Childhood

ORIGINS, EVOLUTION, AND IMPLICATIONS

Edited by Courtney L. Meehan and Alyssa N. Crittenden

2016

Development Plus Social Selection in the Emergence of "Emotionally Modern" Humans

SARAH B. HRDY

Introduction: A More Other-Regarding Ape

It was an inspired guess when Charles Darwin proposed that humans evolved in Africa from now-extinct predecessors resembling today's gorillas and chimpanzees (1974). On the basis of fossil and genetic evidence analyzed since then, we now estimate that apes in the line leading to the genus *Homo* split from that leading to gorillas between ten and seventeen million years ago, and split from that leading to today's chimpanzees and bonobos between six and eleven million years ago (Langergraber et al. 2012). Common descent explains overlap in genomes as well as capacities such as producing and using tools in multiple ways (Roffman et al. 2012). It also helps explain why developmental profiles of a baby chimpanzee can be evaluated using the same Brazelton Neonatal Behavioral Assessment Scale that pediatricians applied to my own infants.

With each passing year, it becomes harder to draw absolute distinctions between the innate capacities of young humans and those of their ape relations. This blurring of boundaries pertains in almost every cognitive realm except those accomplishments requiring language or the kind of sophisticated teaching along with cumulative culture that language facilitates (L. Dean et al. 2012; Matsuzawa, Tomonaga, and Tanaga 2006; Whiten and Van Schaik 2007). Even in tasks such as watching and learning from someone else's demonstration or tasks requiring mentalizing about what someone else is likely to know ("Theory of Mind"), where humans typically test better, considerable overlap exists between the scores of orangutans and chimpanzees and those of two-and-a-half-year-old humans (Herrmann et al. 2007: fig. 2.2; see also L. Dean et al. 2012). In terms of working memory, young chimpanzees can actually

outperform human adults. Some specially trained chimpanzees remember ordered symbols briefly flashed onto a computer screen as well as or better than humans do (Matsuzawa 2012:101).

Within minutes of birth, humans are attracted to face-like patterns. By two months of age they recognize their mother's face. But so do other ape newborns. They too occasionally gaze into their mother's face (Bard 2005; Okamoto-Barth et al. 2007), scan expressions of whoever is holding them, even seek to engage this caretaker by imitating what they see there—sticking out their own tongues or opening their mouths (Bard 2007; Myowa 1996; Myowa-Yamakoshi et al. 2004). Whether their face-to-face partner is another chimp or a human caretaker, little chimpanzees respond in kind to all sorts of emotionally charged expressions, suggesting that underlying subjective emotions are being shared. But there are also key differences.

Even though other apes occasionally share food, the possessor is rarely eager to do so (Silk et al. 2005) and typically does so only after being begged (Yamamoto, Humle, and Tanaka 2009). In the wild, an alpha male chimpanzee may tear off a bit of meat from captured prey to proffer to a strategic ally, but only after persistent solicitation (D. Watts and Mitani 2000). A mother chimp or bonobo may allow her infant to take food from her mouth but rarely volunteers it. Bonobos, generally less competitive over food than common chimpanzees (Hare et al. 2007; Hare and Kwetuenda 2010), have been known to open a cage door so that another bonobo can share in a feeding bonanza (Hare 2012). But in no wild ape is voluntary sharing the routine part of life that it is in every human society ever studied.

Clearly, socialization influences willingness to share. But we are left to explain why the social sharing of food that is universal in human societies is rare in other apes. "Mealtime" simply does not mean the same thing among other apes that it does among humans. In the bonobo case, allomaternal provisioning entails little more than an adult not bothering to object when a youngster removes food from her mouth (Kano 1992). By contrast, among humans, parents and alloparents alike routinely proffer food to children, and to each other. Even very young humans spontaneously offer food (figure 2.1) and by eighteen months may select just the item they have reason to believe that another will prefer—even if it differs from their own preference (Repacholi and Gopnik 1997).

Such ingratiating impulses go beyond food sharing. More than two centuries ago in *The Theory of Moral Sentiments* (1750), Adam Smith spelled out how

Figure 2.1. From an early age, humans will select and proffer an item that they have reason to believe someone else will enjoy, even if it differs from their own preferences. Photo: S. Hrdy.

vitally interested people are in the subjective feelings, underlying motivations, and values people use to judge others. Humans also exhibit powerful desires for others to receive information about their own thoughts and feelings and, moreover, to approve of them. From an early age children are eager to learn appropriate "rules," techniques, and social customs, and as David Lancy describes in chapter 8, to fit in. *What I focus on here is the recent realization of just how early in development such ingratiating tendencies combined with mentalizing and questing for intersubjective engagement emerge, and to explore why they would have been crucial for the survival of entirely dependent (but not quite entirely helpless) immatures.*

My starting point is the proposal by Michael Tomasello and Malinda Carpenter that such "intersubjective sharing" (defined by them as two humans "experiencing the same thing at the same time and *knowing together that they are doing this*") is the key sociocognitive difference between humans and other apes. As they put it, following Trevarthen (2005), creating "a shared space of common psychological ground" lays the foundation for a broad range

of collaborative activities with shared goals as well as human-style cooperative communication (Tomasello and Carpenter 2007:121–122, emphasis in original, following Trevarthen 2005).

There is an emotional component to this questing for intersubjective engagement that goes beyond "Theory of Mind," or being able to attribute mental states or beliefs to others. By one year of age, even before human babies talk, they respond with pride to praise, and with shame when they sense someone else's disappointment (Darwin 1877; Reddy 2003; Trevarthen 2005). Alone among animals, by age two humans respond to others' assessments by blushing, that peculiarly manifest signal of self-consciousness that led Darwin to wonder why "the thought that others are thinking about us" could "alter our capillary circulation" (1998:335). By age four such coy "aspirations-to-appeal" develop into full-fledged perspective-taking, escalating into outright (not infrequently deceptive) flattery (Fu and Lee 2007), while the underlying concern for what others think emerges even earlier (Reddy 2003). From around age three, most humans are motivated to reveal their "inner selves" to someone else, especially when expressing motivations (e.g., behaving generously) likely to elicit admiration from others (Leimgruber et al. 2012). The same neural regions activated by anticipation of tasty food (the mesolimbic dopamine system and the ventral tegmental area) light up when people talk about themselves (Tamir and Mitchell 2012).

Rather than viewing language as a unique faculty that evolved so that people could coordinate with others in collaborative endeavors, I prefer to assume that questing for intersubjective engagement came first, prompting apes already adept at declarative signaling to become apes capable of producing infinitely recursive symbol-rich vocalizations. On this, I follow psychiatrist Peter Hobson, who argued that "before language, there [had to be] something else . . . that could evolve in tiny steps. . . . That something else was *social engagement with each other*. The links that can join one person's mind with the mind of someone else, especially, to begin with, emotional links" (2004:2, emphasis in original). Colwyn Trevarthen makes a similar point when he suggests the "cooperative awareness" or "secondary intersubjectivity" that permits one-year-old infants to communicate experiences, feelings, and intentions provides the foundation on which language is built (2005:70). Givón similarly argues that grammar emerged so as to communicate information in a way that takes into account someone else's knowledge and current state (2005).

If emotional transformations rendering hominins eager to read, influence,

and appeal to mental and subjective states of others preceded the evolution of uniquely human language, it should not be surprising that human toddlers do not just call out for help, utter commands, or announce what they want. They also express feelings, commenting on what seems to them "good" or "bad." By the time a child can talk, perhaps one-third of his or her speech informs others about subjective evaluations, as when Darwin's twenty-seven-month-old son exclaimed, "Oh kind Doddy, kind Doddy" on observing his father give the last piece of gingerbread to the toddler's younger sister (1877). Youngsters may be especially prepared to express inner assessments of others if they are surrounded by encouraging and indulgent others, as is typical among hunter-gatherers (Hewlett and Lamb 2005).

No question, the evolution of language produced potent downstream consequences in terms of cooperation and cultural transmission (Gergely and Gergely 2011; Tomasello and Carpenter 2007). But what I emphasize here is that the apes who first felt a need for forms of communication that went beyond imperative use of communicative signals were already more other-regarding. They were not only cognitively but also *emotionally very different from our last common ancestor with other extant apes.*

How to Explain the Origins of Other-Regarding Impulses?

Efforts to explain humankind's planet-populating, world-dominating "success story" emphasize the cognitive and social processes that facilitate acquisition and transmission of cultural information (Tennie, Call, and Tomasello 2009; Tomasello 1999; Whiten and Van Schaik 2007). Three prerequisites seem especially relevant: closer attention to others, including imitation and observational learning; intentional teaching (including verbal instruction) (L. Dean et al. 2012); and mutual tolerance and other-regarding, helpful impulses (e.g., Burkart, Hrdy, and Van Schaik 2009; Whiten and Van Schaik 2007). But whence such attributes?

Comparative psychologists have done a brilliant job of demonstrating that human social learners focus more on others' actions than do other apes (e.g., Horner and Whitten 2005). They have shown that "uniquely human forms of cooperation" can thus be built up through teaching and transmission of conformity to norms, resulting in a "cultural ratchet" (Tennie, Call, and Tomasello 2009:2413 as cited in L. Dean et al. 2012:1117). It is because our language-using ancestors benefited from new forms of social learning and teaching that, by

100,000 years ago, anatomically modern humans had evolved into fully enculturated ones capable of higher levels of social coordination. But this sequence begs the question: How did the emotional scaffolding facilitating mutual tolerance, interest in the mental states and thoughts of others, and eagerness to please and share with them emerge in the hominin line in the first place? It also fails to explain why these hyper-social impulses evolved in humans but not other apes. Why do they appear so early and in both sexes?

It is increasingly apparent that other extant apes possess neural prerequisites to process what someone else does or does not know, read their intentions, and even figure out how to help them accomplish specific goals (discussed below). But ingratiating themselves by running over to help another or spontaneously offering food is not something other apes do. Such behaviors are, however, observed in some other primates. Humans have not shared a common ancestor with marmosets and tamarins for over thirty-five million years, yet these distantly related, tiny-brained monkeys behave in extraordinarily helpful
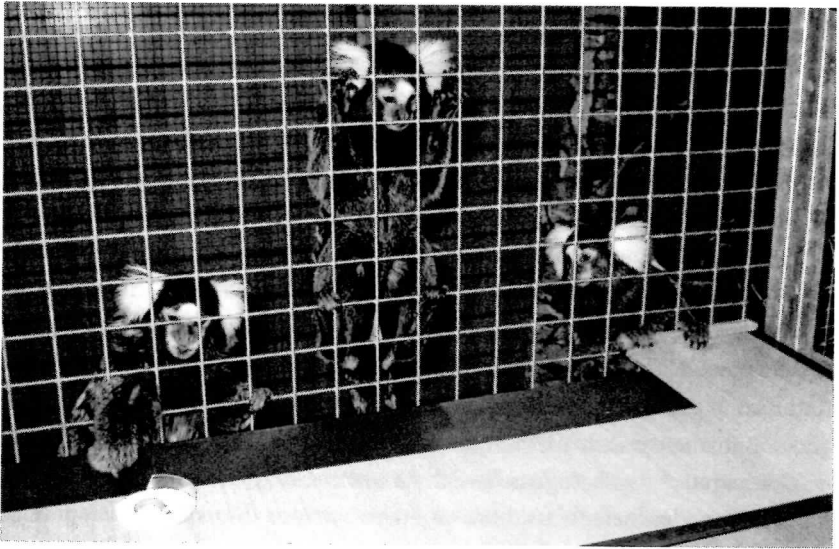

Figure 2.2. The marmoset (*Callithrix jacchus*) on the right has run over to pull in a tray that will deliver a mealworm to a marmoset on the other side of the cage. This photograph was taken with the assistance of Judith Burkart, illustrating methods she devised to compare levels of spontaneous prosociality across species (Burkart and van Schaik 2012). Photo: S. Hrdy.

Table 2.1. Human-Callitrichid Parallels

Thirty-five million years have elapsed since large-brained human foragers last shared a common ancestor with tiny-brained New World monkeys in the subfamily Callitrichidae (marmosets and tamarins), yet there are remarkable convergences in these otherwise distant taxa that both rely on extensive alloparental as well as parental care and provisioning to rear costly young, including:

1. Extensive alloparental care + provisioning
2. Prolonged post-weaning dependence
3. Reliance on hunting + gathering with learning-intensive extractive foraging
4. Adapted to colonizing new habitats
5. Unusually conditional maternal commitment with high rates of abandonment in situations lacking allomaternal support
6. High levels of foraging cooperation
7. Provisioning by multiple males encouraged by polyandrous mating accompanied by either real chimerism as in marmosets or fictitious beliefs about it as in the human case
8. Nonadvertised ovulation + mating throughout cycle
9. Weakly developed dominance hierarchies where food concerned
10. Variable group compositions + adults of both sexes moving between groups
11. Other-regarding impulses manifested in food sharing + information transfer
12. Endocrinological parallels such as elevated prolactin and reduced testosterone levels in males caring for infants

ways in both the wild (Garber 1997; Bales, French, and Dietz 2002) and in well-replicated captive experiments, as depicted in figure 2.2 (Burkart et al. 2007; Cronin, Schroeder, and Snowdon 2010; Hauser et al. 2003). Striking parallels between humans and this phylogenetically distant subfamily of New World monkeys (among whom, as in humans, mothers also rely on allomaternal care and provisioning to rear surviving young as humans also do) are listed in table 2.1. As discussed elsewhere, this convergent evolution cannot be understood without taking cooperative breeding into account (Burkart, Hrdy, and Van Schaik 2009; Hrdy 2009; Burkart and Van Schaik 2012).

Interestingly, marmosets readily follow others' gazes and eagerly assist them, but they do not appear to take the "mental" perspective of another into account the way humans do (Burkart and Heschl 2007). Other apes are

better at doing so, just not as interested in helping. Nor, apart from mutual grooming, do nonhuman apes go out of their way to please others the way marmosets (in their more automatic, "less thoughtful" way) or humans do. In the human case, reward centers in the brain are stimulated just by giving something to someone else (Rilling et al. 2002), but whether such "charitable acts" have comparable effects in any other primate remains unknown. Based purely on behavioral observation, however, other apes do not appear particularly interested in ingratiating behaviors or eager to satisfy another's personal preference. Possessors have to be actively solicited before resources are shared. Apparently other apes do not find it as inherently pleasurable to please others as humans do.

So far, explanations for humankind's peculiarly prosocial impulses have mostly focused on obligate cooperative foraging, especially collaborative hunting and with it the need for equitable sharing (Bullinger et al. 2011; Tomasello et al. 2012) or on the "parochial altruism" needed by a "band of brothers" competing against neighboring bands (Choi and Bowles 2007). Bowles vividly showcases his proposal that "generosity and solidarity toward one's own [group] may have emerged only in combination with hostility toward outsiders" (2008a:326) by asking whether humans "engage in mutual aid because evolution is red in tooth and claw" (2008b). Yet *Pan troglodytes* is also meat-loving and probably even more competitive and dominance-striving than humans are, not to mention xenophobic to the point of reflexively attacking outsiders (Wrangham and Peterson 1996). Hunting and intergroup conflict are integral to chimpanzee life as well. So why didn't their ancestors also spend the past six million years evolving more other-regarding impulses so as to reap manifest benefits of "parochial altruism"? Nor do warfare or hunting models explain why other-regarding impulses characterize both sexes (and indeed may even be more expressed in females, de Waal 2013:51). Nor do they explain why prosocial impulses emerge so early in development. Surely vulnerable immatures would do better to remain self-servingly focused on staying safe, fed, and growing bigger, as earlier generations of behaviorists assumed babies naturally did (e.g., Watson 1928).

Other-regarding impulses lay the groundwork for cooperative potentials that unquestionably have served humans well—as evidenced by all the enterprises, institutions, factories, and gravity-defying machines that coordination with others facilitate. But Mother Nature (my metaphor for Darwinian natural selection) had no way of foreseeing such eventual payoffs. It seems circular

to argue that humans evolved other-regarding, culture-acquiring attributes in order to become other-regarding, culture-bearing animals. Rather, we need to ask under what circumstances does an ape benefit from responding to the mental states, desires, and needs of others? From seeking to appeal to and please them? And why should such impulses emerge so early? Rather than viewing prehuman ancestors as already "exceptional," I prefer to view them as creatures subject to the same evolutionary processes that pertain across the animal world.

Such challenges drew my attention to the unusual way that apes in the line leading to the genus *Homo* must have reared their young (Hrdy 1999a). While shared care is typical of human foragers and widespread across primates, it is not found among our closest great ape relations; it was almost certainly absent among the last common ancestor humans shared with them. Why then, and when, did such extremely un-apelike modes of childcare emerge in the hominin line? And what were the ramifications?

Shared Care, Provisioning Immatures, and the Evolution of More Generalized Food Sharing

There is an ongoing paradigm shift in how evolutionary anthropologists reconstruct family life among hominins struggling to stay fed and rear offspring in the unpredictably fluctuating climates of Pleistocene Africa. As has long been recognized, all apes are born relatively helpless, maturing slowly through a prolonged infancy, followed by a juvenile period and adolescence. Debate persists over just how similar or different these growth stages are in humans and other apes (Thompson, chapter 4, this volume). Indisputably though, humans remain nutritionally dependent longer. Nonhuman apes tend to be weaned later, but thereafter provision themselves. By contrast, humans continue to be subsidized as late as early adulthood. No one knows how far back in time such dependency extends. But the emergence of *Homo erectus*, with an adult brain more than twice the size of either the brain of australopithecines or that of today's chimpanzees, presumably meant that the diets of immatures, and perhaps their mothers as well, were subsidized at least by the beginning of the Pleistocene, 1.8 million years ago (O'Connell et al. 2002; Cofran and DeSilva 2013).

Based on data from twentieth-century foraging peoples, it takes ten to thirteen million calories beyond what a child provides for himself to grow

from birth to age eighteen, more than a foraging mother could ordinarily provide by herself (Kaplan 1994). Furthermore, shorter interbirth intervals meant another dependent born before older offspring were independent. Even with a father on hand and willing to help, the success rate of a Plio-Pleistocene hunter-scavenger would not have come close to meeting the requirements of a *H. erectus* juvenile needing to be fed several times each day (O'Connell et al. 2002). Alloparental in addition to parental provisioning and processing was essential to ensure that growing children had sufficient palatable foods.

Survival of young required multiple providers. Indeed, fluctuating rainfall together with unpredictable resources (Potts 1996; Wells 2012), specifically in east Africa during the period between 1.8 and 2 million years ago when *Homo erectus* was emerging (Magill, Ashley, and Freeman 2013), produced conditions that, in other animals, tend to be associated with the evolution of cooperative breeding (Jetz and Rubenstein 2011), and with it, prolonged dependence (Hrdy 2005b; Langen 2000). In the early hominin case, opportunistic inputs from multiple scavenger/hunters must have been backed up by more reliable gatherers and processors of plant foods. Other apes exhibit some division of labor (e.g., chimpanzee females fish for termites and crack nuts whereas males do almost all hunting) but the fruits of such gender-specific endeavors are rarely shared, and meat is largely consumed by adult males. So, given notably self-serving, often competitive apes, how does food sharing get underway?

Across primates, voluntary provisioning is uncommon. Humans excepted, it is virtually absent among apes. Shared care is a different matter. Infants are universally attractive to at least some other group members, and are protected and even carried by them. Some form of shared infant care is reported for the majority of species in the Primate order (Hrdy 2009, 2010). Apart from humans and one lesser ape, however (siamang fathers carry older infants [Lappan 2009]), hominoid mothers do not permit access to new infants. Yet so deeply entrenched is responsiveness to infant cues among primates that, even among great apes who do not regularly share care, normally aloof males sometimes respond to signals of need as when chimpanzee males adopt an orphaned youngster (Boesch et al. 2010). Some primate mothers also occasionally allow another female's infant to suckle or to take food. Nevertheless, with the exception of humans, extensive alloparental provisioning is confined to the subfamily Callitrichidae.

Occasionally, sharing food with another's infant does not mean that adults share food, but provisioning young—whether by parents or alloparents—may

act as a gateway to sharing among adults. Compiling evidence for sixty-eight species of primates, Jaeggi and Van Schaik (2011) found that adult-to-adult food sharing was disproportionately likely to evolve in taxonomic groups where adult-to-offspring provisioning was already established. This is consistent with the observation that, as with cooperative breeding itself, allomaternal provisioning is more likely to evolve when foods utilized require strength or extractive skills that immatures do not yet possess.

Hamilton's Rule predicts that helping should evolve whenever benefits to the recipient exceed costs to the helper weighted by degree of relatedness. Thus, even a distantly related group member who has already had his fill of a resource may provide some to immatures unable to access it themselves. Exact costs and benefits vary but, across the natural world in species with biparental and/or alloparental care, in thousands of species of birds as well as quite a few mammals, adults transport food back to a nest, den, or other site where immatures are creched. Social carnivores such as African wild dogs and wolves provide classic examples. Adults return from a kill with predigested meat in their bellies, regurgitating it into the mouths of begging pups waiting at a den or central place. In the case of the genus *Homo*, adult provisioning of immatures would have set the stage for more generalized food sharing and, in time, cooking as well (Wrangham and Carmody 2010).

By 800,000 years ago, perhaps earlier, routine cooking would release further energy from "pooled" resources (Kramer and Ellison 2010; Reiches et al. 2009) in a self-reinforcing feedback loop, while adult-to-infant transfers facilitated guided transmission of knowledge about appropriate foods and how to obtain them. As it happens, the best-documented nonhuman instances of "tutoring" come from species where alloparents take the initiative in providing age-appropriate foods to immatures (e.g., Rapaport 2011; Rapaport and Brown 2008; Thornton and McAuliffe 2006). Going beyond merely tolerating a youngster taking food or responding to a beggar (e.g., Jaeggi, Van Noordwijk, and Van Schaik 2008; Jaeggi, Burkart, and Van Schaik 2010; Kano 1992; Silk 1978), callitrichid providers proactively deliver food to infants around weaning age (e.g., Burkart et al. 2007). Allomothers also emit special vocalizations signaling novel foods and actively intervene to prevent youngsters from ingesting inappropriate or toxic items (Byrne and Rapaport 2011; Rapaport and Ruiz-Miranda 2002). Such mentoring helps explain why foragers growing up in groups with many helpers may be more adept at harvesting (e.g., Langen and Vehrencamp 1999:138 for cooperatively breeding magpie jays).

Provisioning of immatures almost certainly preceded the emergence of more generalized adult-to-adult food sharing. This sequence is consistent with accumulating evidence that Pleistocene humans could not have reared young without allomaternal provisioning. Among virtually all Africans still living as hunter-gatherers when first studied, mothers relied on assistance from a fluctuating array of group members of both sexes from as young as ten to over sixty (Blurton Jones, Hawkes, and O'Connell 1997; O'Connell, Hawkes, and Blurton Jones 1999; Burkart, Hrdy, and Van Schaik 2009; Crittenden, chapter 7, this volume; Crittenden, Zes, and Marlowe 2010; Hawkes, O'Connell, and Blurton Jones 1989, 1998; Hewlett and Lamb 2005; Hill and Hurtado 2009; Ivey 2000; Konner, chapter 6, this volume; Meehan, Helfrecht, and Malcom, chapter 9, this volume). According to this Cooperative Breeding Hypothesis, human life histories evolved as byproducts of alloparental supplementation of parental provisioning (Hawkes and Paine 2006; Hrdy 1999a, 2005b; Konner 2010: chap. 16; K. Kramer 2005a; Newson and Richerson 2013). In particular, inclusive fitness benefits accruing to foragers who remained productive and willing to provision younger kin provide the most plausible explanation to date for why human females go on living for decades after menopause (Hawkes et al. 1998; Kim, Coxworth, and Hawkes 2012).

Enhanced buffering of young against food shortages reduces costs of slow maturation and prolonged post-weaning dependence. Even in the face of fluctuating rainfall and unpredictable resources (Potts 1996; Newson and Richerson 2013) hominins could afford to grow up slowly. They could also accommodate steep learning curves and other challenges stemming from migrating into novel habitats (Hrdy 2005b). Meanwhile, stacking offspring improved the capacity of populations to bounce back after crashes (Hawks et al. 2000; Hawkes and Paine 2006).

Augmentation of energy available to mothers and infants probably also played a role in encephalization (Isler and Van Schaik 2012; Navarrete, Van Schaik, and Isler 2011). Isler and Van Schaik (2012) propose that provisioning during periods of rapid brain growth at the end of gestation and during lactation stabilized resource availability. They view this as the "first step" in the threefold increase in brain size characterizing anatomically modern humans. Again, sequence matters. Rather than needing 1,350 cc brains to orchestrate cooperative care, shared nurturing was essential for the evolution of such big brains (Hrdy 1999a:287, 2009).

Changing Our Minds: Psychological Corollaries of Cooperative Breeding

Modern developmental psychology is currently construed as the study of how children's minds grow within the context of their relationships with family. Revising our ideas about exactly who constituted "family" in humankind's Environment of Evolutionary Adaptedness (EEA) means rethinking neural development. Thus, new modes of child-rearing mean changing our minds— literally. This ongoing paradigm shift within evolutionary anthropology requires reassessing assumptions about the ubiquity of exclusive maternal care during humankind's EEA (e.g., Bowlby 1971:228–229), even as new findings from social neuroscience confirm Bowlbian Attachment Theory's central premise regarding the importance of early social experiences (Carter et al. 2005). If infants first develop a sense of self and "internal working models" about their world through responding to others' responses to them, and if, as psychiatrist Daniel Siegel puts it, interaction with "the mind of another seems to catalyze the development of self-awareness" (2012:43), then early social interactions affect both the formation of neural connections and regulation of gene expression.

As in all primates, maternal nurture was critical for hominin infants' survival. Frequent breastfeeding along with co-sleeping continued to guarantee this very special relationship (Konner, chapter 6, this volume). But as new circumstances made allomaternal as well as maternal care and provisioning increasingly essential, the hominin infant's own mother ceased to be the sole source of security, warmth, mobility, and nutrition. Nor could infants rely on their mother to obsessively maintain contact with them day and night for the first six months of their lives as is typical of other extant apes, mothers who thereafter continue to suckle them and remain reliably within eye- or earshot for four or more years. Hominin infants' need for care and feeling secure remained unchanged (Bowlby 1971), but they could no longer count on nearly single-minded dedication from a mother who prioritized their well-being above that of all other current and future offspring.

Prior to conception, all through gestation, lactation, early and late childhood, and beyond, this hominin mother's nutritional status depended on how much social support she had. Her lifetime reproductive success depended on how strategically she allocated maternal investment between costly, closely spaced offspring. In the hours and days immediately after birth, a postpartum mother's perception of social support influenced how primed she would be

to pick up and hold close the little stranger who had just emerged from her body, how likely that infant would be to successfully latch onto nipples and, through initiating lactation, promote continued contact and, over time, the formation of a profoundly close social bond. With the exception of very young or inexperienced first-time mothers or unusually dire circumstances (Hrdy 1999a:181–183), most primate mothers are remarkably undiscriminating, displaying nearly unconditional dedication (e.g., Matsuzawa 2012; Turner et al. 2012). The main exceptions fall among marmosets, tamarins, and humans who, unlike other primates, discriminate on the basis of both infant attributes and availability of allomaternal support. They may abandon, actively reject, or kill specific newborns (Bardi, Petto, and Lee-Parritz 2001; Culot et al. 2011; Tirado Herrera, Knogge, and Heymann 2000 for callitrichids; Hrdy 1999a:288–317, 351–380 for review of human evidence).

Increased reliance on allomaternal assistance must have been accompanied by both increased maternal sensitivity to cues of social support and selection on infants favoring aptitudes for eliciting it. At the same time, shorter interbirth intervals combined with prolonged juvenile dependence (and perhaps also a greater need for group consensus regarding a specific infant's viability?), intensified pressure on mothers to evaluate attributes and prospects of each newborn in relation to prospects for older but still dependent siblings, as well as prospects for any future sibling, the arrival of whom might be delayed or accelerated by the fate of this one. Over generations, a mother's reproductive success and that of close relatives would depend upon how well she negotiated cost/benefit trade-offs implicit in Hamilton's Rule. Thus was a newly conditional maternal commitment overlain upon the single-minded dedication typical of most primate mothers, helping to explain the curious ambivalence documented for human mothers (Hrdy 1999a: chap. 20; Parker 1995).

And what of fathers? As in many primates, paternal commitment would be influenced by both paternity probabilities and alternative mating options. But among cooperatively breeding hominins, fathers also needed to take into account availability of alternative nurturers (Meehan 2005a; Meehan, Helfrecht, and Malcom, chapter, 9, this volume). When feasible, hunters preferentially channel meat to their own offspring (Marlowe 2010), but genetic progenitors were not the only hunters bringing back meat to share (R. Lee 1979; Kaplan et al. 2000; Hill and Hurtado 2009). Furthermore, taking advantage of occasional protein and fat bonanzas was only practical if people could count

on more reliably provided plant foods gathered by women to tide them over when hunters returned empty-handed (R. Lee 1979; Marlowe 2010: fig. 3.11). As reported by Hawkes and colleagues (1989) and subsequently confirmed by Marlowe (2010: fig. 3.11), postreproductive women without infants of their own forage more diligently and bring in more calories than do mothers of childbearing age, with patrilineal as well as matrilineal grandmothers making substantial contributions to child well-being (Meehan, Helfrecht, and Malcom, chapter 9, this volume). In some African habitats, children as young as ten also share gathered food with younger siblings and more distant kin (Blurton Jones, Hawkes, and O'Connell 1997; Crittenden, Zes, and Marlowe 2010; Crittenden, chapter 7, this volume). Just who contributed how much varied so that fungibility of nurture as well as residential mobility would have been essential for maintaining fits between local conditions and an appropriate mix of providers.

Like other mobile fission-fusion primates (Schreier and Swedell 2012), human hunter-gatherers gravitate away from adversity and toward opportunities including better access to food, water, and security. Add to such incentives the need for allomaternal assistance and variable impulses among postreproductives to provide it (e.g., Blurton Jones, Hawkes, and O'Connell 2005; Scelza 2011). Fortuitously, our last common ancestors with other apes were probably characterized by more flexible transfer patterns than is usually assumed. Far from typical, extreme male philopatry and xenophobia reported for chimpanzees look more like derived troglodytian outliers than hominoid norms (Koenig and Borries 2012). Even among chimpanzees, females remain in their natal range when benefits of doing so outweigh costs of staying (Pusey, Williams, and Goodall 1997). Over time, long-distance relationships maintained with kin and as-if kin alike would have facilitated flexible group composition among hominin foragers and, with it, more flexible parenting.

Porous social boundaries meant that newcomers with useful services to offer, whether skilled hunters or productive older kinswomen, would have been particularly welcome while groups with adept hunters or healers (often older men) might be especially attractive (Wiessner 2002b). In this way, flexible group compositions essential for cooperative breeding would have also enhanced exposure to novel artifacts and technologies, not only laying the groundwork for the more formalized exchanges that eventually became hallmarks of hunter-gatherer lives (Wiessner 1977, 2002a) but also for more far-flung kin and as-if kin networks (Wiessner 2002b). Concurrently, psychological

corollaries of alloparental provisioning, such as enhanced mutual tolerance and dependence along with the tutoring impulses seen in many cooperative breeders, would have further encouraged social transmission of knowledge (Burkart and Van Schaik 2010; Byrne and Rapaport 2011; Rapaport and Ruiz-Miranda 2002).

But what of the implications for infants on the receiving end of all this investment by others? Heightened maternal discrimination would have produced selection pressures on neonates to emerge looking full-term and robust and, after birth, to expeditiously get to the critical task of initiating lactation. Should a mother's commitment falter, infants would do well to catch her attention, vocally reminding her of their vulnerability. Over the course of development, hominin infants and children needed to monitor not only their mother's location and intentions but also those of other potential caretakers. In the process, infants become conditioned by rewards when solicitations succeeded, and disappointed or worse when they misgauged. Such social conditioning affects phenotypic outcomes—what a neuroscientist conceptualizes as the individual's "neural net profile" (Siegel 2012:24; also see Gopnik 2010).

When availability of allomaternal care is correlated with child survival, as has been repeatedly documented for cooperatively breeding monkeys and, to a lesser extent, for humans (e.g., see Bales, French, and Dietz 2002 and Garber 1997 for callitrichids; Ivey 2000; Mace and Sear 2005; Sear and Mace 2008, and Lahdenperä et al. 2004 for humans),[1] it produces directional social selection favoring infant phenotypes better at soliciting nurture.

Social Selection Favoring Other-Regarding Aptitudes

Social selection (sensu West-Eberhard 1979, 1983, 2003) entails competition with conspecifics for access to some resource. "Competition" need not imply individuals directly duking it out over a desirable tidbit or location. Consider the conspicuous natal coats typical of many infant-sharing monkeys. Their flamboyance attracts attention from available allomothers while diverting care from other infants born that season (Hrdy 1976; 2009). The situation for human babies is different. Right after birth, it is mothers, not allomothers, that infants need to appeal to. Lacking flamboyant natal coats, human neonates are much fatter than other apes. These fat deposits fuel thermoregulation and stockpile energy for a fast-developing brain (Kuzawa 1998), but plumpness

also makes neonates appear full-term and robust, advertising to their mothers that they merit the prolonged investment that will ensue once she allows the baby to suckle, initiating lactation and with it a concatenation of bonding processes (Hrdy 1999a: chap. 21). Even though no other baby is in sight, this newborn is competing with both older siblings in whom the mother might otherwise continue to invest and an as yet unborn sib the mother might produce were she to resume cycling sooner. As they mature, babies need to appeal to others as well through monitoring their tastes and intentions—a psychological dimension to Lorenzian *Kindschenschema*. Mothers also have a stake in making their babies attractive since they, too, are competing with other mother-offspring dyads for allomaternal assistance (Hrdy 2009:225ff).

Conspicuous natal coats presumably attract the attention of predators as well as caretakers, while fetal fat deposits built up just prior to birth can impede passage through narrow birth canals. Such costs must be offset somehow. As with Darwin's example of the peacock's tail, otherwise disadvantageous traits continue to be favored if they increase chances of being "chosen" by another (Lyons and Montgomerie 2012; West-Eberhard 2010). Anyone who doubts the existence of this infantile equivalent of "sex appeal" should consider how reliably reward centers in the brains of human alloparents as well as parents react when looking at cute babies (Glocker et al. 2009; Kringelbach et al. 2008).

"Runaway social selection" has been invoked in other contexts where humans benefit from appealing to others. For example, psychiatrist Randolph Nesse invokes it to explain why humans depart from rational self-interest by remaining loyal to a person or an ideal, behaving generously or otherwise engaging in selfless conduct exceeding reasonable expectations of return (2007, 2010; see also Flinn and Alexander 2007). People do so, Nesse argues, because selflessly generous or honest behaviors enhance that individual's likelihood of being chosen by an advantageous social partner. Such a partner may in turn benefit from that choice. Such "runaway" social selection is possible when signal and response are genetically or culturally correlated and both coevolving. According to Nesse, people's acute sensitivity to embarrassment and the powerful constraining self-consciousness that we call "conscience" (and with it perhaps blushing) evolved through social selection as part of the internal monitoring system that helps an individual "behave well" so as to compete with others directly or, more often, indirectly, to be chosen by advantageous social partners (see also Boehm 2012).

With such logic in mind, consider how early humans manifest self-conscious

emotions. I hypothesize that such sensibilities first emerged as corollaries of cooperative breeding in an ape lineage. That is, our ancestors were emotionally preadapted for self-consciousness because, in the high child mortality environments that presumably prevailed throughout the Plio-Pleistocene, prolonged dependence on caretakers with contingent levels of commitment generated novel selection pressures such that, over generations, dependents neurologically disposed to be more "other-regarding" were better cared for. Darwinian social selection would have favored those who grew up more interested in the thoughts, feelings, and needs of others, an emotionally quite distinctive kind of ape prepared to recognize what expressions, vocalizations, or behaviors would appeal to specific others.

Primate Preadaptations for Cooperative Breeding

Old World monkeys and apes navigate complex, emotionally mediated relationships. They remember who they grew up around (and thus are probably related to), who is currently dominant over whom or likely to soon be so. They recognize special competences and track reciprocal interactions over time so as to differentiate between useful versus unreliable, potentially harmful, associates (Cheney and Seyfarth 2007; Mitani 2006; Schino and Aureli 2009). If death of a high-ranking relative disrupts an advantageous relationship, primates opportunistically seek substitutes, related or not (Seyfarth and Cheney 2012).

Internalized systems for emotionally based "bookkeeping" similar to that found in cercopithecine primates (Schino and Aureli 2009) and modern humans (Hrdy 1999a:171) surely characterized early hominins as well. Add to this the neurophysiological scaffolding for registering the whereabouts and current condition of tiny individuals outside themselves that first evolved in mammalian mothers some two hundred million years ago (Carter et al. 2005). Elaborations on these ancient bauplans help mothers decide whether or not to allow allomaternal access to vulnerable newborns. Although all primate infants are attractive to at least some would-be allomothers, voluntary shared care only occurs when mothers feel sufficiently confident of their infants' safe return to permit another to hold them. I suspect this is why shared care is only observed in primates where would-be allomothers can be trusted, as in the case of close matrilineal kin or probable progenitors (Hrdy 2009a, 2010).

Most allomaternal care in nonhuman primates involves pre-reproductive

females or else likely progenitors. Less attention has been paid to females nearing the end of their reproductive careers even though selfless impulses often increase as reproductive value declines, as in the case of old female langurs who opt out of competition for food yet risk mortal injury defending younger relatives against infanticidal males. This obvious preadaptation for cooperative breeding did not lead to longer postmenopausal life spans in other primates, as Hawkes hypothesizes it did in humans. Without food sharing, opportunities for postreproductives to enhance the fitness of kin would have been more sporadic than chronic (Hrdy 1999a, 2009).

Meanwhile, over millions of years, as maternal horizons expanded to include caring relationships with others besides their own infants, so did cortical capacities for mediating between complex social experiences, long-term bonds, and emotions (Carter et al. 2005). Given this legacy, it is unsurprising that social experiences early in life continue to shape both brain development and subsequent social relationships across primates, especially in humans (reviewed in Siegel 2012, esp. p. 22ff.). But how can we test the proposition that prehuman apes who relied on multiple caretakers develop different cognitive and emotional aptitudes than apes reared exclusively by their mothers?

Virtual and Real "Tests" of Assumptions Integral to the Mothers-Plus-Others Model

None of us has a machine to go back in time to observe how hominin infants responded to mothers and allomothers. What we do have are observations from collateral lines of extant Great Apes (mostly *Pan troglodytes*) and from modern descendants of those early hominins. They allow us to study how hominoid infants respond to different caretaking regimens. In addition, new findings from neuroscience are beginning to enable us to compare brain development in chimpanzees and humans.

Elsewhere (Hrdy 2009), I reviewed such limited evidence as I could then find that infants with several attachment figures grow up better able to integrate multiple mental perspectives (e.g., Van IJzendoorn, Sagi, and Lambermon 1992). Allomaternal support, whether from a grandmother in the same household or just transient visits by "as-if" supportive kin, accelerates and enhances social awareness and an infant's sense of security. This holds both for infants born to young, inexperienced, or unmarried mothers who

might otherwise be at risk of insecure attachments (Hrdy 2009:124–141; Olds, Sadler, and Kitzman 2007; Spieker and Bensley 1994), and for infants among Aka foragers securely attached to their own mothers plus four to six familiar, trusted others (Meehan and Hawks, 2013). Such findings are consistent with my assumption that shared care and provisioning among already highly social, clever, tool-using, bipedal apes produced phenotypes increasingly attuned to others. Then, assume also that in each generation infants a little better at reading the mental states of others and motivated to appeal to them would be better cared for and better fed. Over evolutionary time, immatures would be subjected to directional social selection favoring other-regarding aptitudes (figure 2.3). Although scarcely conclusive, indirect evidence from comparative infant development and comparative neuroscience helps us evaluate the plausibility of these underlying assumptions and also helps to generate new predictions or tests. Let's begin.

DOES ALLOMATERNAL INVOLVEMENT AFFECT
DEVELOPING APE PHENOTYPES? IF SO, HOW?

As Bowlby noted long ago, all higher primates are born with innate capacities for emotional engagement and become attached to their most reliable care-taker—usually the mother. Chimpanzee infants cling tightly to this caretaker and calm when held close by her (Bard 2012:228). At night, infant chimpanzees held by their mothers cry even less than co-sleeping human infants do (Mat-suzawa 2012:295). By one month of age, both human and chimpanzee infants recognize and preferentially respond to their mother's face. Human infants, however, continue to distinguish between their mother's face and the faces of other individuals long after the stage at which infant chimpanzees cease to do so. By the age of two months or so, infant chimpanzees no longer discriminate between a photo of their own mother's face and that of a composite digitally generated by averaging chimp faces (Tomonaga et al. 2004:229).

The frequency of mutual gazing between chimpanzee infants and their mothers is inversely correlated with how much physical contact they have. Between birth and two months, as the chimpanzee mother cradles her infant less, the incidence of mutual gazing rises (Bard 2005). Experimental psychologists and cross-cultural anthropologists report a similarly inverse correlation for humans. A baby being held by his mother will look into her face less than if securely propped up on a couch nearby (Lavelli and Fogel 2002). Thus, it

MOTHERS-PLUS-OTHERS THOUGHT EXPERIMENT

Start with an intelligent, bipedal primate with the cognitive and manipulative potentials and rudimentary theory of mind found in all great apes.

Lore Ruttan

Rear this ape in a novel developmental context where maternal care is contingent on social support and where offspring survival depends on nurture elicited from multiple caretakers.

Lore Ruttan

This results in a novel ape phenotype in turn subjected to directional social selection such that over generations, those youngsters better at ingratiating themselves with others will be better cared and fed, and hence most likely to survive. The predicted evolutionary outcome is apes more interested in and adept at intersubjective engagement.
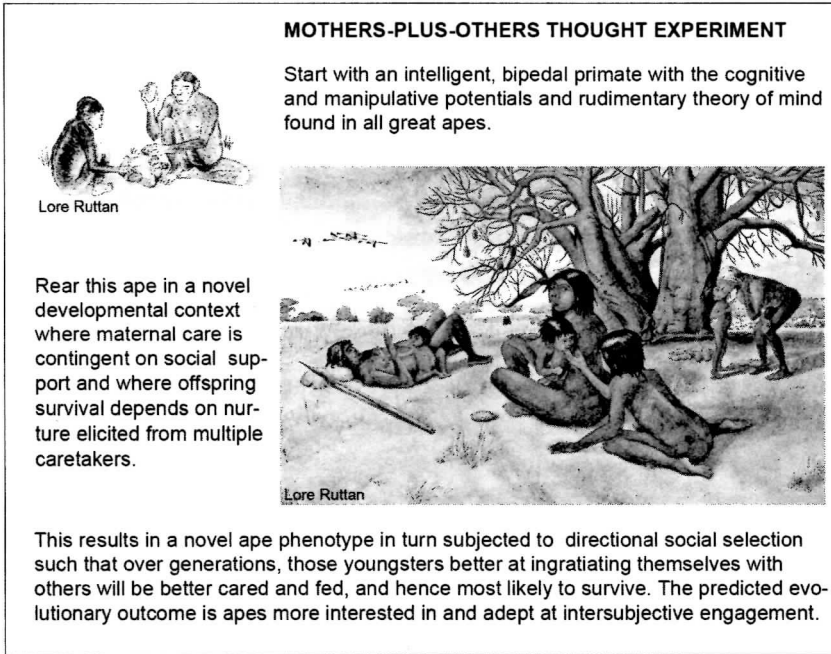
Figure 2.3. The Mother-Plus-Others hypothesis attempts to explain the initial emergence of "emotionally modern humans" through development's role in the production of selectable variation as in this graphically presented three-step thought experiment. Art by L. M. Ruttan.

is not surprising that in traditional societies that are characterized by more direct tactile contact between infants and their mothers, babies gaze into their eyes less than do babies who spend more time off their mothers (Keller 2007; reviewed in Bard 2012).

Like chimpanzee infants, human infants out of direct contact with their mother (but still in non-anxiety-provoking situations) feel a need to "stay in touch without touch," monitoring their mothers' expressions more and frequently "checking back" (cf. Falk 2004a, b). Being off the mother alters behavioral phenotypes, increasing how often infants attend to faces and the motivations of those nearby. Apparently, at some point in the past, human infants also became more discriminating about the identity of caretakers. Both observations are consistent with a legacy of multiple caretakers and with it more conditional maternal commitment.

Social referencing like pointing rarely occurs among wild chimpanzees or among captive-born ones with limited human exposure. But even though nothing like the eager questing for intersubjective engagement characteristic of humans has been reported, human-reared chimpanzees do communicate intentions to others and even refer someone else to look at something they are interested in (Bard 2012; Leavens, Hopkins, and Bard 1996; Menzel 1999).

Clearly, rearing conditions, including extent of allomaternal experience (albeit with allomothers of a different species), alter ape phenotypes. Chimpanzees reared in human families (some being trained to use sign language) prove better than their wild counterparts at communicating likes and dislikes through gestures, following with their eyes what someone else is pointing to, and even pointing themselves at what they want. Human-reared chimpanzees are also better at reading human intentions and emotional states, and are more inclined to coordinate activities with others (e.g., R. Fouts 1997; James Marsh's 2011 documentary *Project Nim*). Life stories of human-reared chimpanzees are problematic on both ethical and scientific grounds. However, we are beginning to have more thoughtful, carefully controlled, and also hopefully more humane case studies confirming that chimpanzees possess the basic neurological equipment to register someone else's goals. Exposure to helpful human caretakers really does seem to enhance apes' capacity to understand what another needs. In innovative recent experiments, Shinya Yamamoto, Humle, and Tanaka (2012) demonstrated that some chimpanzees (all had experienced relationships with trusted human caretakers in addition to their own mothers) could correctly identify the intended goal of another chimpanzee in an adjacent cage and sought to help with the task.

Five of these mother-reared/experimenter-trusting, human-socialized chimpanzees were caged beside five other chimpanzees who were either close kin or as-if kin. In one set of experiments, a window in the partition separating the cages permitted the tool-provider to see which tool (from an array of seven) was needed to access a sweet juice reward. In a second set of experiments, the provider was prevented from seeing what the other chimp was trying to do. With vision obscured, tool selection was random. But when the provider could see what the other chimp was trying to do, he almost always selected the correct tool (a brush or a straw), qualifying the assistance as "targeted help" that takes into account the intentions of the recipient. Such findings are consistent with characterizations of chimpanzees and bonobos as possessing capacities for rudimentary empathy and concern for others, as has

long been advocated by Frans de Waal (for updates see de Waal 2006, 2012; de Waal and Ferrari 2012; Warneken et al. 2007).

Of Yamamoto's five subjects, a chimp named Ayumu stood out as the most "other-regarding." Like the other chimpanzees in the experiment, Ayumu was cared for by his own mother (Ai) while also repeatedly exposed to the same trusted tester. The chimps in these studies are described as having a "strong bond" with these testers (e.g., Hayashi and Matsuzawa 2003:226). But in Ayumu's case, allomaternal exposure went further. Right from birth, Ayumu had interacted face-to-face with a particularly responsive experimenter in the person of Tetsoro Matsuzawa, who had spent years patiently interacting with Ai and cultivating her confidence. When Ayumu was born, Matsuzawa became the first scientist ever voluntarily granted access to a newborn by a mother chimpanzee. As a consequence, Ayumu was reared as few chimpanzees ever have been. Was it a coincidence then that when paired with his own mother in the experimental condition where the tool provider was prevented from seeing what the other chimp needed, Ayumu was the only one of the five subjects motivated to clamber up the wall and peek over the barrier before handing his mother exactly the tool she needed?

It is not clear whether Ayumu was just innately more resourceful or curious, or whether prolonged and intimate exposure to a human allomother conditioned him to be more interested in what someone else might need. There are few reports of helping behaviors from the wild (e.g., Snare 2012). Nevertheless, even if such capacities usually remain latent, I think we can say that other apes, certainly chimpanzees, possess the basic neural wiring for targeted helping under some conditions. From the wild, the best-documented exceptions in which chimpanzees appear to cooperate involve monkey-hunting by adult males at Taï Forest. As they pursue their prey, one may post himself below a tree where dinner is likely to descend. Depending on the actual intention behind this mutually beneficial act (whether self-serving, other-regarding, or both), it might count as targeted helping (see Boesch and Boesch-Achermann 1990; Boesch, Boesch, and Vigilant 2006; Tomasello et al. 2012). Nevertheless, compared with humans, wild chimpanzees simply do not engage in targeted helping or cooperation as much or as readily as humans do. So, does rearing by multiple responsive caretakers enhance the requisite perspective-taking?

The closest thing to the relevant experiment we have derives from a long-running project that Kim Bard and coworkers set up while seeking ways to improve psychological well-being in captive-born chimpanzees. To this

end, Bard monitored outcomes for chimpanzees under three rearing con-
ditions. Infants were either reared by their own mothers or, when maternal
care proved inadequate (as is all too often the case in captivity), removed and
reared in communal nurseries under one of two conditions, either in "Stan-
dard" communal nurseries where their physical needs were met by a series of
human caretakers or else in special "Responsive Care" communal nurseries.
In the Responsive Care situation, familiar, specially trained human caregiv-
ers, essentially allomothers-of-another-species, interacted with and stim-
ulated infants for several extra hours five days a week (Bard 2005, 2012). In
what follows, I summarize Bard's findings as if they represented results from a
"natural" experiment exploring how "proxies" for humankind's last common
ancestors with other apes might have responded to socioenvironmental con-
ditions requiring shared care.

The Responsive Care infants who interacted with multiple (albeit human)
allomothers engaged in more frequent and more sustained mutual eye gazing
than either wild chimpanzees or captive infants cared for exclusively by their
mothers (Bard 2005). By three months of age, they also exhibited more fre-
quent social smiles. Tested at nine months using the Bayley Scale for Infant
Development (no language required), chimpanzees receiving extra attention
from responsive allomothers exhibited more advanced cognitive development
than nursery-reared chimpanzees who had not received extra attention. Bard
refers to this "responsivity to social interaction" found in both human and
chimpanzee infants during face-to-face gazing as "primary intersubjectivity"
(different from Trevarthen's "secondary intersubjectivity").

Under suboptimal captive conditions, emotionally deprived chimpanzee
infants exhibit similar behavioral disturbances to those observed among
institutionalized human children. Infants receiving inadequate personal
attention may be unable to mount any organized response to attachment fig-
ures—freezing, for example, instead of running to them for comfort. Bard col-
laborated with Dutch developmental psychologists who had been comparing
attachment styles in children from intact nuclear families versus those reared
in understaffed orphanages. Their collaboration (Van IJzendoorn et al. 2009)
was the first to document "disorganized attachment" in another species of
primate. It was also the first "prospective" intervention study to evaluate how
care differing in quality and quantity of interactions affects cognitive develop-
ment and emotional security in nonhuman apes.

For obvious reasons, infant-care regimens were quite different for

colony-reared chimpanzees and children. Twenty-nine infant chimpanzees were placed in Standard Care after being removed from mothers deemed inadequate. They were placed in nurseries with a small group of other infants attended by one of four staff members who provided minimal human contact, feeding them and changing their diapers several times a day. Another seventeen received Responsive Care, spending some four hours, five days a week with one of five caretakers, all familiar and trained to sensitively engage chimpanzee infants (Van IJzendoorn et al. 2009). When tested at nine months using various measures, including the first-ever application of Ainsworth's Strange Situation procedure to nonhuman apes, chimpanzee infants reared with Standard Care exhibited attachment disorders similar to those in institutionalized human children. However, infants from the Responsive Care program tended to be emotionally more secure and also tested significantly better on cognitive development than Standard Care chimpanzees.

Clearly, interpersonal experiences in the months after birth had a profound impact on resulting phenotypes. None of these captive infants were reared under species-typical conditions, but those exposed to multiple responsive others developed to be more other-regarding than their exclusively mother-reared counterparts. Presumably, infants in Bard's Responsive Care nurseries were expressing cognitive and emotional capacities that otherwise remain latent among chimpanzees in continuous one-on-one contact with mothers in natural settings. Nevertheless, "other-regarding" does not mean the same thing in a year-old chimpanzee as in a human.

Among the more striking differences is the relative eagerness with which an infant accustomed to responsive care seeks to share experiences with someone else by calling their attention to some object in a triadic interaction. By nine months of age a human infant will hold out an object to a caretaker while eagerly monitoring their reaction to it (Tomasello 1999), as if inquiring, "What do you think of this? And, what should my response be?" By that age, however, young chimpanzees (even though interested earlier) are losing interest in that game (Tomonaga et al. 2004). It is not that infant chimpanzees never exhibit such joint attention. Outside the lab, young chimps have been observed interacting with other chimpanzees, cueing off one another's responses to an object. The differences seem to lie in frequency and enthusiasm for mutual engagement during shared attention or, as Kim Bard puts it (pers. comm., 2012), the amount of "positive affect" surrounding joint attention.

Like Tomasello (1999), researchers at the Primate Research Institute in Kyoto

considered "object-showing" and "object-giving" indicative of "referential communication in a triadic relationship." They specifically set out to learn whether a "nine month revolution" comparable to that in humans occurs in chimpanzees. Given similarities in terms of mutual gazing, smiling, and so on, up until that point, it seems odd that apes endowed with mirror neurons and capable of monitoring and imitating the expressions of others would not develop the same level of interest in sharing another's experience of an outside object that nine-month-old humans do. But they do not, nor do they develop it later on (Tomonaga et al. 2004:232–233; Tomonaga 2006; see also Matsuzawa 2007).

Humans' interest in what others think about something else starts to emerge before language. Six to nine months is also when humans start noting sounds others use to identify specific things and first learn to recognize common nouns (Bergelson and Swingley 2012). This convergence prompts us to ask if the human infant's enthusiasm for triadic interaction might be due to the need to get ready to acquire language. Or, did language evolve among our ancestors because early hominin infants were already interested in monitoring the mental states of others, already prone to "babble?"

Humans start to emit recognizable strings of phonemes around five to seven months of age. I agree with anthropologist Dean Falk (2004a, b) and others (Locke and Bogin 2006) that such babbling probably first emerged as a by-product of infants seeking to attract attention. We differ, however, in our reconstructions of the conditions under which babies did so. In line with this proposed "attention-getting" function, pygmy marmosets as well begin emitting similarly nonsensical but highly appealing vocal streams at just the age when infants in this cooperatively breeding species need to attract allomaternal attentions (cf. Elowson, Snowdon, and Lazaro-Perea 1998). As in marmosets, human "babbling" coincides with the developmental stage at which interactions with allomothers begins to be most relevant (Hrdy 2009:81ff.). In humans this is about six months when the milk teeth come in; infants are fed premasticated or soft foods via kiss-feeding and, among the Aka at least, there is a marked increase in "attachment behaviors" with allomothers (Meehan and Hawks 2013). Thus, I hypothesize that the babbling that eventually provided practice for language first emerged as a solution to a challenge other apes rarely confronted—the need to stay in touch without touch. Elicitation of attention and even, occasionally, tasty rewards would have provided contingent reinforcement (the most powerful kind) for continued elaboration and refinement of vocalizations (Goldstein, King, and West 2003).

Beyond maintaining contact and learning through such conditioning how best to appeal to others, infants relying on multiple caretakers would also benefit from being able to assess intentions. In this respect, humans are notably precocious. When Yale University cognitive psychologists showed six-month-old babies cartoons of a red ball struggling to roll up a hill, either helped by a yellow triangle nudging the ball upward or hindered by a blue square shoving it back down, babies subsequently looked longer and were more likely to reach out to the helpful symbol (Hamlin, Wynn, and Bloom 2007). As early as three months and certainly by six—still before language—infants preferred looking at the helpful character (Hamlin, Wynn, and Bloom 2010; Hamlin et al. 2011). They were, it seems, discerning who is potentially helpful and who is not.

By eight months of age, not only are babies making fairly sophisticated social judgments, but they begin to assign "reputations." By two, toddlers preferentially provide treats to third parties who behaved positively toward someone else who behaved prosocially, withholding treats from obstructive individuals (Hamlin et al. 2011). By ages three to five, children's own experiences of being shared with influence their decisions about how much to share with another depending on that individual's past contributions or "merit" (Kanngiesser and Warneken 2012).

In other words, as Henry Wellman and colleagues put it, "social cognition develops in infancy, revolving around understanding of human agents as intentional goal-directed beings and this understanding develops into preschool understanding of persons as mental beings" (2008:622). Those attending to intentional behavior early in development (at fourteen months) also test better at Theory of Mind tasks as preschoolers. Furthermore, as reported earlier, infants with more older sibs and caretakers manifest Theory of Mind at younger ages (Perner, Ruffman, and Leekam 1994; Ruffman et al. 1998).

Adult chimpanzees can also assess competence and, in laboratory tests, prefer reliable partners (Melis, Hare, and Tomasello 2006). They too respond more positively to "cooperative" versus obstructive others (Hamann, Warneken, and Tomasello 2011). But, to my knowledge, no one has tested infant chimpanzees or bonobos using the sort of experimental protocols Hamlin and colleagues used. Thus, we do not yet know at what age or under what circumstances chimpanzees develop these assessment capacities. Do chimpanzees register social reputations of others as early as human infants do? And do they do so in the wild, or only when socialized in human settings? Nor do we know

if social selection operated on earlier humans so as to enhance such discriminative capacities. However, preliminary evidence from the Primate Research Institute in Japan suggests that the neural capacity to make such judgments may indeed develop earlier in humans than it did in our last common ancestor with other apes.

WAS THERE SELECTION FOR EARLIER DEVELOPMENT OF
OTHER-REGARDING CAPACITIES IN HOMININ INFANTS? EVIDENCE
FROM COMPARATIVE NEUROSCIENCE

No mammal takes longer than humans to grow up (Bogin 1997) as reflected in slower brain maturation and later eruption of deciduous (or "milk") teeth and molars (see Bernstein, chapter 5, this volume; Bogin, Bragg, and Kuzawa, chapter 3, this volume). Indeed, the human brain's metabolic demands do not actually peak until around age four or five, after a hunter-gatherer youngster would ordinarily be weaned (Kuzawa et al. 2014), further highlighting the importance of allomaternal provisioning for synapse formation. Whereas the larger part of adult-like myelination in chimpanzees occurs before birth, in humans neocortical myelination takes place throughout childhood, with prolonged neocortical maturation, and synaptic pruning in the prefrontal cortex still ongoing in the thirties (Miller et al. 2012:16482). These are early days in the comparative study of anthropoid brain development, a field outside of my own expertise. Yet it strikes me as noteworthy that, given this general scheme of prolonged development, parts of the brain devoted to interpersonal judgments develop earlier in humans than in chimpanzees.

I rely here on a single study still awaiting replication. Using magnetic resonance imaging, Sakai et al. (2010, 2011) compared trajectories of development for prefrontal white matter in twenty-eight human children between the ages of one month and 10.5 years, three mother-reared chimpanzees between six months and six years, and thirty-seven rhesus macaques between ten months and 5.3 years. Not surprisingly, absolute brain sizes were larger in humans than chimpanzees, and much larger than in macaques. Both human and non-human apes exhibit delayed maturation of the prefrontal cortex, the brain region mediating working memory, motivation, temporal awareness, decision making, self-awareness, and, in humans at least, language (Sakai et al. 2010). The right prefrontal cortex also seems peculiarly implicated in inequity aversion and in how subjects respond to "fair" versus "unfair" offers in

experimental ultimatum games. When functioning of the right prefrontal cortex was temporarily disrupted, people tended to respond in a self-serving way regardless of whether the offer made to them was equitable or extremely inequitable (Knoch et al. 2006). Presumably this brain region also played a role when infants in Kiley Hamlin's experiments (described above) distinguished "helpful" from "obstructive" cartoon characters.

In the case of unusually clever and Machiavellian, tool-using apes—be they human or chimpanzee—extension of formative periods is assumed to be correlated with neuronal plasticity and enhanced mental flexibility owing to extra opportunities for exploration early in life (e.g., Gopnik 2012). According to this view, prolonged neural plasticity allows for learning through both trial-and-error and observation. Anthropologists have long believed that such extended periods of neuronal plasticity were essential for the evolution of characteristically human higher cognitive functions (e.g., Montagu 1955). Indeed a need for flexibility is often invoked to explain why human brains are so immature at birth and, in this respect "secondarily altricial" (e.g., Portmann 1962). Hence, Sakai and colleagues propose that "brain connection development, particularly in the prefrontal portion, may have been under intense selection pressure to remain immature, producing a brain that is more susceptible to acquiring chimpanzee- and human-specific social and technical skills based on early postnatal experience" (Sakai et al. 2011:5). But Sakai and colleagues also reported something else. When controlled for absolute size, white matter development in the frontal cortex develops more rapidly in humans than in chimpanzees. This faster growth trajectory seems paradoxical since humans absorb more cumulative culture than chimpanzees do. Following Montagu's logic they presumably would benefit from more prolonged neural plasticity and slower development in this respect.

The rapid trajectory of growth in the human prefrontal cortex begins around the second half of the first year of life (a phase marked by increased allomaternal interactions and provisioning among hunter-gatherers), then continues and levels off around age three (Sakai et al. 2011: fig. 3). This faster rate of prefrontal cortical development contrasts with development in other neural systems—for example, those controlling physical coordination and mobility. In contrast to those ungulates with highly precocial infants off and running within minutes of birth, all apes enter the world dependent on someone else for locomotion. Humans are born most helpless of all (see Konner, chapter 6, this volume). With even less muscle tone or coordination than a

newborn chimpanzee, human neonates also do not have the option of catching hold of maternal body hair. Unless held up by their mother, the only way a human neonate could reach her nipples would be to inch along caterpillar-like, but only if she was horizontal.

By three to five months of age, chimpanzee infants grasp and mouth objects more competently than human babies can. Chimpanzees will be weaned later, but develop chewing capacities earlier with deciduous teeth erupting at least a year earlier than in children (Bernstein, chapter 5, this volume). Yet by one year of age, chimpanzees still do not perform as well as human infants at collaborative tasks, pointing out objects, turn-taking, or completing puzzles (e.g., Bard 2012:236). This is so even though humans and chimpanzees seem equivalently precocious in terms of manipulating objects, exhibiting great competence in object-object combinations and inserting a stick into a hole by one year of age.

In terms of overall motor maturation, nonhuman ape infants develop faster than their human counterparts, a difference apparent to anyone who has watched infant chimpanzees or bonobos crawl, climb, scamper, or swing circles around humans of comparable ages. In predator-free, captive environments where less-restrictive chimpanzee mothers allow baby chimpanzees to more fully demonstrate innate abilities, youngsters crawl by four months and walk bipedally by nine. By contrast, human babies are only beginning to crawl at that age and do not walk until the end of the first year. These different rates of development are reversed however when assessing or discriminating between others is required. The white matter in the human prefrontal cortex develops faster in humans than in chimpanzees.[2] Apparently, the brains of human infants are *only selectively altricial*. In respect to assessing others and distinguishing intentions, human infants appear surprisingly precocious. Why?

Apes in the line leading to *Homo sapiens* were walking bipedally by four million years ago, so perhaps the brain-body coordination needed for walking required earlier development in the prefrontal cortex. But it takes many months before the irregular stepping motions of a baby become anything like balanced upright walking. Recent analyses reveal that the neural components at work this early are little different from those in other mammals. What distinguishes human bipedality are extra components emerging later in the course of development (Dominici et al. 2011; Grilner 2011)—perhaps only emerging "as needed" when needed.

This speculation brings me to the explanation I favor, that being able to make interpersonal assessments emerges so early because such capacities helped hominin infants judiciously and effectively elicit maternal and allo-maternal care. They developed earlier in hominins than physical coordination or other, arguably useful, abilities because precociality in this interpersonal realm was advantageous. This hypothesis is not mutually exclusive with more conventional "head start" explanations by which infants begin early to build the neural scaffolding and infrastructure for later cognitive development (Leigh 2004:162, cited in Falk et al. 2012) or begin to accumulate experiences acquired through observation, social trial and error, or play that will eventually be useful for negotiating the social and technical complexities of a successful human life (Gopnik 2012).

Various counterarguments involve metabolic costs inherent in building neural connections as well as the many specialized capacities that do not develop until needed (and that might even be disadvantageous if they emerged too early). But glossing over these and taking the "early start" logic at face value, rapid development of prefrontal connections during infancy might facilitate complex social interactions, providing opportunities for such interactions to continue shaping neuronal connectivity as experience-dependent knowledge and skills build up over time (as in Sakai et al. 2011; see also Luby et al. 2012). An early start might build necessary scaffolding essential for language acquisition or other social competencies that evolved later for reasons outside of my scope here. What I want to emphasize here is the sequence. Neither "early start" explanations nor common assumptions about the need for prolonged childhoods in order for humans to fill unusually large, anatomically modern 1,350 cc brains with "social capital" needed for a successful life (Kaplan et al. 2000) are mutually exclusive with the proposal that infants with multiple providers took longer to grow up. All three may have played roles in shaping modern humans. What I hypothesize here, though, is that alloparental care, food sharing, and, with it, youngsters beginning to take longer to grow up, characterized our ancestors prior to the emergence of anatomically modern humans.

Rather than long childhoods evolving to accommodate growing big brains, prolonged dependence emerged as a corollary of cooperative breeding. But with alloparental care came more rapid postnatal development of the frontal cortex and areas of the brain that help infants monitor and assess commitment levels and intentions of others as well as adjust their facial expressions,

vocalizations, hand movements, and other actions in ways that engaged and appealed to them. These little apes were already emotionally more similar to modern humans. Shared provisioning permitted the evolution of anatomically modern brains in response to selection pressures favoring them, while "emotional modernity" preadapted these apes to eventually evolve (through processes and feedback loops described elsewhere by Boehm, Flinn and Alexander, Bowles, Tomasello, Knight, and many others) such behaviorally modern human capacities as language, cumulative culture, or consciences peculiarly attuned to the evaluation of others.

My working assumption is that the duration of childhood in *Homo erectus* by 1.8 million years ago fell someplace in between the prolonged childhoods typical of modern humans and the much shorter ones typical of both the genus *Pan* and their anatomically similar australopithecine cousins. There are fascinating hints in the fossil record that larger babies (e.g., DeSilva 2011) and more rapid postnatal expansion of the prefrontal cortex (e.g., Falk et al. 2012; Tague 2012) might go back in the hominin lineage even further than I conservatively postulated in *Mothers and Others*. Either way, it seems unlikely that mothers would have been selected to produce such costly, slow-maturing young without reasonable prospects of assistance. The big question relevant to the evolution of childhood, just when hominins began to be characterized by prolonged nutritional dependence and longer postreproductive life spans, continues to be debated (summarized by Voland, Chasiotis, and Schiefenhövel 2005a: table 1.1).

Evolving "Emotionally Modern" Underpinnings for Cooperation: Recap and Conclusions

As a branch of tool-using, bipedal apes equipped with "Machiavellian" social intelligence traversed the ecologically unstable savanna-woodlands of Plio-Pleistocene Africa, selection favored those with broader diets (including meat and tubers) provided by an array of provisioners. Cooperative breeding is especially likely to evolve in animals living in habitats with unpredictable rainfall and abrupt swings in available resources. Meanwhile, food delivered to immatures produced situations conducive to more generalized (adult-to-adult) food sharing. Such sharing increased chances of survival in famine times while permitting shorter intervals between births when conditions improved, enabling at least some populations to bounce back after crashes.

Cooperative breeding was accompanied by changes in the life history and psychology of all parties concerned: mothers, fathers, alloparents, and especially immatures upon whom selection impacted most immediately and heavily. I hypothesize that, to survive, infants became connoisseurs not only of mothers but of others as well. This transformation was mediated via development's role in the production of selectable variation (West-Eberhard 2003). Over generations, immatures buffered from acquiring and processing their own food could afford to delay costly adult size and dentition as well as bigger brains (see Bogin, Bragg, and Kuzawa, chapter 3, this volume; Bernstein, chapter 5, this volume). But the need to solicit care required speeding up and refining development of other capacities important for perspective-taking, understanding how to appeal to others and assess their intentions—critical preadaptations for the role reputations would increasingly play in human social organization.

In the absence of direct evidence, I attempted to "test" underlying assumptions of this mothers-plus-others model (figure 2.3) by reviewing evidence for how the best available proxies we have for humankind's last common ancestor with other apes (chimpanzees and modern human infants) respond to different rearing conditions. Findings from these "as if" experiments reveal that infants spending time off mothers, interacting with and attended to by multiple caretakers, develop in the predicted directions. They pay more attention to faces and expressions of potential caretakers, strive to attract their attention and to appeal to them, attend better to their communicative cues and goals, and are more likely to engage in targeted helping. Differences between human and chimpanzee infants in brain development during the first years of life appear consistent with the mosaic pattern of physically altricial/emotionally precocial development hypothesized here.

I am not proposing that humans are cooperative because their ancestors were "cooperative breeders." Rather I believe that more other-regarding (and in this sense "emotionally modern") youngsters were predictable corollaries of this mode of child-rearing and as a byproduct of it, preadapted apes in the hominin line for greater social coordination. At the same time, food sharing would have magnified opportunities for already highly social apes to interact with the same individuals over time, benefiting from exchanges and providing fertile ground for selection to specifically favor cooperative responses (e.g., Axelrod and Hamilton 1981; Fehr and Fischbacher 2003; Rand, Greene, and Nowak 2012).

Of course, many other factors and processes were simultaneously at work. My point is that no foresight on Mother Nature's part would have been required to favor the evolution of cooperative breeding in a highly social species struggling to rear altricial young in the face of difficult-to-extract and unpredictable resources. Thus, there is no need to invoke "exceptional" processes to account for the evolution of other-regarding capacities that initially emerged as predictable corollaries of immatures relying on mothers-plus-others. It was because predictable developmental and evolutionary processes impacted what was already a cognitively sophisticated, relatively large-brained ape that foundations were laid for the eventual emergence of such uniquely human attributes as language, conscience-based moral systems, and multifaceted collaborations.

Acknowledgments

Notes

1. Note that, depending on ecological and customary circumstances (usually having to do with inheritance of property), child survival can also be inversely correlated with the presence of allomothers, including grandmothers (e.g., Voland and Beise 2005; Sear 2008 for the Malawi; Strassmann and Garrard 2011). However, such exceptions have never been reported among band-level hunter-gatherers and thus fall outside of the scope of this chapter.

2. Sakai's sample size was small, but it is tantalizing that Ayumu, the chimpanzee co-reared by his mother and human others, was also the chimpanzee exhibiting both unusually well-developed capacities for perspective-taking in targeted help experiments (described above) and the fastest trajectory of prefrontal white-matter development of the three chimpanzees scanned (Sakai 2011: fig. 2.2).