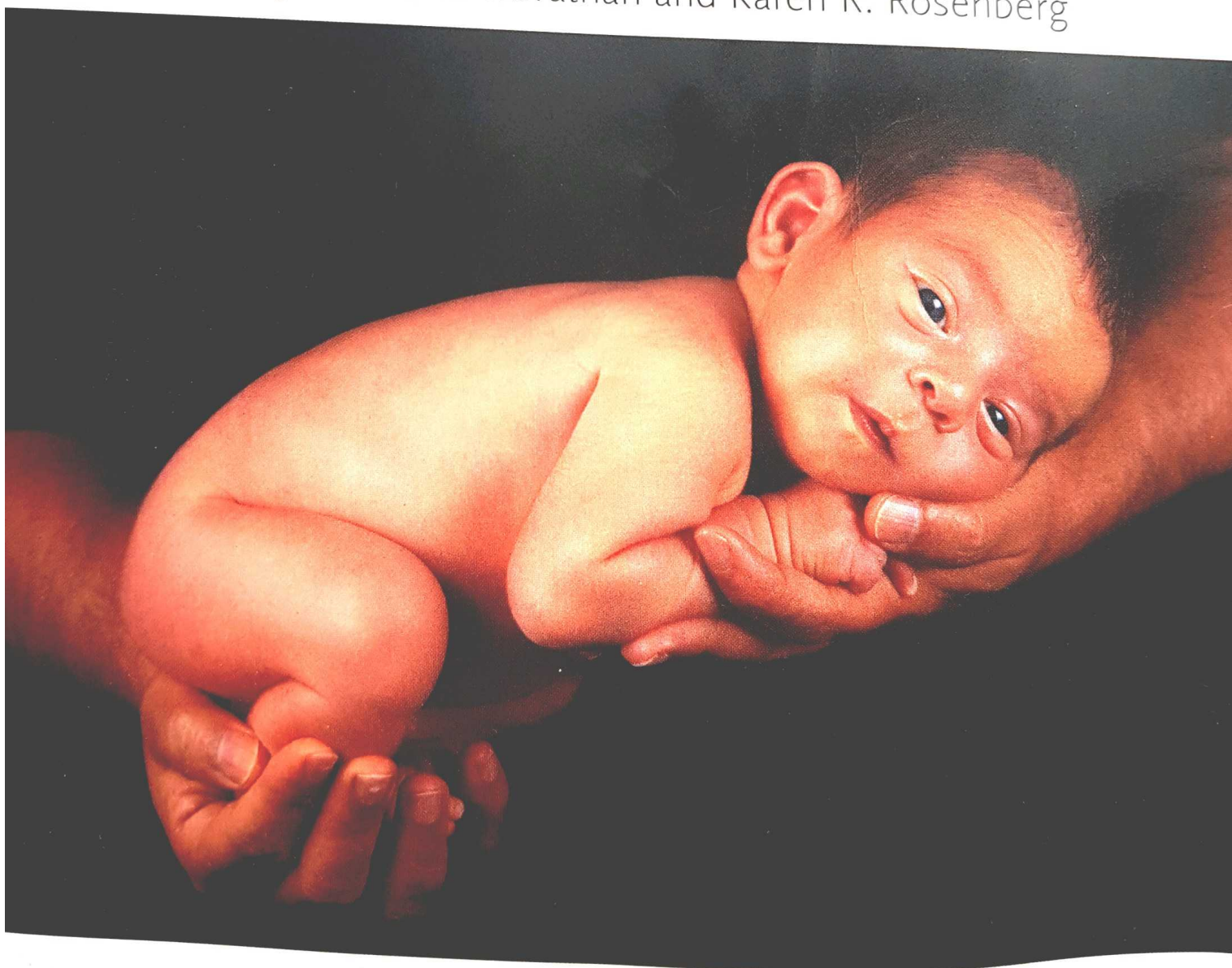


Costly and Cute

HELPLESS INFANTS AND
HUMAN EVOLUTION

Edited by Wenda R. Trevathan and Karen R. Rosenberg



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Human Evolution and the Helpless Infant

WENDA R. TREVATHAN AND KAREN R. ROSENBERG

We know from literature, films, and our own personal experience that human newborns are very adept at demanding and occupying the attention of others. They are helpless, dependent creatures who need our care, and they have evolved attractive characteristics and a range of captivating behaviors that are very effective at soliciting and obtaining that attention. This topic has long been of interest to evolutionary biologists and anthropologists. In his influential book *Mankind Evolving*, Dobzhansky was unequivocal in stating that it was humans' helplessness at birth and utter dependence on parents and other caretakers that favored learning and socialization "on which the transmission of culture wholly depends" (1962:196). We agree but argue here that it is more than the transmission of culture that derives from this helplessness. Many of the distinctive characteristics that make us human can trace their origins (or at least their significance) to the fact that we give birth to infants who are highly dependent on others; babies are afforded the opportunity to learn how to be human while their brains are experiencing growth unlike that seen in other mammals, including the nonhuman primates.

In the 1960s and earlier, most models of human evolution featured "man the hunter" (Lee and DeVore 1968) as the key player; in the 1970s (in the context of the women's movement), it became obvious that such an approach examined only a limited part of the human adaptation, and many anthropologists turned their attention to the other half of the species, namely "woman the gatherer" (Dahlberg 1981). The pivotal books that carried those names sought to explain and contextualize a number of distinguishing characteristics of humanness: bipedalism; language; increased reliance on tools and meat eating; expanded kin and other social networks; large, complex, and metabolically expensive brains; prolonged lifespan after menopause for women; sharing of food,

childcare, and other resources; art; symbols; rituals; and social and emotional intelligence. While we recognize that single-cause explanations of the human adaptation are simplistic, we propose that an equally important player in the story of human evolution, and one who can account for most of the characteristics listed above, is the helpless, attractive human infant. In a parallel phrase to the previous models, Dean Falk refers to this model as “baby the trendsetter” (chapter 6, this volume).

As anyone who has cared for them will attest, human newborns are truly dependent creatures that arrive in the extrauterine world in an undeveloped, helpless state and that mature even more slowly and over a longer period than any other primate. In spite of these challenges, our ancestors were able to find ways for their infants to survive while maintaining mothers' health *and* reducing the spacing of births relative to apes so that human parents (and alloparents) are able to care for not just one, but several needy offspring at a time (see Lovejoy 1981). This costly developmental pattern is unprecedented among primates and is surely related to other aspects of our biology and behavior and to our adaptation as a cultural species. The chapters in this book examine both the costs and benefits of giving birth to such immature offspring, and the contributors propose that infant helplessness and social and cultural adaptation evolved hand in hand in many significant ways.

We came to our interest in the developmental status of human infants at birth from our work on the evolution of human childbirth. In previous publications (Trevathan 1987, 1988; Rosenberg and Trevathan 2002), we have argued that the evolution of the complex and constrained way in which human babies are born was made possible because of human birth assistance, a behavioral adaptation that may have characterized bipedal hominins even before encephalization. In our early thinking, we saw the timing of birth as one of the variables that can be altered (because of humans' ability to culturally buffer our infants from the extrauterine environment) to mitigate the constraints of the obstetrical dilemma. As a result of a number of developments in the field (reviewed by Dunsworth in chapter 2), our attention has shifted from birth to the developmental status of the newborn. The timing of birth relative to infant development is not only a way to mitigate obstetrical constraints (by being born sooner when head size is smaller and passage through the birth canal easier) but also creates challenges that confer advantages in a species in which the chances of survival and future reproduction are enhanced by attracting the attention (and protection and provisioning) of alloparents. This book

investigates the proposition that helpless human infants are costly but that their attractiveness (“cuteness”) helps to mitigate those costs and that great benefits balance those high costs. In order to investigate the potential costs and benefits of being born early relative to developmental status, we brought together a group of scholars who we thought could bring fresh perspectives to this issue.

In 2014, the average cost to raise a middle-income American child to age eighteen approached a quarter of a million dollars. This seems expensive to most of us, but costs like these, while not necessarily stated in monetary terms, have been part of the human heritage for millions of years. Infancy is an especially expensive time in the life course, largely due to the extreme dependence and helplessness of the infant. An enduring question is why we have evolved to have such highly dependent infants. Given the costs of pregnancy, childbirth, breastfeeding, and other aspects of caring for these dependent infants, what has our species gained? What have been the trade-offs of this reproductive strategy that have made it worth it? We demonstrate in this book that infant helplessness is central to the human adaptation, and we argue that the only way humans could have adopted such a costly reproductive strategy is with extensive care from others, cooperative caretaking in addition to and beyond that provided by the parents. (Following Hrdy in her chapter in this volume, we define “cooperative breeding” as a characteristic of “any species with allo-parental as well as parental care and provisioning of offspring.”) Bogin and colleagues (2014) have called this set of behaviors “biocultural reproduction” in recognition of the fact that, unlike most other cooperatively breeding species, human allomothers are not necessarily genetic relatives of the young they care for. Kramer and Otárola-Castillo (2015) have pointed to cooperative breeding as central to the distinctive aspects of human life history.

Human infants are like other primate babies in many ways, but they appear to reach extremes in two significant characteristics: (1) exhibiting a higher degree of helplessness and dependence at birth and therefore (2) needing an inordinate amount, duration, and intensity of parenting and caretaking. The two are obviously related, as has been discussed for centuries. The relationship between the helpless infant and strong family bonds was recognized by Alexander Pope in his *Essay on Man* (1733, noted by Gould 1977), when he observed that most mammals and birds leave their young after a relatively short time to take care of themselves, whereas “A longer care man’s helpless kind demands / That longer care contracts more lasting bonds.” Bolk, Gould,

Portmann, and Montagu were among the early influential writers who argued that slow development (Bolk's "retarded life course" or "fetalization theory of anthropogeny") was "what is the essential in Man as an organism" (Bolk 1926:469-470). Cohen (1947, cited in Gould 1977) argued that the long period of human infancy is more important than any anatomical differences in distinguishing us from other animals.

Many scholars have written about the significance of extended childhood (delayed maturation or adulthood) for the learning and socialization that are part of our adaptation as cultural animals (e.g., Bogin 1997; Mann 1972; Portmann 1990), but a focus on infant helplessness at the time of birth is less common, and rarely has it served as the focus of an entire book. In this volume we concentrate on late pregnancy to weaning, considering this time period in the human life cycle as a developmental continuum. In this view, birth is neither a beginning nor an end of a developmental stage; rather, it is a point when the neonate leaves the relative isolation of the biological womb of the uterus and enters the larger, more stimulating cultural womb of the mother and her social group.

Historical Overview of Perspectives on the State of the Human Newborn

Across mammals and birds, a continuum of life history patterns is recognized and distinguished by the extremes: altriciality and precociality. Altricial species (like mice) tend to be born after a short gestation, in large litters, with eyes and ears sealed by membranes at birth, without hair, and unable to locomote, regulate their own body temperature, or find food independently. They tend to spend the first period of their extrauterine lives in a nest. Precocial species (like horses) are generally born covered in hair after a long gestation, in small litters, with well-developed sensory organs that are open, and are able to locomote, thermoregulate, and find food on their own (Sacher and Staffeldt 1974; Martin 1992; Harvey 1992). Primates as an order are precocial in the pattern of their development, and humans generally fit this pattern (e.g., Smith and Tompkins 1995). The interesting ways in which humans fail to fit the precocial pattern make it difficult, however, to use either of these terms or even to locate a place along the continuum to describe the state of the infant at birth.¹

Finding a working phrase to describe this state has been challenging. Terms used by earlier scholars include "helpless," "neotenus," "paedomorphic,"

“fetalized,” “immature,” “highly dependent,” “secondarily altricial,” “semi-altricial,” “extergestate fetus,” “altricial-precocial,” and “precocial-altricial.” Portmann was among the first to write about the significance of the human infant being born in a more helpless and less developed state than the infants of most other primates. In his earliest writings, he used the German terms *Nesthocker* (nest hocker or squatter) and *Nestflüchter* (nest flier), which were usually translated as altricial and precocial. He recognized that human infants are difficult to categorize in these terms and suggested that, for the human infant to be considered truly altricial, he² would have to be born at 5 months of gestation, when the sensory organs are still closed and undeveloped. In contrast, as in other precocial mammals, the sensory organs, locomotor organs, and central nervous system of human infants develop and grow in utero and are largely functional at the time of birth. As further evidence of the precocial state of human infants, Portmann cited the composition of human milk, which is like that of mammals with precocial infants in being very dilute and thus necessitating frequent nursing. Portmann argued that we should see human helplessness at birth in its context: “not as the primitive, somatic immaturity of an altricial infant, but as a very exceptional situation within the mammalian group. In fact, with respect to the full precocial type, humans are secondarily altricial” (Portmann 1990:38; phrase actually first introduced in 1942).

Portmann continued his discussion of the unusual nature of the human infant compared to other mammals by noting that most precocial infants are “miniature versions” of the adults of their species with behaviors and locomotion little different from theirs. But the human infant does not match other primates in relative body proportions, locomotion, and communication until he has matured for approximately 1 year after birth. On the basis of this, Portmann suggested that the functional human gestation period might be considered to last 21 months: “Our preliminary conclusion is only that the actual length of human pregnancy is much less than it should be for typical mammalian development at our level of organization” (1990:51). He further argued that in spite of the fact that our infants are much larger at birth than those of our closest relatives, growth in the first year of life is more like that of a fetus than of an infant: “At the end of the first year of life the moment comes that must be considered as the time of parturition for any true mammal of humanlike organization” (54).

Portmann called the first year of life in humans the “extrauterine spring,” referring to the season of growth. It is during this year that the human infant

becomes a walker, a talker, and a doer. The important thing both to Portmann and to the contributors in this volume is that these maturational events take place in the relatively stimulating cultural and social environment of the postnatal world, not in the “all-purpose environment of the womb but under unique circumstances; each phase of postpartum life intensifie[s] this uniqueness by increasing the possibilities for divergent, individual situations” (Portmann 1990:91). Portmann concluded this line of thought by proclaiming that it is the existence of this extrauterine spring that accounts for us. “It will gradually become clear that world-open behavior of the mature form is directly related to early contact with the richness of the world, an opportunity available only to the human!” (93). In this sense, we can interpret the term “spring” in its meaning “to move upward or outward” and as in the root of “wellspring.” (See Dunsworth, chapter 2, this volume, for more discussion of the extrauterine spring.)

Bostock (1958), a psychologist, proposed that the human infant should have two birthdays: the first upon leaving the womb and the second when “exterior gestation” ends and quadrupedal movements (i.e., crawling) begin. Perhaps anticipating Washburn’s (1960) obstetrical dilemma hypothesis, Bostock argued that the first birthday occurs when the neonatal head is as big as it can be and still pass through the birth canal. Recognizing that being born “early” has costs, Bostock further argued that the exterogestate fetus (referred to by him as the “neogestate”) needs a great deal of care: “The pelvic barrier has been overcome, but at the cost of all the hazards of keeping alive naked helpless foetuses under difficult and changing conditions” (1962:1034).

Montagu also wrote a great deal about the state of the human infant at birth: “man is born as immaturely as he is because—owing to the great increase in the size of his brain and consequently of his head—if he weren’t born when he is, he wouldn’t be born at all” (1961:56). In his view, gestation is not complete at birth; rather, it consists of “uterogestation” or “interogestation” in the womb and then “exterogestation” outside the womb. According to him, the length of uterogestation matches the period of exterogestation, both at 267 days. He claimed that “it is important that most of the brain growth be accomplished during the first year, when the infant has so much to learn and do” (57). Publishing his views in the *Journal of the American Medical Association*, Montagu used a clinical journal for physicians as a platform to decry the “modern” view of infancy and the disruption in mother-infant interaction:

“The separation begins from the moment of birth, so profound has our misunderstanding of the nature of human beings grown. Perhaps the hypothesis of uterogestation and exterogestation proposed here may cause us to reconsider the meaning of the infant’s immaturity and dependency” (57). His concern was that the “symbiotic union” of mother and infant is too frequently disrupted, with potentially negative effects on development. Bostock (1962) also decried the “complete revolution in infant care” that occurred in the first half of the twentieth century; he was particularly concerned for the potential deleterious effects of bottle feeding. He called for an “evolutional approach to infant care” (1035) and claimed that many social ills could be traced to the first few months of life, when the infant should be treated as an exterogestate fetus and kept close to the mother’s body, receiving the same intense nurturing and support as he did in utero.

Although often portrayed for illustrative purposes as a unidimensional continuum, the distinction between altricial and precocial is complex and multidimensional. Despite historical discussions of human infants as altricial or precocial, it is clear that the terms have limited utility when applied to humans. Our babies are not helpless, blind, and hairless/featherless, as expected for altricial young, nor are they able to move about on their own, as expected for precocial young; rather, our babies at birth show a mixture or mosaic of altricial and precocial features.³ Like other precocial primates, human infants have eyes and ears that are fully open. Also similar to precocial mammals, humans have long gestation periods and usually give birth to one infant at a time. Our babies are large, relative to adult body size, and we reproduce later in life, like other precocial mammals. Human milk is dilute at 88% water, similar to that of other precocial primates, who are able to keep up with their mothers and nurse frequently, in contrast to animals who remain in a nest and can only nurse at discrete intervals (Milligan 2013). Certainly we recognize that infants of many species are rarely completely altricial or completely precocial, but may possess a mosaic of the features usually used to characterize these extremes. The human infant, who is born with eyes fully open but who is utterly helpless in motor skills, has a particularly unusual constellation of features. Rather than describe humans as secondarily altricial, could it be more accurate to say that human infants are simply “precocial babies born at a relatively early stage in their development,” as we have suggested elsewhere (Rosenberg and Trevathan 2007:94)?

In an effort to find a single term, most of the contributors to this volume have chosen to use "helpless." It is important to note, however, that this refers only to somatic immaturity and locomotor limitations. Indeed, we argue that it is the precise combination of this helplessness with the fact that human infants are highly engaged with their caretakers and able to manipulate aspects of their environment through their attractiveness (cuteness) and to take in so much sensory stimulation that makes humans unusual and so difficult to place on the altricial-precocial continuum. In addition to motor development, however, there are a number of other ways in which human infants seem to be underdeveloped at birth in comparison with our closest relatives, the monkeys and apes.

What Is Undeveloped about the Human Infant?

BODY PROPORTIONS AND SKELETAL MATURATION

As noted by Portmann (1990:38), human newborns are not "miniature versions of their parents," as in most precocial species. Rather, they are very different from their parents in their body proportions, making them more like altricial infants. In the chimpanzee, the length ratios between infant and adult torsos, legs, and arms are similar, whereas in humans the ratios differ considerably. For example, human legs are much longer relative to the rest of the adult body than they are in infancy.

With regard to skeletal maturation, humans show less ossification at birth than most other primates. In the rates of ossification of long bones and digits, human neonates are as developed as the fetuses of macaques and do not reach the level observed in macaque newborns until several years after birth (Schultz 1949, cited in Gould 1977). Even at 3 months of age, human infants are more immature than newborn chimpanzees with regard to hand and wrist ossification (Watts 1990). Dental eruption also shows similar delays. Cranial plates are open in human infants until several months after birth, when they reach a stage seen in infant monkeys and apes at the time of birth (Gould 1977). The skull bones remain unfused and flexible until brain growth is completed: in early adulthood for humans but in early childhood for apes. This degree of flexibility is important during the birth process because it allows the skull to mold as it passes through the birth canal, reducing the diameter of the head and facilitating birth (Posner et al. 2013). (The occiput is the most developed

Table I.I. Newborn and Adult Brain Size for Selected Primate Species

| | Neonatal Brain Size | Neonatal Sample Size (n) | Adult Brain Size | Neonatal- Adult Brain Size Ratio |
|---------------------------------|------------------------|--------------------------------|---------------------|--|
| <i>Chlorocebus aethiops</i> | 47.6 | 13 | 66.7 | 71.4 |
| <i>Macaca mulatta</i> | 58.6 | 79 | 91.1 | 64.3 |
| <i>Macaca nemestrina</i> | 61.8 | 93 | 104.6 | 59.1 |
| <i>Saimiri sciureus</i> | 14.7 | 43 | 26.2 | 56.1 |
| <i>Cercocebus atys</i> | 57.5 | 43 | 107.9 | 53.3 |
| <i>Papio anubis</i> | 82.9 | 35 | 161.4 | 51.4 |
| <i>Cebus albifrons</i> | 33.7 | 12 | 71.0 | 47.5 |
| <i>Callithrix jacchus</i> | 3.5 | 28 | 7.6 | 46.1 |
| <i>Pan troglodytes</i> | 150.9 | 22 | 381.7 | 39.5 |
| <i>Homo sapiens</i> | 373.8 | 729 | 1330.5 | 28.1 |

Note: Data are courtesy of Jeremy DeSilva and include species for which samples of 10 or more neonatal individuals were available.

of the cranial plates, which is why it can sustain the intense force of uterine contractions during birth; it is also the least likely cranial bone to be damaged during birth; Redfield 1970.) Interestingly, Gould (1991) cited cranial molding as a way to pass a large head through a tight birth canal as an example of something that evolved as an “exaptation” rather than “adaptation.” All of these ossification delays are consistent with the overall slowed development in hominins compared with other hominids and haplorrhines.

BRAIN DEVELOPMENT AND GESTATION LENGTH

The average human gestation of 38 weeks is not very different from the gestation periods of the other great apes—32 weeks for chimpanzees and 38 weeks for gorillas and orangutans—making it very unlikely, as some scholars have suggested (Trinkaus 1984; Gould 1975), that the gestation length of our ancestors was significantly greater in either absolute or relative terms compared to humans today (Martin and MacLarnon 1990; Rosenberg 1992). What is really

different about human newborns is the relative size of their brains compared to adults' brain size. This is achieved by a shift in the position of birth relative to the rapid period of brain growth. In most primates, birth takes place at about the point where fetal brain growth slows down and the brain growth curve shows an inflection. In humans, brain growth continues at fetal rates well past the time of birth (see Falk, chapter 6, this volume, and figure 6.2). This postponement of brain maturation makes human infants helpless in several domains (see Falk, chapter 6, and Semendeferi and Hanson, chapter 7, both this volume). By 18 months of age, brain growth rates for humans and chimpanzees are similar (Leigh 2004). Table 1.1 (from data generously shared with us by Jeremy DeSilva) shows infant brain size as a percentage of adult brain size (what Portmann called the "multiplier factor"). At birth, humans have achieved only about 28.1% of their adult brain growth; the numbers for other primates range from 39.5% (in *Pan troglodytes*) to 71.4% (in *Chlorocebus aethiops*). This means that compared to most anthropoids, human infants have a great deal of brain growth still to accomplish.

Much of the discussion of the human infant brain at birth focuses on size and makes comparisons with adult brain size to highlight the degree of underdevelopment at the end of gestation. But brain size alone does not tell the full story. In comparing neural development during gestation and shortly thereafter in a number of primate species, Clancy and colleagues (2001:14) conclude that human infants have a "precocial brain although somewhat disguised by an unwieldy body." What they mean is that although human infants are motorically undeveloped at birth, they are neurally advanced in comparison to the other species studied. For example, at 7 months' gestation, the human brain has the neural maturation level of a newborn macaque, a week-old kitten, and a 2-week-old rat. This lends further support to the concept of mosaic development in the human newborn, as proposed by DeSilva in chapter 4 (this volume). The extensive neural and cognitive development that takes place in the first year of life is highly dependent on sensory interaction with others in the infant's environment (Bruner 1972; Bjorklund 1997; Bjorklund and Pellegrini 2000; Gopnik et al. 1999; Kinnally 2013). As the contributors to this volume argue, this may be one of the most significant advantages of being born relatively early in the course of brain growth and development. Of course most neural development occurs before birth, but this view emphasizes the importance of the outside world for continuing neurological maturation, which we discuss below, as do Semendeferi and Hanson in chapter 7.

VISION

Human infants are not born blind, as would be expected for an altricial mammal or bird, but neither is their vision fully developed at birth (Mercuri et al. 2007). Apparently they can focus on objects 12–18 inches from their faces (conveniently, approximately the distance to their mothers' eyes when they are breastfeeding) (Brazelton et al. 1966). Newborns' preference for the human face has been demonstrated as early as the first 10 minutes of life (Goren et al. 1975), a phenomenon that has been shown for chimpanzees and macaques as well (Tomonaga 2007; Kuwahata et al. 2004). According to Haith (1980), the light and dark areas of a human face are optimal for stimulating maximum neural firing rates. Infants engage in visual searching soon after birth, helping to activate neural areas for further visual development.

Eye contact is important in forming social attachments in humans (Guastella et al. 2008) and appears to be a significant mechanism for forming parent-infant bonds in the first hours after birth (Trevathan 1983). Rivinus and Katz (1971) suggested that as clinging abilities at birth diminished over the course of human evolution, eye contact became more important for maintaining connections between mothers and infants. The ability of human infants to maintain eye contact and to visually follow movements in the early hours and days of life facilitated these attachments, placing a selective premium on the early emergence of visual function even when neural abilities to locomote were limited. Like chimpanzees, right from birth, human infants seek out faces, focusing especially on the eyes, but by 9 months or so, when chimpanzees tend to lose interest, human infants become more interested (Okamoto-Barth 2012; Hrdy 2016).

LOCOMOTION

In considering the various aspects of human development at and soon after birth, perhaps the most conspicuous and consequential undeveloped characteristic is locomotion. Human babies are extremely helpless motorically at birth and are dependent on others for mobility for several years. As a rule, precocial mammals tend to move about in ways very similar to adults, albeit a bit wobblier in the beginning. At birth, human infants can make alternating stepping movements with their legs that are similar to those used in locomotion, but they lack the equilibrium and postural control that is developed embryonically in precocial animals (Muir 2000). These aspects of locomotion

develop postnatally in altricial infants and in humans, who are unable to maintain the upright posture of bipedalism until they are at least a year old; it often takes several years beyond that before their movements are smooth and efficient.

At first look, humans appear to be qualitatively different from other primates with regard to when they begin walking, but it turns out that this assessment depends on what point in the life course is selected as a baseline. When measured from birth, humans appear to be greatly delayed in locomotor independence, but if another beginning point is selected, that difference diminishes. Garwicz and colleagues (2009) argue that the onset of walking in humans, when measured from conception rather than from birth, is not different from that of other mammals and is highly correlated with adult brain mass. Their research into the age of walking onset across terrestrial mammals indicates that humans begin walking when their brains reach a certain developmental level and at the time predicted based on adult brain size. They conclude that the neural basis for walking onset is similar across mammalian species with respect to brain development and that it is a highly conserved trait shared by a wide range of placental mammals. So humans walk when their brains reach a maturation level comparable to that of other mammals, but like brain maturation, that point is greatly delayed in the human life course. This observation fits well with the data of Clancy and colleagues (2001), which showed that what is different across mammals is not motor maturation rates but the timing of birth.

GASTROINTESTINAL AND IMMUNE FUNCTION

The human infant's intestinal tract is essentially sterile at birth, but by the end of the first year of life, a baby's intestinal microbiota resemble those of adults (Levy 2007). Most of these come from the vaginal passage during birth, colostrum, and breastmilk (Dominguez-Bello et al. 2010). The birth process provides the first source of gut bacteria via exposure to the perineal region; further colonization comes through breastmilk (Newburg and Walker 2007; Abrams and Miller 2011). The importance of this process is highlighted by the increasing concern today that infants born by cesarean section and fed only formula may find challenges to their GI function in later life (Martin and Sela 2013; Neu and Rushing 2011; Cho and Norman 2013; Mueller et al. 2015; see also Quinn, chapter 5, this volume).

Although human infants are not immunologically naïve at birth (Holt and Jones 2000), their immune systems are far from fully developed, partly due to the very invasive hemochorial placenta (a characteristic of all haplorrhines), which requires immune suppression from both mother and fetus to prevent rejection during pregnancy (Morein et al. 2007). For example, although most immunoglobulins are not expressed until after birth, limiting the newborn's ability to fight off infections (McDade 2005), some (such as immunoglobulin G) can cross from the mother to the infant via the placenta during gestation. Antibodies are acquired from the mother through contact with the vaginal passage during birth and via colostrum and breastmilk early in infancy, as noted above with regard to gut bacteria. There is also evidence that newborn infants acquire bacterial nasal flora directly from their mothers (and others) when their faces are close together. The mother's strains of respiratory organisms develop in the infant's respiratory and gastrointestinal tracts, providing protection from potentially pathogenic bacteria (Klaus and Kennell 1982). It seems that the fact that development of proteins critical for surviving outside the womb is delayed until after birth contributes to the delayed maturation of the infant and his high dependence on the mother and others.

In summary, human infants are undeveloped in several aspects of physiology, anatomy, and neurological development. Although they may not be unique in their state of development (see Robson et al. 2006; Leigh 2004; Finlay and Workman 2013), the needs of human infants for intensive caretaking and inordinate investments of time and energy for a large portion of the life course have both been impacted by and have an impact on almost all aspects of human evolutionary history.

Factors Influencing the Birth of the Helpless Infant

Figure 1.1 proposes a number of factors influencing the helpless state of the infant and factors that flow from that state (originally published in Trevathan 1987:32; factors not in the original model are in italics here). On the left side of the diagram are factors that may contribute to the birth of a helpless infant: an encephalized neonate who must pass through a relatively constricted bipedal pelvis; the deeply invasive hemochorial placenta, which may impact the infant's state in late pregnancy; the advantage of being born before most of brain growth is completed; and metabolic limits to the mother's ability to support the pregnancy. On the right side of the diagram are features that

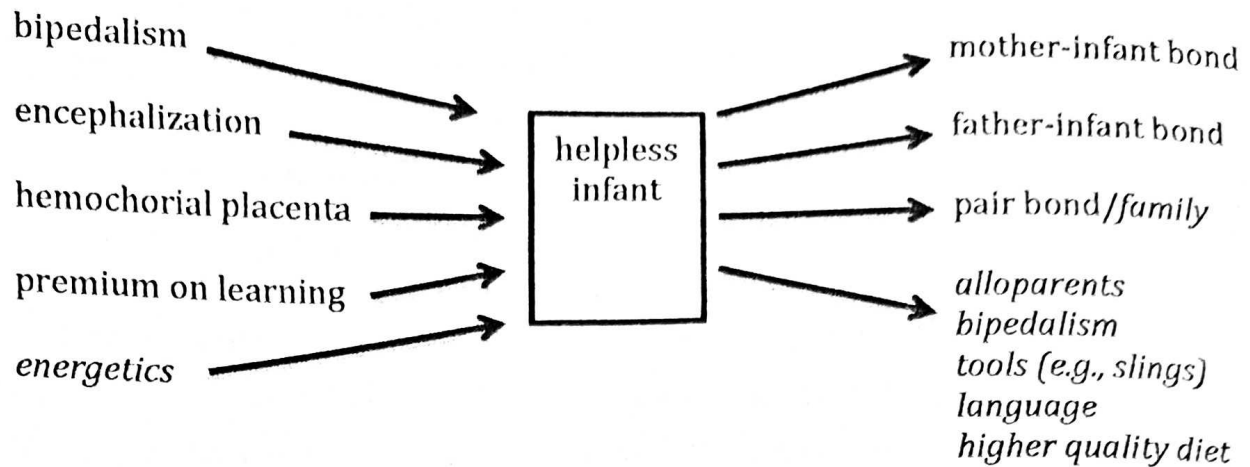


Figure 1.1. Factors in human evolutionary history that have contributed to the birth of the helpless infant. Modified from Trevathan 1987:32.

may flow from the helpless state of the infant at birth: the mother-infant and father-infant bonds; the pair bond and extended family, including alloparents; contributions to selection for bipedalism, tool use, and language; and dietary adaptations that increase diversity, nutrient density, and nutrient quality. Some of these are the subjects of other chapters, but we briefly discuss some features here.

OBSTETRIC FACTORS

For more than half a century, the reigning paradigm to explain why human infants are so helpless at birth has been the obstetrical dilemma, first proposed by Washburn in 1960. If selection is to favor encephalization in a lineage, he reasoned, there must be a way to escape the constraints on brain and body growth imposed by the bipedal pelvis. The dilemma was solved by delivering the fetus at an earlier stage of development. As encephalization evolved in the human lineage, more and more of brain growth had to occur postnatally, placing more and more demands on mothers (and, as we now increasingly recognize, others as well) to care for the increasingly helpless and vulnerable infant. But more than 40 years ago, Epstein (1973) suggested that the pelvis would only have to expand 4 cm (which he described as “readily evolvable”) in order to accommodate the birth of an infant with an adult’s full brain size. In

other words, he concluded that the obstetrical dilemma could not explain why the human infant has only a quarter of its brain size at birth.

The obstetrical dilemma as an explanation for the timing of birth and hence human helplessness at birth has come under further fire from scholars directly assessing the biomechanics and energetics of bipedalism and the metabolic requirements of pregnancy and lactation (Dunsworth et al. 2012; Wall-Scheffler and Myers 2013; Warrener et al. 2015; see Dunsworth, chapter 2, this volume). Length of gestation is determined by a number of proximate and ultimate factors, including both metabolic and obstetrical constraints.

Although maternal metabolism may play an important role in the timing of birth, pelvic shape and size are likely still subject to obstetric selection. Furthermore it is difficult to explain human sexual dimorphism in pelvic morphology (in which females are greater than males, in contrast to body size dimorphism, in which males are larger than females on average) without invoking selection from obstetrical constraints. The discussions about challenges to the birth process usually focus on cephalopelvic disproportion, but there are other maternal and fetal dimensions that pose challenges because of bipedalism and encephalization. Often, midwives are as concerned about shoulder dystocia as they are about cephalopelvic disproportion (Trevathan and Rosenberg 2000) and severe tearing of the vaginal opening and perineum, which may result when a large baby is born through a bipedal birth canal. A third-degree laceration (tearing from vagina to anus), often resulting in what today is called an obstetric fistula, would have had serious impacts in the past on a mother's health and her ability to care for her infant, just as it does today.

As noted above, the cranial plates of human infants do not fuse until several years after birth. This may make the infant somewhat vulnerable to damage if dropped or hit, but the fact that the cranial bones can slide over each other (referred to as "molding" by birth attendants) means that the circumference of the fetal head can be decreased temporarily to allow easier passage through the birth canal. The shoulders of the human infant do not have that degree of flexibility, however, and may actually provide more obstruction to the birth process than do the head and the rest of the body. Monkeys' shoulders are narrower than their heads, so the monkey head provides more resistance to passage through the birth canal than the shoulders do. (Apes, which, like humans, do have broad shoulders, have infants that are much smaller than their mothers' birth canals so shoulders have limited impact in the birth process for those animals.)

ENERGETICS

Although pelvic constraints provide an ultimate factor limiting gestation, most contemporary scholars—beginning at least with Epstein's work (1973) and continuing through Martin's contributions (1983, 2007) and those of Ellison (2001a, 2009)—agree that a primary proximate factor limiting brain growth before birth is the ability of the mother's metabolism to support the fetus in utero. In other words, it is most likely a metabolic trigger that serves as a proximate factor to signal the end of the 38- to 40-week gestation period, which ends with delivery of a highly dependent infant with only about a quarter of its ultimate brain size, a hypothesis proposed by Ellison (2001a), Dunsworth (Dunsworth et al. 2012), and others and discussed further by Dunsworth in chapter 2.

PLACENTAL EFFECTS

Preeclampsia is another constraint on the human developmental state at birth (Rosenberg and Trevathan 2007). Humans, like other haplorrhine primates, have highly invasive placentae with fetal nutrient and oxygen needs met by direct contact with the maternal vascular system (Martin 2003). In the third month of pregnancy, the human placenta undergoes a secondary invasion, or burrowing in, when brain development takes off and nutrient and oxygen needs increase significantly. Sometimes this secondary invasion is incomplete, compromising nutrient and oxygen delivery later in pregnancy and occasionally resulting in preeclampsia. The resulting cost is often a compromised pregnancy or even maternal and/or fetal death. The major indicator of preeclampsia is high blood pressure resulting from resource diversion from the mother to meet increasing fetal needs in the context of limited vascular support of the incomplete invasion. The only cure for preeclampsia is delivery of the infant. Perhaps one of the explanations for a 9-month gestation period is that it prevents a higher rate of preeclampsia than the 10% reported in the world today. (Preeclampsia and the secondary deep invasion of the trophoblast were believed to be unique to humans, but see Crosley et al. 2013 for evidence that preeclampsia is found in other ape species that have the same degree of invasion as humans.)

The deeply invasive placenta is also causally related to the high rate of postpartum hemorrhage (it takes longer to detach from the uterine wall), a prominent contributor to birth-related morbidity and mortality throughout history

(Abrams and Rutherford 2011). Two other placental disorders related to degree of invasiveness and perhaps unique to humans are *placenta abruptio* (premature separation from the uterine wall when invasiveness is too shallow) and *placenta accreta* (invasion is too deep, and detachment does not occur when it should), both of which contribute to maternal and infant mortality today. It is likely, as with other pregnancy and birth complications reviewed here, that preeclampsia and other problems related to the placenta are more common in contemporary populations than they were in the past.

IT IS BETTER OUTSIDE

A great deal of our discussion so far has focused on factors that select *against* developing too long in utero, but there are a number of reasons that it may be better for a species with a cultural adaptation to be outside rather than inside the uterus during important neurological and cognitive development. Oxygen is of utmost importance to brain growth, of course, and the amount of oxygen available to the infant outside the womb is five times what is available in utero (Nathanielsz and Vaughan 2001). Prolonging time in utero may lead to the infant “starving to death” with regard not only to energy, but also to oxygen. Clearly, continued brain growth requires adequate oxygen, so in one view, birth occurs when the fetal lungs are mature enough to utilize the higher levels of oxygen in the environment outside the womb.

Size undoubtedly puts limits on how much brain growth can occur before birth, but the fact that most neuronal and synapse development occurs in the first few months and years of postnatal life suggests that beyond size, there are advantages to having this growth occur in the stimulating environment of the outside world and a dense social network. Miller and colleagues (2012:16482) note that “activity-mediated myelin growth early in human life has the capacity to be shaped by postnatal environmental and social interactions to a greater degree than in other primates, including chimpanzee,” suggesting advantages to being born “early.”

Costly and Cute

COSTS OF GESTATION

Gestation is costly for all mammals. Human infants are unusually large, and the energetic demands increase dramatically in late pregnancy (see Dunsworth,

chapter 2, this volume). At birth, the human infant is notably fatter (around 16% of body weight) than most other mammals (Cunnane 2005; Kuzawa 1998). Fat accumulation in the last weeks of pregnancy is important for maintaining the expensive and rapidly growing brain, for preparing the baby for postnatal life, and for preparing the mother for lactation. The last trimester of pregnancy requires an additional 300 calories a day in the mother's dietary intake to maintain this fat deposition. Cooperative caretaking in the form of provisioning to supplement what she was able to gather herself was probably important throughout human evolution in providing sufficient caloric intake for a late-term pregnant woman (Dufour and Sauthier 2002). Although metabolic efficiency increases in pregnant women, there comes a point when they simply cannot metabolize any more calories, no matter how much food is available (Dunsworth et al. 2012). One way to meet caloric needs is to divert calories from herself to her fetus by reducing physical activity (Dufour and Sauthier 2002). An important contribution that members of her social group can make is to help reduce her workload and physical activity so that more of the calories she consumes go to her developing fetus. In a sense then, cooperative child-rearing really begins in the late stages of pregnancy.

COSTS OF GIVING BIRTH

Unlike other primate species, in which females most often give birth in isolation from other members of their social group, it is difficult, risky, and unusual (but not impossible) for humans to give birth alone. Monkey infants have sufficiently developed motor skills at birth that they can help themselves in the birth process (Trevathan 1987, 2015). Human babies have never been reported to use their hands or otherwise actively assist in their own delivery; this is not surprising given the poorly developed motor skills of our infants and the lack of a hairy substrate to cling to. Therefore, delivering a human infant is entirely up to the mother and her birth assistants.

Despite motor immaturity and neonatal brains that are small relative to adult brains, our infants have large brains and large bodies that pose challenges to the birth process. We have argued elsewhere that giving birth to large-bodied, large-brained infants and the way in which the infant emerges from the birth canal have placed a selective advantage for humans on seeking assistance during birth (Trevathan 1987; Rosenberg 1992; Rosenberg and Trevathan 1995, 2002). The costs of complicated childbirth are thus met by another form

of social cooperation: assistance during birth, or midwifery. Birth is a time in the human life cycle when the costs of reproduction are shared.

COSTS OF BREASTFEEDING

Like all mammals, humans lactate to nourish their infants, and they incur energetic costs through milk production. As noted above, one of the reasons that caloric intake is so important in the late stages of pregnancy is that it prepares the mother for lactation, which is even more expensive than the late stages of pregnancy (Quinn, chapter 5, this volume). The costs of lactation are balanced by the benefits gained from the provisioning of calories, protein, and immunological protection (Piperata 2009; Quinn, chapter 5, this volume). These costs are shared when other members of the group augment the mother's diet beyond what she can obtain for herself and help to reduce her caloric needs by taking on some of her workload and, in some cases, even serving as wet nurses.

COSTS OF CARE IN INFANCY AND CHILDHOOD

Caring for highly dependent babies during infancy involves more than breastfeeding. Unlike other primates, whose infants can cling to their mothers' fur using four limbs within days of birth, human infants, with only two clinging limbs and nearly hairless mothers, must be carried for at least the first year of life in the arms or in a carrying device like a sling. Even after humans begin walking, they cannot do so very efficiently and must be carried when their families cover long distances (Lee 1980). Carrying an infant in her arms is costly for the mother and has the potential to be even more energetically expensive than lactation (Wall-Scheffler et al. 2007). This is another point where cooperation may be important; there is value in having others (e.g., fathers, grandparents, older siblings) help carry the infant (Gettler, chapter 8, and Hrdy, chapter 9, both this volume).

This burden can also be eased by the use of a carrying device, such as a sling (Tanner and Zihlman 1976), which can reduce the energetic costs of carrying by as much as 16% (Wall-Scheffler 2012). Furthermore, traveling long distances while carrying infants has been proposed to increase the interbirth interval by diverting calories from reproduction (Lee 1980). Cooperative caretaking in conjunction with long-distance travel probably served to decrease the

interbirth interval. There is abundant cross-cultural evidence for family members, including older siblings, and other members of the social group sharing the job of carrying babies.

BUT THEY ARE CUTE

Certainly, cuteness is, to some extent, in the eyes of the beholder, but by all accounts human infants tend to be immensely appealing to those who matter—not just their mothers but often others as well (Hrdy 1999, 2009). A growing body of neurological, endocrinological, and observational evidence indicates that such caretakers have evolved to find looking at and even caring for infants rewarding and in some cases even socioendocrinologically transformative (Gettler, chapter 8, this volume; Hrdy 2009 and chapter 9, this volume). Returning the favor, human infants enter the world primed to interact with parents and alloparents alike. And why not? From birth, the human infant enters a social world that is not only critical to his survival, but that introduces likely contexts for his ensuing social life. Within months, Hrdy (2009, 2015) argues, human infants are far more capable than chimpanzees with regard to their cognitive and interactive potentials, particularly their interest in monitoring others, assessing their potential to help or hinder, and determining how best to appeal to them.

Human babies exhibit a mosaic of physical helplessness and sophisticated social, manipulative skills. As Turke puts it, human babies exhibit “the combination of physical altriciality and precociality in which children who cannot jump off the ground with both feet can control and manipulate every adult they come in contact with” (P. Turke, pers. comm., 2015). Or, as Trivers (1985:155) has put it, “An offspring cannot fling its mother to the ground and nurse at will. . . . [Rather] it should attempt to *induce* more investment than the parent is selected to give.” Human newborns’ motor helplessness is paired with socially and emotionally manipulative skills.

It has been argued that the human infant is more helpless at birth than most monkeys and apes, but in the first few hours after birth, the infant has unusual behavioral and physical characteristics that enhance his attractiveness to his mother and others who are present. These behaviors include “primary walking,” the Moro reflex, crawling movements, and even smiling. The infant state referred to as the “quiet-alert state” is typically short and fleeting in the first weeks after birth, but it is prolonged in the first hour after birth

(Desmond et al. 1963; Widström et al. 2011). This is the state when the infant is wide awake, can follow voices and faces, and can focus on objects and people, and it is the state in which most learning takes place. It is also a time when the mother is alert and when the baby is highly attractive to her and others. It is an optimal time for social bonds to form. Right after birth, when oxytocin and other socioendocrinological transformations are enhancing the mother's affiliative responses (Carter 2014), is also an opportune time for her infant to engage in ways that "prove" that he is worth the prolonged investment that human young require (Hrdy 1999). In addition to fueling a rapidly developing brain, Hrdy proposes, fetally induced fat accumulation just prior to the infant passing through a tightly constrained birth canal may secondarily serve the neonate as a signal of robustness, effectively saying, "Mom, go ahead and bond. I am a good bet for surviving." Thus, even in his first hour of life, the human infant, seemingly helpless in so many ways, has an array of emotionally and socially manipulative behaviors and characteristics that lead others to invest heavily in him for decades.

Of course, being born early cannot be only costly (and risky), or it would have been selected against. Human babies must gain some advantages to being born when the brain is still undergoing rapid growth, most notably the advantage of being exposed to external stimuli in the environment, which they soak up at a remarkable rate and use to manipulate the world. For example, at a very early stage of life, human babies interact socially and emotionally with those around them. Decades ago, Meltzoff and Moore (1977) showed that newborn babies between 12 and 21 days old imitate a number of different facial and hand gestures that they see in adults. Mandel and colleagues (1995) showed that long before they are able to produce language, 4.5-month-old human infants are able to recognize sound patterns (such as their own names) that have "special personal significance for them." Ferry and colleagues (2013) showed that human infants quickly tune in to the patterns of human language. They are born preferring to listen to primate vocalizations (either human or nonhuman) over artificial sounds, but within months they come to prefer human speech and finally the language most commonly spoken around them. Trevarthen and Aitken (2001:4) claimed that the "existence of specialized innate 'human-environment-expectant' social regulatory and intersubjective functions in the infant mind has been firmly established." Trevathan (1987:149) argued that the advantages that come from being born before much brain growth has occurred include the fact that the infant is exposed to a rich set of sensory stimuli in the

environment at an earlier stage in development, encouraging greater plasticity and flexibility, which are important components in learning. Hrdy (2009), Konner (2011), and Martin (2013) all have reviewed literature emphasizing the point that in addition to the adaptive benefits of lengthening (i.e., prolonging) childhood, there are advantages to exposing the human infant to his social, emotional, and physical environments at an earlier stage in brain growth and development and hence at a more helpless and also malleable developmental stage (Semendeferi and Hanson, chapter 7, this volume).

Organization of This Volume

~~The contributors to the SAP advanced seminar and this book represent~~