Childhood

ORIGINS, EVOLUTION, AND IMPLICATIONS

Edited by Courtney L. Meehan and Alyssa N. Crittenden
**CHAPTER TWO**

*Development Plus Social Selection in the Emergence of “Emotionally Modern” Humans*

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**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 relatives. 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 Tanaka 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 2011).

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 younger removes food from her mouth (Kano 1992). By contrast, among humans, parents and alloprenes 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 vitally interested people are in the suffering and values people use to judge others for others to receive information about how to behave, and moreover, to approve of them. From the appropriate “rules,” techniques, and the mentalizing and questing for intersubjectivity, why they would have been crucial for quite entirely helpless immatures.

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vitality 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 asking 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

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 prefer-
ences. Photo: S. Hrdy.
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 that “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 Whiten 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 2009:241) as cited in L. Dean et al. 2012:117). 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 en-culturated 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 ways in both the wild (Garber 1997; replicated captive experiments, as Cronin, Schroeder, and Snowdon 2011) between humans and this phylogenetically distant species of monkeys (among whom, as in humans, there is no costly care and provisioning to rear surviving offspring). As discussed elsewhere, they are capable of an unusual level of cooperation (Van Schaik 2009; Hrdy 2009; Burkard 2011).

Interestingly, marmosets readily adopt these behaviors toward humans, but they do not appear to exhibit them in the wild. To be sure, we need to also take into account the way humans do (Table 2.1).

Table 2.1. Human-Marmoset Parallels

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<tr>
<th>Human Trait</th>
<th>Marmoset Trait</th>
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<tr>
<td>Extensive alloparental care + primate care</td>
<td>lavish alloparental care</td>
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<td>Prolonged post-weaning dependence</td>
<td>care of nestlings</td>
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<td>Reliance on hunting + gathering</td>
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<tr>
<td>Adapted to colonizing new habitats</td>
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<td>Unusually conditional maternal abandonment in situations lacking maters</td>
<td>care of nestlings</td>
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<td>High levels of foraging cooperation</td>
<td>care of nestlings</td>
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<td>Provisioning by multiple males</td>
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<td>accompanied by either real chimp</td>
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<td>care of nestlings</td>
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<tr>
<td>Nonadvertised ovulation + mating</td>
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<td>Weakly developed dominance hierarchy</td>
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<td>Variable group compositions + culture</td>
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<td>testosterone levels in males carieing</td>
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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.
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<td>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:</td>
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<td>1. Extensive alloparental care + provisioning</td>
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<td>2. Prolonged post-weaning dependence</td>
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<td>3. Reliance on hunting + gathering with learning-intensive extractive foraging</td>
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<td>4. Adapted to colonizing new habitats</td>
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<td>5. Unusually conditional maternal commitment with high rates of abandonment in situations lacking allomaternal support</td>
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<td>6. High levels of foraging cooperation</td>
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<td>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</td>
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<td>8. Nonadvertised ovulation + mating throughout cycle</td>
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<td>9. Weakly developed dominance hierarchies where food concerned</td>
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<td>10. Variable group compositions + adults of both sexes moving between groups</td>
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<td>11. Other-regarding impulses manifested in food sharing + information transfer</td>
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<td>12. Endocrinological parallels such as elevated prolactin and reduced testosterone levels in males caring for infants</td>
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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

on the right has run over to pull in a set on the other side of the cage. This Judith Burkart, illustrating methods she sociality across species (Burkart and
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 impulses in order to become other-regarding, and that the only way to ask under what circumstances do our nonhuman primate conspecifics exhibit mental states, desires, and needs of the sort that might please them? And why should such a capacity persist as creatures subject to the same evolutionary pressures that characterized our animal world?

Such challenges drew my attention to the idea that leading to the genus Homo must have been a process of cooperative care shared care is typical of human foraging societies. Yet shared care is not found among our closest great ape relatives. Did Pan and Homo diverge from a common ancestor some 4 million years ago? When, did such extremely un-apelike behavior first emerge in the human line? And what were the ramifications for future human evolution?

Shared Care, Provisioning, and the Evolution of More Generations

There is an ongoing paradigm shift in our understanding of the way early humans lived and interacted with their environment. Until recent years, the predominant view was that human ancestors lived as nomadic foragers with relatively small family groups. However, recent research suggests that early humans may have lived in larger, more permanent communities. This new understanding of human evolutionary history has important implications for our understanding of the human mind and behavior. For example, it has been suggested that the evolution of larger groups may have facilitated the development of more complex social structures and cooperative behavior. This, in turn, could have led to the emergence of more advanced cognitive abilities and cultural practices. Overall, the idea that early humans lived in larger, more permanent communities provides a new perspective on human evolution and has important implications for our understanding of the human mind and behavior.
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-ape-like 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 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 younger (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.

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mother’s infant does not mean that adults
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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. As 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 Carney 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., Rapoport 2011; Rapoport and Brown
2008; Thornton and McAuliffe 2000). Going beyond merely tolerating a
younger 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 Rapoport 2011; Rapoport
and Ruiz-Miranda 2003). Such mentoring helps explain why foragers growing
up in groups with many helpers may be more adept at harvesting (e.g., Langen
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, Hel- frecht, 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:257, 2009).

Changing Our Minds: Psychologically

Modern developmental psychology suggests that children’s minds grow within the context of early care. Revising our ideas about exactly what the Environment of Evolutionary Adaptation means to development. Thus, new modes of cognitive operation require reassessing assumptions about the role of early care during humankind’s EEA (e.g., see C. B. Jones, 2006; Kazen et al., this volume; K. Kramer 2005a; Hunt 2005). If infants first develop a sense of self and then learn about their world through responsive care, as psychiatrist Daniel Siegel puts it, infants develop skills to engage with other minds. It is not surprising that these early interactions affect both the formation of the child’s social brain and the regulation of gene expression.

As in all primates, maternal nurturance is crucial for survival. Frequent breastfeeding along with physical warmth constitutes this very special relationship (Konner 2010). Circumstances made allomaternal care increasingly essential, the hominin mother no longer the primary source of security, warmth, mobility, and protection. This maternal bond on their mother to obsessively maintain the first six months of their lives and thereafter continue to suckle in earshot for four or more years. Hominin mothers remained unchanged (Bowler 2005) in their nearly single-minded dedication for their young, becoming above that of all other current hominins.

Prior to conception, all through childhood, and beyond, this hominin mother demanded much social support she had. Her brain size may have been directly linked to how strategically she allocated maternal care to spaced offspring. In the hours and days after birth, the mother’s perception of social support...
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 Bowlby’s 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 overlaid 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 2005; Meehan, Helfrechtd, 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 1975; Kaplan et al. 2000; Hill and Hurtado 2009). Furthermore, taking advantage of occasional protein and fat bonanzas was only practical if people could count
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ring back meat to share (R. Lee 1979;
09). Furthermore, taking advantage of
as 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 oppor-
tunities including better access to food, water, and security. Add to such
incentives the need for allomaternal assistance and variable impulses among
postreproductive to provide it (e.g., Blurton Jones, Hawkes, and O’Connell
2009; Sclaza 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 Boarios 2012). Even among chimpanzees, females remain
in their natal range when benefits 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 of-
er, 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 2002c). 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” (Siegal 2012:24; also see Gopnik 2010).

When availability of allomotheral 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. 2009 for humans), 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 allomotheres 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 allomotheres, 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, so that they merit the prolonged investment in baby to suckle, initiating lactation and its processes (Hrdy 1999: chap. 21). Every newborn is competing with both older and otherwise continue to invest and any that produce were she to resume cycling in appeal to others as well through more psychological dimension to Lorenzi’s stake in making their babies attractive to other mother-offspring dyads for all.

Conspicuous natal coats presumed as well as caretakers, while fetal fat deposits passage through narrow birth canals. With Darwin’s example of the peacock’s tail to continue to be favored if they increased their fitness (Lyons and Montgomery 2012; Weidman, the existence of this infantile equivalent reliably reward centers in the brains of other infant’s, react when looking at cute babies (Gross 2004). “Runaway social selection” has humans benefit from appealing to others. Nesse invokes it to explain why humans remaining loyal to a person or an idea, engaging in selfless conduct exceeding one’s survival requirements (2010; see also Flinn and Alexander 2004). Selflessly generous or honest behavior, say, of being chosen by an advantageous person, is a near benefit from that choice. Such signal and response are genetically coevolving. According to Nesse, people and the powerful constraining self-image (and with it perhaps blushing) evolved the internal monitoring system that guides humans to compete with others directly or, as in the case of advantageous social partners (see also Flinn and Alexander 2004).
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 *Kindsfaltung*. Mothers also have a stake in making their babies attractive since they, too, are competing with other mother-offspring dyads for allomaternal assistance (Hrdy 2009:229ff).

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 Montogomerie 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 (Glöckler 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 selfishly 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. Late in the end of their reproductive value, often increase as reproductive value decreases in langurs who opt out of competition for younger relatives against infanticidal males. Cooperative breeding did not lead to long-term primate, as Hawkes hypothesizes it does in humans. Opportunities for postreproductive survival have been more sporadic than chronic (Hrdy 2009).

Meanwhile, over millions of years, human brains include caring relationships with other species as well as those with long-term bonds, and emotions (Carey 2008). It is unsurprising that social experiences of human development and subsequent social roles in humans (reviewed in Siegel 2012) support the proposition that prehuman apes were more likely than human apes to have different cognitive and emotional approaches to the care of their mothers.

Virtual and Real “Tests” to the Mothers-Infant Bond

None of us has a machine to go back in time to respond to mothers and allomothers, but we can look at the modern descendants of those early hominoid infants who respond to different stimuli. Findings from neuroscience are beginning to suggest how development in chimpanzees and humans is shaped.

Elsewhere (Hrdy 2009), I reviewed the evidence for a maternal system that integrates multiple mental perspectives (Lamermon 1992). Allomaternal support within the same household or just transient visits to the same household and enhances social awareness and growth of both for infants born to young, inexperienced mothers.
Responsibilities first emerged as corollaries of kinship. That is, our ancestors were emotionally because, in the high child mortality phase throughout the Plio-Pleistocene, with contingent levels of commitment such that, over generations, dependents “other-regarding” were better cared for. Have favored those who grew up more and needed of others, an emotionally quite recognize what expressions, vocalizations, others.

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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. 2ff). 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 2009:141; Olds, Sadler, and Kitzman 2007; Spieler 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 caretaker—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 (Matsuzawa 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 2009). Experimental psychologists and cross-cultural anthropologists report a similarly inverse correlation for humans. A baby 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 is not surprising that in traditional cultures that did not provide opportunities for direct tactile contact between infants and caregivers, human infants spend many more hours looking into their caregivers’ eyes than do babies who spend much time in their caregivers’ arms (reviewed in Bard 2012).

Like chimpanzee infants, human infants are born attached to the mother (but still in non-anxiety-producing proximity) and remain in touch without touch,” monitoring and signaling frequently “checking back” (cf. Faller 1999). In each generation, behavioral phenotypes, increasing brain capacity, and the motivations of those nearby. Apparently, when human infants also became more discriminating, both observations are consistent with the idea that more conditional maternal commitment is associated with offspring that may receive more care and are thus more likely to develop ties to the mother. The Mother-Plus-Others hypothesis would predict that the emergence of “emotionally modern humankind” is associated with the evolution of selective variation in the environment, and that human infants are better cared for and fed than their chimpanzee counterparts.
Attachments (Hrdy 2009:124–141; Olds, and Bensley 1994), and for infants among their own mothers plus four to six familiar, (Harlow 1959; 1968), and (Olds and Field 2013). Such findings are consistent with provisioning among already highly social, primates. As predicted, infants increasingly attuned to their caregivers and the cues they give, each generation infants a little better at projecting their needs and motivations to appeal to their primary caregiver. During this period of rapid change, immature infants in the wild seem better motivated to appeal to them would be more likely to have their needs met. In the long term, the transition favoring other-regarding appetites and abilities to individuate from other individuals. Indirect evidence from comparative studies suggests that the ability to read and respond to facial expressions helps us evaluate the intentions of others and also helps to generate new social interactions.


caregiver.

Figure 23. 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 extended family care, direct contact between infants and their mothers, babies gaze into their mothers' 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 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 chimpanzee was trying to do. With vision obscured, tool selection was random. But when the provider could see what the other chimpanzee 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 and Ferrari 2012; Warneken et al. 2006.

Of Yamamoto’s five subjects, a child named “other-regarding.” Like the other chimpanzees cared for by his own mother (Ai) who was a trusted tester. The chimps in these studies (e.g., Hayashida 1999; in Ayumu’s case, allomaternal exposure was in the form of face-to-face interaction with a participant of Tetsuro Matsuzawa, who has also been cultivating her confidence. While the first scientist ever voluntarily to live with a chimpanzee. As a consequence, Ayumu has been. Was it a coincidence that the chimpanzee was the experimental condition where the chimpanzee needed. Ayumu was motivated to clamber up the wall and into the mother exactly the tool she needed.

It is not clear whether Ayumu was conditioned him to be more interested. There are few reports of helping behaviors in animals, even if such capacities usually exist in apes, certainly chimpanzees, possessing under some conditions. From the way, in which chimpanzees appear to cooperate males at Tai Forest. As they pursue a tree where dinner is likely to be found, behind this mutually beneficial activity (for both), it might count as targeted help (Boesch 1990; Boesch, Boesch, and Vigant 1999). Compared with humans, wild chimps helping or cooperation as much or more by multiple responsive caretakers ever.
Development Plus Social Selection in Emergence of “Emotionally Modern” Humans

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 Tetsuro 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., Struwe 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
Hrdy

end, Bard monitored outcomes for chimpanzees under three rearing conditions. 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 “Standard” 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 caregivers, essentially allmothers-of-another-species, interacted with and stimulated 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 conditions requiring shared care.

The Responsive Care infants who interacted with multiple (albeit human) allmothers engaged in more frequent and more sustained mutual eye gazings than either wild chimpanzees or captive infants cared for exclusively by their mothers (Bard 2005). By three months of age, they also exhibited more frequent social smiles. Tested at nine months using the Bayley Scale for Infant Development (no language required), chimpanzees receiving extra attention from responsive allmothers 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 gazings 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 figures—freezing, for example, instead of running to them for comfort. Bard collaborated 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 development and emotional security in nonhuman apes.

For obvious reasons, infant-care regimens were quite different for colony-reared chimpanzees and children. All infant chimpanzees and children were placed in Standard Care after birth; responsive care, on the other hand, was not provided. They were placed in nurseries attended by one of four staff members in every social context, feeding them and changing them every few hours. Seventeen received Responsive Care, one week with one of five caretakers, all five typically human caretakers. Van IJzendoorn and colleagues used various measures, including the Strange Situation procedure to nonhuman primate with Standard Care exhibited attachment to nonhumanized human children. However, the group tended to be emotionally more secure than Standard Care infants.

Clearly, interpersonal experiences have a marked impact on resulting phenotypes. Not surprisingly, mothers under species-typical conditions, but others did not. Mothers who were more highly reared counterparts. Presumably, infants were expressing cognitive and emotional development among chimpanzees in contrasting care forms in natural settings. Nevertheless, “other thing in a year-old chimpanzee as in a child.”

Among the more striking differences was an infant accustomed to responsive care, who one by one by calling their attention to objects. Nine months of age a human infant would go eagerly monitoring their reaction to it. What do you think of this? And, what should we do? Young chimpanzees (even though they are not the same as human infants) show much joint attention. Outside the lab, young chimpanzees interacting with other chimpanzees, caregivers, or objects. The differences seem to lie in the level of engagement during shared attention (Bard 2012), the amount of “positive affect” displayed by the infant.

Like Tomasello (1999), researchers at
chimpanzees under three rearing conditions: their own mothers or, when maternal care was removed (often the case in captivity), removed and fostered to two caregivers, either of the same or opposite sex. In one condition, either a male or a female caregiver was present, and in the other condition, both a male and a female caregiver were present. The two caregivers were of the same species, and the chimpanzees were not exposed to external stimuli. The caregivers were trained to provide a series of social and physical needs in a communal setting.

In terms of interactions, the chimpanzees exhibited a range of behaviors, including mutual grooming, play, and social play. The caregivers also provided physical care, such as feeding and grooming. The chimpanzees were observed to develop attachments to the caregivers, which were measured through various methods, including the use of the Bayley Scale for Infant Behavior Development.

The study found that the chimpanzees reared under these conditions showed differences in cognitive and emotional development. For example, chimpanzees reared with a single caregiver showed more advanced cognitive development, as measured by the Bayley Scale, compared to those reared in the communal setting.

The authors argue that human infants also experience similar social and emotional development, and that caregivers play a crucial role in this process. They suggest that the findings from this study have implications for the development of more effective caregiving practices for human infants.
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 hominins 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 Lazar-Perea 1998). As in marmosets, human “babbling” coincides with the developmental stage at which interactions with allomother begins to be most relevant (Hrdy 2009:8ff.). In humans this is about six months when the milk teeth come in; infants are fed premaxicated or soft foods via kiss-feeding and, among the Aka at least, there is a marked increase in “attachment behaviors” with allomother (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 siblings 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 (Bogen 1997) as reflected in slower brain maturation and later eruption of deciduous (or “milk”) teeth and molars (see Bernstein, chapter 5, this volume; Bogen, 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 53 years. Not surprisingly, absolute brain sizes were larger in humans than chimpanzees, and much larger than in macaques. Both human and nonhuman 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 particularly implicated in inequity aversion and in how subjects respond to “fair” versus “unfair” offers in experimental ultimatum games. But the wet cerebral cortex was temporarily disrupted in a way regardless of whether the offers were inequitable (Knoch et al., 2006).

The role when infants in Kiley Hamlin’s studies distinguished “helpful” from “obstructive”

In the case of unusually clever chimpanzees, they human or chimpanzee—extreme in the way correlated with neuronal plasticity—were offered extra opportunities for exploration. In support of this view, prolonged neural plasticity and the extended periods of neuronal plasticity characteristic of human higher cognition, particularly in the prefrontal cortex, are increasingly recognized. The need for flexibility is often invoked both at birth and, in this respect, in childhood. Hence, Sakai and colleagues proposed, particularly in the prefrontal portion of the brain, that infants are under pressure to remain immature, postponing the process of acquiring chimpanzee- and human-like maturity on early postnatal experience” (Sakai et al., 2010). The study also reported something else. With maturation, the relative development of the prefrontal cortex of chimpanzees. This faster growth helps them absorb more cumulative culture and language. The logic they presumably would be more flexible and slower development in this region.

The rapid trajectory of growth rates may continue around the second half of the first year. In contrast to many other neural systems—for example, the somatosensory and motor systems—for example, the visual and auditory systems—prefrontal cortex continues and levels off around six years, and the rate of prefrontal cortical development continues to decline. In contrast to those younger systems, the many others, including cognition and social cognition, are still running within minutes of birth, at least slow rate of development. Human infants outlive both chimpanzees and monkeys, so they may have been more rapidly expanding human brains so rapidly.
The development of the human brain as reflected in the eruption of deciduous (or "milk") teeth in hominins was a critical period for neural development, particularly in the prefrontal cortex (Knoch et al. 2006). This region of the brain is crucial for social cognition and decision-making, particularly in response to ultimatum games. When functioning of the right prefrontal cortex was temporarily disrupted, participants 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 neural 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 alltricial" (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). 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. 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 point. Make interpersonal assessments enable helped human infants judiciously acquire the parental care. They developed earlier or other, arguably useful, abilities because the neural scaffoldings and infrastructures (Leigh 2004:162, cited in Falk et al. 2011) acquired through observation, social interaction, and abilities be useful for negotiating the successful human life (Gopnik 2012).

Various counterarguments involve the neural connections as well as the much later, still develop until needed (and that might be too early). But glossing over these anomalies, rapid development of prefrontal cortex facilitates complex social interactions, allowing social actions to continue shaping neuronal knowledge and skills build up over time (Falk et al. 2012). An early start might build the biological acquisition or other social cognitive systems, outside of my scope here. What I want to argue is that neither “early start” explanations nor for prolonged child rearing in order for biologically modern 1,550 cc brains with “social roles” (Kaplan et al. 2000) are mutually exclusive. Multiple providers took longer to grow these mental capacities shaping modern humans. What I hypothesize about early altricial care, food sharing, and, with it, social growth, characterized our ancestors and us, modern humans.

Rather than long childhoods evolving into prolonged dependence emerged as a result of altriciality, with altriciality care came as a result of parental care. The prefrontal cortex and areas of the brain that had emergent levels and intentions of others...
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 australopithocene 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 Schieffenhövel 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.

Development Plus Social Selection in Emergence of Emotionally Modern Cooperation

Cooperative breeding was accompanied and, I hypothesize, selected for by and psychology of all parties concerned, especially immatures upon whom selection seemingly focused heavily. I hypothesize that, to some extent, selection favored the role of mothers but of others as well. Cooperative breeding appears to have been the development’s role in the production of bigger brains (see Bogin, Bragg, and Kurzban chapter 5, this volume). But the need to refine development of other capacities may be needed to understand how to appeal to other species and how to respond to other capacities for appeal to others. Other species and their behavioral and social organization.

In the absence of direct evidence for the role of maternal care in the development of a species with a common ancestor with other apes (chimpanzees), these assumptions may not be directly applicable. Yet, as studies of infant development in non-human primates show, infants respond to different rearing conditions. Some primate species, for example, develop relatively high levels of attachment to a single caregiver, while others develop a broader range of attachment patterns. These differences may be due to factors such as the availability of food resources and the presence of other individuals that can provide support. Regardless, the idea that infants are capable of learning to use tools and participate in social activities is supported by observations of infant behavior in the wild and in controlled settings. These observations suggest that infants are capable of learning to use tools and participate in social activities.
other actions in ways that engaged and were already emotionally more similar to those events that permitted the evolution of anatomical selection pressures favoring them, while these apes to eventually evolve (through cited elsewhere by Boehm, Flinn and Patat, and many others) such behaviorally change, cumulative culture, or consciences of others.

The duration of childhood in Homo erectus are in between the prolonged childhoods of the australopithecine cousins. There is that larger babies (e.g., DeSilva 2011) of the prefrontal cortex (e.g., Falk et al. hominin lineage even further than I and Others). Either way, it seems unlikely to produce such costly, slow-maturing of assistance. The big question relevant when hominins began to be characterized and longer postreproductive life spans, by Voland, Chasiotis, and Schiefenhövel

Underpinnings for Cooperation: Conclusions

Hominins equipped with “Machiavellian” social unstable savanna-woodlands of Pliocene, those with broader diets (including herd of provisioners. Cooperative breeding of quadrupeds living in habitats with unpredictable resources. Meanwhile, food delivered conducive to more generalized (adult-to- increased chances of survival in famine intervals between births when conditions regulations to bounce back after crashes.

Cooperative breeding was accompanied by changes in the life history and psychology of all parties concerned: mothers, fathers, allopairs, 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 the predicted behaviors. 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

This chapter benefited from discussions over many years with Kristen Hawkes, Steve Emlen, Mel Konner, J. Anderson Thomson, and Polly Wiessner, from comments and corrections provided by Kim Bard, Judith Burkart, and Mary Jane West-Eberhard, and from the talented assistance of Lore M. Ruttan and June-el Piper. Additional thanks are due to participants at both the 2012 S.A.R. workshop on the Evolution of Childhood and the 2016 University of California, San Diego Center for Academic Research and Training in Anthropogeny (CARTA) Symposium on the Evolution of Altruism.

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. Sakal’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).

Life-history theory is a branch of evolutionary biology that focuses on the allocation of life cycles, which are a product of growth, reproduction, and survival. Life-history theory is a set of biological and behavioral traits, such as size, growth rate, number of offspring, age at first reproduction, life span, and the pace of senescence. The central question is not how traits evolve, but instead may be understood as evolutionary trade-offs through natural selection because traits that are costly to maintain or are disselected traits carry costs. Life-history traits are recognized as evolutionary trade-offs or compromises. The central question of this chapter is: How are life-history traits shaped by life-history trade-offs that help define the horizons of our lives? What can we infer about human life-history traits from our nearest relatives and other primates such as the chimpanzees and bonobos? How do life-history traits influence the way we live and interact with others?

Does Childhood Exist?

We see “children” everywhere. We speak to them in a special language, or, as Lancy (2008) phrases it, “kids rule” (373). We are so preoccupied with children that we are often too generous in our interpretation of what we mean by “the child,” or more accurately, “the childhood.” Some are based