Puberty and Adolescence: An Evolutionary Perspective

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Glossary

Adolescence: A stage in human life cycle covering the years after the onset of puberty until the onset of adulthood (approximately ages 9–19 years). The adolescent phase is characterized by a growth spurt in height and weight, the development of secondary sexual characteristics, sociosexual maturation, and intensification of interest and practice in adult social, economic, and sexual activities.

Biocultural reproduction: The human type of cooperative breeding, which is the pooling of resources such as food and shelter which increase the reproductive success of adults in the social group.

Childhood: A stage in the human life cycle that occurs between the end of infancy and the start of the juvenile growth period (about the ages 3.0–6.9 years). Children are weaned from all breast-feeding (or bottle feeding) but must be provided specially prepared foods due to immaturity of their dentition and digestive systems. Children require intensive care by older individuals due to the child's motor, neurological, and cognitive immaturity.

Juvenile: A stage of growth and development of some mammals that occurs between the end of infancy (cessation of feeding by lactation) and the onset of adulthood (reproductive maturity). The human juvenile stage is an exception, in that it begins at approximately ages 7.0, after the human childhood stage, and ends at about age 10 years in girls and 12 years in boys, when human adolescence begins.

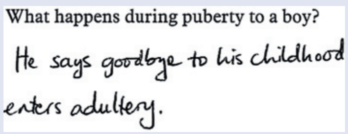
Natural selection: Defined by Darwin (1859) as the differences in fertility (production of offspring) and mortality (deaths of offspring) between individuals of a population. Physical or behavioral traits that increase fertility and/or decrease mortality will become more frequent in the population over time. Traits that reduce fertility and/or increase mortality will decline in frequency from generation to generation.

Puberty: In biology, a short-term physiological event, taking place over a few weeks, of the central nervous system, which reinitiates positive feedback within the hypothalamic–pituitary–gonadal axis and promotes sexual maturation. In people, puberty occurs at the end of the juvenile stage and the beginning of the adolescent stage of the life cycle (approximately age 9–10 years).

Rites of passage: Culturally patterned ritual or ceremonial activities to mark such events as birth, puberty, adulthood, courtship, marriage, death, accession to office, admission to membership, and expulsion. In various forms, rites of passage are found in all human societies, although particular individuals may or may not participate in them. Rites of passage seem to be unique to the human species.

Sexual selection: Defined by Charles Darwin (1871) as, "... the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." The 'advantage' may take the form of a physical trait, such as bright plumage in birds or horns/antlers in some mammals, or may take the form of a behavioral trait such as singing or dancing, as found in many animals including the human species.

Introduction



An incorrect answer to an examination question.

In this article, we discuss puberty and adolescence from a biological and anthropological perspective. This perspective differs from that taken by many social and psychological treatments. Each view of puberty and adolescence has merits. The emphasis here is on those aspects of puberty and adolescence which are best explained in terms of human evolution and the patterns of culture found in human societies throughout time and around the world.

The nature of human puberty and adolescence are best understood as part of the entire pattern of human biological growth. Table 1 lists the stages of human development from conception to death, their approximate ages, and several defining features of each stage. Human development before birth follows many of the patterns seen in other animal species, but after birth there are some special features. Humans share with other social mammals, such as most monkeys and apes, three postnatal life stages: infancy, juvenile, and adult. Human life history is unusual due to the addition of childhood, adolescence, and grandmotherhood (postmenopausal stage) as biologically and behaviorally definable stages of the life cycle. The pattern of human growth in height from birth to adulthood is shown in Figure 1 (body weight follows very similar curves). The distance curve (part a) indicates the amount of height achieved at a given age. The velocity curve (part b) indicates the rate of growth at a given age. The velocity curve best illustrates the human postnatal growth stages of infancy (I), childhood (C), juvenile (J), and adolescence (A).

Definitions of these life stages may be given in terms of how people of different ages are fed, especially in the traditional human societies of hunter-gatherers, horticulturalists, and

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Table 1 Stages in the human life cycle (modified From Bogin B, *Patterns of Human Growth*, 2nd edn. Cambridge University Press, 1999)

Stage	*Duration*	*Events*
First trimester of pregnancy	Fertilization to week 12	Embryogenesis
Second trimester of pregnancy	Months 4 to 6	Rapid growth in length
Third trimester of pregnancy	Month 7 to birth	Rapid growth in weight and organ maturation
Neonatal period	Birth to 28 days	Extrauterine adaptation, most rapid rate of postnatal growth and maturation
Infancy	Month 2 to end of lactation (usually by 36 months)	Rapid growth velocity with steep deceleration in velocity with time, feeding by lactation, deciduous tooth eruption, many developmental milestones in physiology, behavior, and cognition
Childhood	3–6.9 years	Moderate growth rate, dependency for feeding, mid-growth spurt, eruption of first permanent molar and incisor, cessation of brain growth by end of stage
Juvenile	7–10 (girls) or 12 (boys) years	Slower growth rate, capable of self-feeding, cognitive transition leading to learning of economic and social skills
Puberty	Brain: 9–10 years Body: girls, 10 years; boys, 12 years	In the brain, puberty is an event of short duration (days or a few weeks) that reactivates the hypothalamic GnRH pulse generator leading to a massive increase in sex hormone secretion; on the body, puberty is noted by a darkening and increased density pubic hair
Adolescence	The 5–8 years following onset of puberty	Adolescent growth spurt in height and weight, permanent tooth eruption virtually complete, development of secondary sexual characteristics; sociosexual maturation, intensification of interest and practice in adult social, economic, and sexual activities
Adulthood		
Prime and transition	18–20 years for women to 45 years (end of child-bearing) and from age 21–25 years for men to about age 50 years	Commences with completion of skeletal growth; homeostasis in physiology, behavior, and cognition; menopause for women by age 50
'Grandmotherhood'	10–20 years following menopause	Culturally defined stage of women's life often characterized by investments of time and energy in the caring for grandchildren
Old age and senescence	From end of child-bearing years to death	Decline in the function and repair ability of many body tissues or systems
Death		

pastoralists. Human biology and behavior evolved in these types of societies, which represent 99% of human history. Even though large-scale agricultural and industrial societies dominate today, these ways of life appeared only in the past few thousand or few hundred years. Typical social behaviors in much of the industrialized world of today such as bottle-feeding infants and separate infant–mother sleeping arrangements did not exist during the evolutionary development of our species.

Human growth and development between birth and adulthood may be divided into four stages: (1) infancy, (2) childhood, (3) juvenile, and (4) adolescent. Infancy lasts from birth to age 30–36 months and is characterized by breast-feeding, with complementary foods added by age 6–9 months. The transition to childhood by about age 3 years is characterized by the termination of maternal lactation and the completion of deciduous tooth eruption. The limitations of a deciduous dentition and small digestive system require that children eat easy to chew and nutrient dense foods. Older members of the social group acquire, prepare, and provision these foods to children. This style of cooperative care frees the child's mother from lactation and much care and feeding of the child. The mother may then accumulate new reserve capacity, such as fat stores and bone mass lost during pregnancy and lactation, and in time, devote her reserves to a new pregnancy and lactation of a new infant. The childhood stage ends at about age 6.9 years.

The juvenile stage spans age 7 years to onset of the adolescent growth spurt (approximately age 10 for girls and age 12 for boys in healthy, well-nourished populations). Juvenile mammals are sexually immature, but physically and mentally capable of providing for much of their own care. Human juveniles have the physical capabilities to eat the adult-type diet, as the first permanent molars and the central incisors have erupted by age 7 years. In many human societies, juveniles perform important work including food production and the care of children, but still require food provisioning by older people to achieve energy balance. Puberty takes place near the end of the juvenile stage and we have more to say about this event below.

Adolescence includes the years of postpubertal growth (approximately ages 10–18 years for girls and ages 12–21 years for boys, including the adolescent growth spurt). Adolescence ends with the eruption of the third molar (if present) and/or the termination of growth of the skeleton. Adulthood and reproductive maturity follow.

Human growth velocity in body length stands in contrast to all other mammals, even our closest genetic cousins the African apes. The childhood stage of relatively moderate and stable

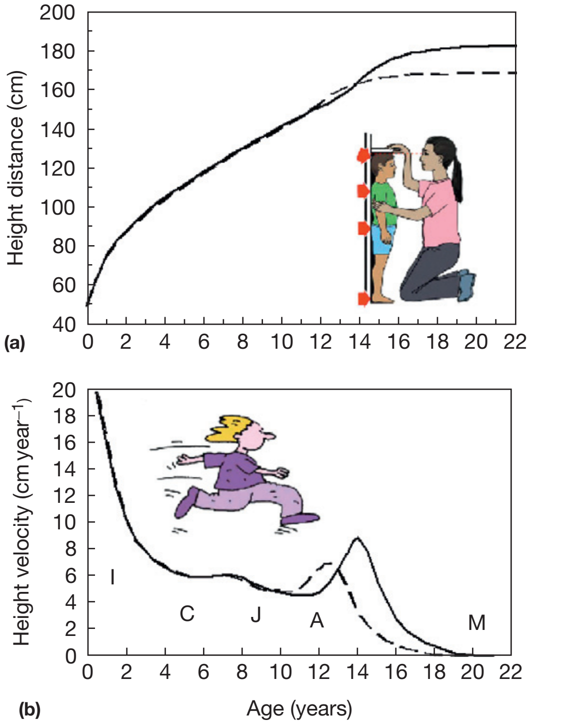

Figure 1 Average distance (a) and velocity (b) curves of growth in height for healthy girls (dashed lines) and boys (solid lines). Distance is the amount of height achieved at a given age. In part (a), the image shows a child's height being measured. Velocity is the rate of growth at a given time, in this case shown as centimeters per year. In part (b), the running figure represents 'velocity.' The velocity curves show the postnatal stages of the pattern of human growth. Note the spurts in growth rate at mid-childhood and adolescence for both girls and boys. The postnatal stages: I, infancy; C, childhood; J, juvenile; A, adolescence; M, mature adult (original figure of the author).

growth velocity and the adolescent growth spurt in virtually all skeletal dimensions are not found in other mammals. The termination of breast-feeding takes place earlier in humans than in the chimpanzee, bonobo, or orangutan. Human female reproductive maturity takes place during the later part of the adolescent stage, and this differs from the apes as well. Healthy, well-nourished girls achieve physiologically defined fecundity (i.e., 80% of menstrual cycles release an ova) at a median age of 18 years. The worldwide median age of human first birth is 19 years. This is up to 6 years later than in the other apes. Human boys may produce fertile spermatozoa by 13.5 years, but are not likely to become fathers until after age 20 years. Even though sexually mature and capable of producing sufficient quantities of food to exceed their own energy requirements, teenage boys and girls remain immature in terms of sociocultural knowledge and experience. To gain sufficient experience for successful adulthood, adolescent boys and girls in all societies engage in many types of economic, social, sexual, and ideological apprenticeships, or rites of passage as they are called by anthropologists. These informal and formal settings for learning lead to greater adult reproductive and sociocultural success. We discuss these apprenticeships/rites of passage in more detail below.

It is hypothesized that the childhood and adolescence stages of human life history evolved due to the selective advantages for increased reproductive fitness. In essence, this reproductive fitness hypothesis predicts that childhood and adolescence: (1) enhance the fertility of mothers, (2) improve the survival of mothers, and (3) lower the mortality of offspring prior to adulthood. This hypothesis emphasizes that early weaning and the transfer of responsibility to other social group members for the feeding and care of children frees the mother to reproduce more quickly than any ape, without increasing the risks for morbidity and mortality of the children. There are also benefits for increased brain growth and learning, but these are secondary outcomes of the selection for increased fertility of the mothers.

Puberty Defined

Physiologically, puberty is a short-term event (taking place over a few weeks) of the central nervous system, which reinitiates positive feedback within the hypothalamic–pituitary–gonadal (HPG) axis and promotes sexual maturation. Puberty is also defined socially, to mean the period of time when sexual development and its related behaviors and emotions are taking place. In this article, we use the physiological definition for puberty and use the term 'adolescence' to refer to the period of time for sociosexual maturation between puberty and adulthood.

Biology of Puberty

Much of human biology is associated with our brain. Adult humans have brains which are 3–4 times larger than the brains of adult chimpanzees. The human advantage is evident at birth and differences increases over time as human brain grows rapidly during infancy and childhood, but chimpanzee brains grow much less after birth. The large and fast growing human brain requires a relatively large amount of metabolic input, for example, energy and oxygen. The human newborn uses 87% of its resting metabolic rate (RMR) for brain growth and function. By the age of 5 years, the percent RMR usage is still high at 44%, whereas in the adult human, the figure is between 20 and 25% of RMR. At comparable stages of development, the RMR values for the chimpanzee are about 45, 20, and 9%, respectively. A trade-off seems to take place between the supply of energy required to support the growth of human brain versus energy to support the growth of rest of the body. The trade-off is seen in Figure 1b as the rapid deceleration of growth velocity during infancy. Relatively slow growth continues through childhood and juvenile stages. Rapid growth returns following puberty, after the brain has almost completed its own growth in size.

The hypothalamus is a brain center of neurological and endocrine control (Figure 2). During fetal life and early infancy, the hypothalamus produces relatively high levels of gonadotrophin-releasing hormone (GnRH). This hormone causes the release of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the pituitary gland, and these hormones stimulate the ovaries or testes to secrete their estrogen or androgen hormones. The latter promote body growth.

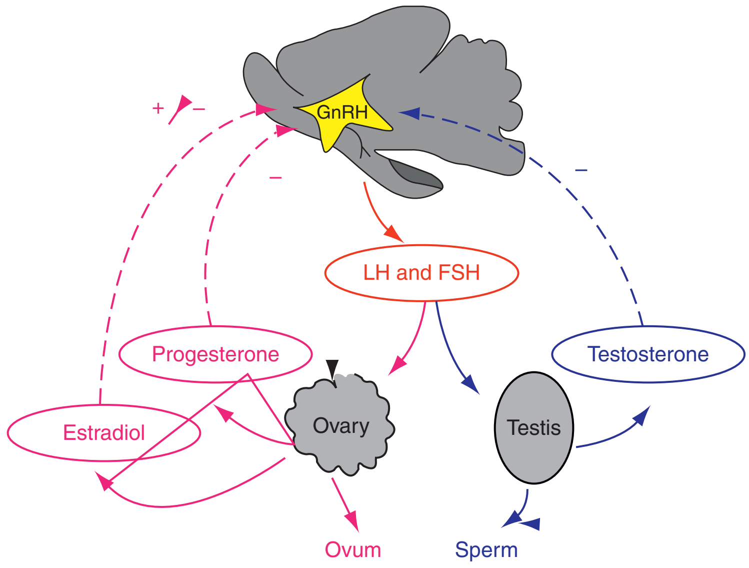

Figure 2 The hypothalmic–pituitary–gonadal (HPG) axis. This simplified cartoon indicates the principle tissues and their connections. The HPG axis is composed of the hypothalamus and its neural connections with the rest of the brain, the pituitary, and the testis (male) or ovary (female). The anterior hypothalamus is responsible for the synthesis of gonadotropin-releasing hormone (GnRH). GnRH reaches the anterior pituitary via neurons and portal veins and stimulates the release of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) into the general circulation. LH and FSH bind to receptors in the ovary and testis and regulate gonadal function by stimulating sex steroid production and gametogenesis (production of ova and sperm). In the male, LH causes testosterone to be produced from the Leydig cells of the testes. LH in combination with FSH is required for maturation of spermatozoa. FSH stimulates testicular growth and increases production of androgen-binding protein by Sertoli cells. Androgen-binding protein concentrates testosterone near the sperm, enabling normal spermatogenesis. In the female, LH stimulates ovarian production of estrogen and progesterone. An LH surge midway in the cycle causes ovulation, and sustained LH secretion stimulates the corpus luteum to produce progesterone. FSH exerts primary control over development of the ovarian follicle, and FSH and LH are responsible for follicular secretion of estrogen. The solid lines indicate the stimulatory cascade from hypothalamus, to pituitary, to gonads. The broken lines and '–' symbols indicate the inhibitory feedback loops. The '+/–' symbols of the estradiol feedback loop indicate the variation of inhibitory/stimulatory feedback during the menstrual cycle (with permission of Prof. C. Rivier, unpublished).

The effect that GnRH production has on the pituitary is associated with the frequency, or 'pulse,' of its release from cells in the hypothalamus. In 1975, Melvin Grumbach and colleagues reported that the gonadotrophin-releasing hormone pulse generator has an on–off–on pattern of activity during postnatal development in humans. Rodents do not show this pattern, instead having a progressive and uninterrupted increase in GnRH production from birth to sexual maturation. Since 1975, much research has been focused on the mechanisms that control this on–off–on pattern (Figure 3). The current understanding of the control of puberty (also called 'gonadarche' in the literature) is that one or perhaps a few centers of the brain change their pattern of neurological and endocrinological activity, and their influence on the hypothalamus. The human hypothalamus becomes, basically, inactive in terms of sexual development by about age 2–3 years. The 'inhibitor' has not been identified but likely is located in the brain and certainly not in the gonads. Human children born without gonads, as well as rhesus monkeys and other primates whose gonads have been surgically removed at birth, still undergo both GnRH inhibition in infancy and hypothalamus reactivation at puberty.

In most species of primates, puberty is followed within a few months or a year by reproduction. In humans, there is a greater delay between puberty and first reproduction, usually on the order of 5–10 years. This interval is the human adolescent growth stage. In humans, the hormones responsible for sexual maturation also cause the adolescent growth spurt in stature and other skeletal dimensions. The ubiquitous nature of the adolescent growth spurt is unique to the human species. Not even our closest genetic relative, the chimpanzee, has anything like it.

Another neuroendocrine event precedes puberty. This event is called adrenarche and is the postnatal onset of secretion of the androgen hormones dehydroepiandrosterone (DHEA) and DHEA-sulfate (DHEA-S) from the adrenal gland. The mechanism controlling adrenarche is not understood because no known hormone appears to cause it. In humans and chimpanzees, adrenarche occurs between the ages of 6–10 years (median age is 7 years). In some other primates, such as the rhesus monkey, the upregulation of DHEA and DHEA-S begins just before or after birth. DHEA acts as an antiglucocorticoid with a wide variety of effects, including promoting immune function, altering glucose metabolism, and being neuroprotective, all suggesting a selective benefit, but the evolutionary origins of adrenarche are not known. It is suggested that adrenarche and DHEA-S may play a role in ape and human evolution in terms of extended brain development and prolonged life span compared with other primates. In humans, adrenarche has been related to the adiposity rebound (regaining of body fat) at the transition between the childhood and juvenile stages of the life cycle.

Current evidence indicates that there is no connection between the occurrence or timing of adrenarche and puberty. Perhaps the evolution of adrenarche may be explained as a mechanism for mental maturation. By this we mean that the physical changes induced by adrenarche are accompanied by a change in cognitive function, called the '5- to 7-year-old shift' by some psychologists, or the shift from the preoperational to concrete operational stage, using the terminology of Piaget. This shift leads to new learning and work capabilities in the juvenile. Adrenarche may function to mark the transition from the childhood to the juvenile growth stage.

Human Adolescence

Biological adolescence begins with puberty and lasts for 5–10 years. The physiological transition in the brain and hormonal system from juvenile to adolescent stages cannot be seen without sophisticated technology. The effects of puberty, however, can be noted easily as visible and audible signs of sexual maturation. In both sexes, there is a sudden increase in the density of pubic hair and often other body hair. In boys, there may be an increased density and darkening of facial hair. The deepening of the voice (voice 'cracking') is another sign of male puberty. In girls, a visible sign is the development of the breast bud, the first stage of breast development, which often precedes the appearance of dense pubic hair. The pubescent boy or girl, his or her parents, and relatives, friends, and sometimes everyone else in the social group can observe one or more of these signs of early adolescence.

Other notable features of adolescence include a growth spurt in height and weight, the completion of permanent tooth eruption, development of secondary sexual characteristics (fat and muscle typical of each sex, Figure 4), and the intensification of interest in and practice of adult social, economic, and sexual activities leading to sociosexual maturation.

Adolescence ends with (1) the cessation of skeletal growth in length, usually due to the closing of the epiphyses of the long bones; (2) the completion of dental development (eruption of the third molar, if it is present, which takes place between 18–21 years of age); and (3) sociosexual maturation, meaning both the biological and social ability for successful parenthood. On a worldwide basis, including living and historical societies, the age of onset of adulthood averages 19 years for women, which is best measured as the median age at first

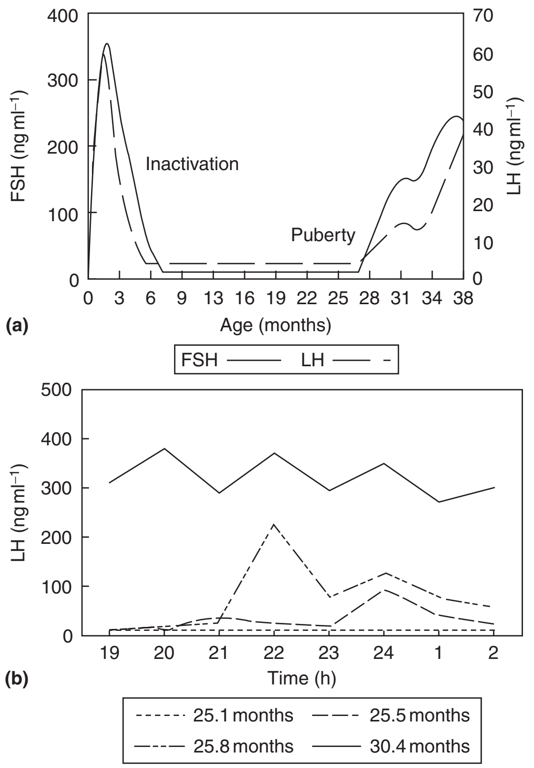

Figure 3 (a) Pattern of secretion of FSH and LH in a male rhesus monkey (genus *Macaca*). The testes of the monkey were removed surgically at birth. The curves for FSH and LH indicate the production and release of GnRH from the hypothalamus. After age 3 months (i.e., during infancy), the hypothalamus is inactivated. Puberty takes place at ~27 months, and the hypothalamus is reactivated.
(b) Development of hypothalamic release of GnRH during puberty in a male rhesus monkey with testes surgically removed. At 25.1 months of age, the hypothalamus remains inactivated. At 25.5 and 25.8 months, modest hypothalamic activity is observed, indicating the onset of puberty. By 30.4 months, the adult pattern of LH release is nearly achieved. This pattern shows increases in both the number of pulses of release and the amplitude of release. In human beings, a very similar pattern of infant inactivation and late juvenile reactivation of the hypothalamus takes place. Adapted, with some simplification, from Plant TM (1994) Puberty in primates. In: Knobil E and Neill JD (eds.) *The Physiology of Reproduction*, 2nd edn., pp. 453–485. New York: Raven.

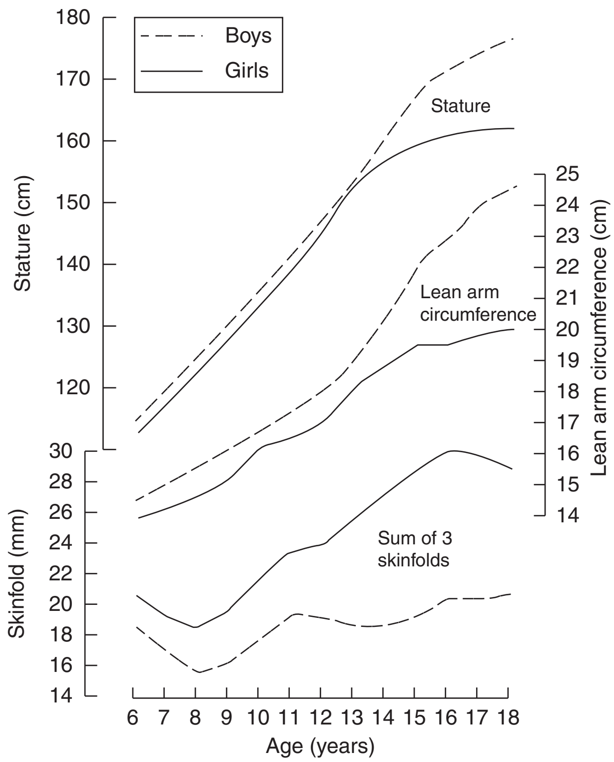

Figure 4 Mean stature, mean lean arm circumference, and median of the sum of three skinfolds for Montreal boys and girls. Notice that sexual dimorphism increases markedly after puberty, from 12–13 years onward. Reproduced from Baughn B, Brault-Dubuc M, Demirjian A, and Gagnon G (1980) Sexual dimorphism in body composition changes during the pubertal period: As shown by French-Canadian children. *American Journal of Physical Anthropology* 52: 85–94.

successful reproduction. The age at adulthood for men is more difficult to measure. Skeletal growth completion for men occurs between 21 and 25 years of age. Adolescent boys can father offspring, and as young as age 13 years in some notorious cases. But, few men become fathers before age 20–25, and many wait longer. We discuss the factors influencing age at fatherhood below.

Biocultural Perspective on Human Adolescence

Clearly, the human pattern of growth and maturation following puberty is quantitatively different in terms of amount, rate, and duration from the pattern for other mammals. Human adolescence, however, is more than skeletal growth and reproductive system maturation. It is also a stage of the life cycle defined by several changes in behavior and cognition that are found only in our species.

Evolution of Human Adolescence

Some theorists hypothesize that the adolescent stage of human growth evolved to provide the time to learn and practice complex economic, social, and sexual skills required for effective food production, reproduction, and parenting. In this perspective, adolescence is a time for an apprenticeship, working and learning alongside older and more experienced members of the social group. The benefits of the skills acquired during adolescence are lower mortality of both first-time mothers and their offspring. This places the 'apprenticeship hypothesis' for the learning and practice value of adolescence firmly within Darwinian natural selection theory. There is much human ethnographic and demographic evidence to support the apprenticeship hypothesis and it is likely that the learning and practice of adult skills play an important role in human growth, development, and maturation.

However, apprenticeship cannot be the primary cause for the evolution of adolescence. Learning for childcare is an example. In most species of social mammals, the juveniles are often segregated from adults and infants. The ethnographic literature, however, documents that in human societies juvenile girls often are expected to provide significant amounts of childcare for their younger siblings. Human girls enter adolescence with considerable knowledge of the needs of young children. Learning about childcare, then, is not the reason why human girls experience adolescence.

Human childhood evolved as a benefit for the mother and not the child, that is, so that the mother could resume reproduction more quickly by weaning early. Similarly, adolescence is likely to have evolved as a reproductive adaptation for adults, and not directly for the adolescent. The reason for this is that natural selection works on differential fertility and differential mortality between individuals. An additional 5–10 years of infertility, or reduced fertility, associated with adolescence could not evolve for all humans, since those individuals who 'cheated' by terminating growth at an earlier age would begin reproducing sooner and would be at a reproductive advantage. All other primates do, in fact, begin reproducing at earlier ages than humans, and none of the nonhuman primates has a human-like adolescent growth spurt, nor many of the other biological and behavioral features of human adolescence. Clearly, a juvenile primate does not need to pass through a lengthy period of adolescence, with apprenticeship type learning, just to be reproductively successful. What factors, then, could give rise to adolescence and further delays in reproduction?

The answer may lie in a type of multilevel model of selection for mating and parenting. Multilevel models in evolutionary biology include selection at the level of the individual and at the level of the social group. Such models allow for time lags between the stage of life when selection takes place and the accrual of reproductive benefits later in life. The complex pattern of human individual growth and development, combined with equally complex human social and cultural behavior, seems to be better explained by multilevel evolutionary models rather than simpler models, for example, those focusing only on fertility or mortality of the adolescent.

Human mating and parenting are of course related, but they are not identical. Charles Darwin identified two types of biological selection, natural selection, and sexual selection, and both are likely to be involved in the evolution of human adolescence. Sexual selection is all about opportunities for mating, while natural selection is, in part, about parenting. Darwin, in 1871, defined sexual selection as "... the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." Today we would replace the word reproduction with mating, as not all mating opportunities result in fertilization and offspring. Darwin also wrote of the many structures and instincts developed through sexual selection, including, "... weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals – their courage and pugnacity – their ornaments of many kinds – their organs for producing vocal or instrumental music – and their glands for emitting odors; most of these latter structures serving only to allure or excite the female." It is known today that sexual selection also works for females, meaning that female-specific physical and behavioral traits may evolve via competition between the females for mating opportunities with males. Some human examples are the waist-to-hip ratio and childlike voice pitch of women that may be alluring to men.

Adolescent Contributions to the Reproductive Success of Adults

Earlier we described the cooperative care of human children by older group members. In biology, such care of offspring by nonparents is called cooperative breeding. It is found in some species of birds and mammals (e.g., wolves and hyenas) and it works to increase net reproductive output. In those species the cooperative breeders are close genetic relatives of the mother. A genetic connection may exist in human cooperative breeding, but often it does not as people have social and cultural rules about marriage and kinship, and these, rather than genes, define the rights and obligations that people have to each other. Due to these social rules, it may be better to call the human type of cooperative breeding biocultural reproduction, because it enhances the social, economic, political, religious, and ideological 'fitness' of the group as much or more than it contributes to genetic fitness.

Human juveniles may hunt, gather, or produce some of their own food intake, but overall they require provisioning to achieve energy balance. In contrast, human adolescents are capable of producing sufficient quantities of food to exceed their own energy requirements. Some of the food that adolescents produce may be used to fuel their own growth and development, creating larger, stronger, and healthier bodies. The surplus production is shared with other members of the social group, including younger siblings, parents, and other immediate family members (defining families in the broad anthropological sense). Adolescent contributions enhance the fertility of adults and the survival of infants, children, and juveniles. The biological trade-off is the delay of years between puberty and first birth for the adolescents. For their valuable services in food production, the adolescents receive care and protection to safeguard their health and survival. This is important because adolescents are immature in terms of sociocultural knowledge and experience.

Girls and Boys: Separate Paths Through Adolescence

The multilevel nature of the evolution of human adolescence may be seen by considering the trade-offs related to biocultural reproduction and the different sequence of biological and behavioral events experienced by adolescent girls and boys. The differences allow each sex to improve opportunities for mating and parenting. Mating will eventually lead to the birth of offspring, but producing offspring is only a small part of reproductive fitness. Rearing the young to their own reproductive maturity is a surer indicator of success. The developmental paths of girls and boys during adolescence may be key in helping each sex to both produce and rear its own young successfully.

The order in which several pubertal events occur in girls and boys is illustrated in Figure 5 in terms of time before and after peak height velocity (PHV) of the adolescent growth spurt. In this figure we use the Tanner Maturation Staging System for the development of secondary sexual characteristics. This system is based on five stages. Prepubertal maturation is denoted as Stage 1, for example, B1 – the absence of breast development in girls, or G1 – the absence of testes or penis enlargement in boys. The adult appearance is stage 5.

In both girls and boys, puberty begins with changes in the activity of the hypothalamus and other parts of the central nervous system (the HPG axis). These changes are labeled as 'CNS puberty' in the figure. Note that the CNS events begin at the same relative age in both girls and boys, that is, 3 years

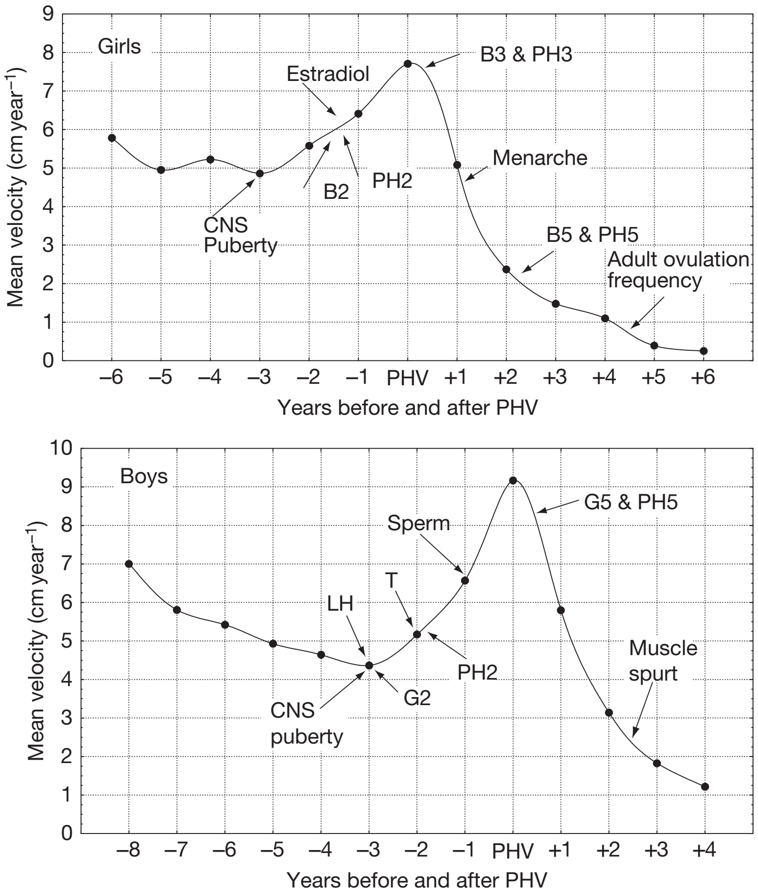

Figure 5 The ordering of several sexual maturation events for girls (top panel) and boys (bottom panel) during the adolescent growth spurt. The velocity curves are calculated using data derived from a sample of healthy, well-nourished girls and boys living in Guatemala. Girls achieve adult levels of fertility near the end of the adolescent growth spurt. Boys are fertile early-on during the growth spurt. See text for an explanation of each labeled event (original figure by the author).

before PHV. This is also the time when growth rates change from decelerating to accelerating. In girls, the first outward sign of puberty is the development of the breast bud (B2) and wisps of pubic hair (PH2). This is followed, in order, by

1. a rise in serum levels of estradiol which leads to the laying down of fat on the hips, buttocks, and thighs;
2. increased velocity of the adolescent growth spurt;
3. further growth of the breast and body hair (B3 and PH3);
4. menarche (first menstruation);
5. completion of breast and body hair development (B5 and PH5); and
6. attainment of adult levels of ovulation frequency.

The path of pubertal development in boys starts with a rise in serum levels of luteinizing hormone (LH) and the enlargement of the testes and then penis (G2). This genital maturation begins, on average, only a few months after that of girls. However, the timing and order of other secondary sexual characteristics is unlike that of girls. About a year after CNS puberty, there is

1. a rise in serum testosterone levels (T) which is followed by the appearance of pubic hair (PH2);
2. about a year later motile spermatozoa may be detected in urine;
3. PHV follows after about another year, along with deepening of the voice, and continued growth of facial and body hair;
4. the adult stages of genital and pubic hair development follow the growth spurt (G5 and PH5); and
5. near the end of adolescence boys undergo a spurt in muscular development.

The sex-specific order of pubertal events tends not to vary between early and late maturers, between well-nourished girls and boys and those who suffered from severe malnutrition in early life, between rural and urban dwellers, or between European and African ethnic groups. In addition to these biological events there are behavioral and social events that also follow a predictable course during adolescence. Indeed, the biological and cultural events are usually tightly correlated. A comparison of the biocultural timing of adolescent events in samples of British (London) and Kikuyu (rural Kenya) girls and boys provides a case study. The London sample represents adolescents who are relatively well nourished and healthy. The Kikuyu are a Bantu-speaking, agricultural society of the central highlands of Kenya. Kikuyu adolescents may suffer from periodic food shortages and a higher incidence of infectious and parasitic diseases.

For both London and Kikuyu girls, the first biocultural event is breast development (B2), and the second event is pubic hair development (PH2). The third event is a rise in serum estradiol concentration, which leads to biological and behavioral changes that are easily detectable, for instance, in the form of fat deposits on hips, thighs, and buttocks and new levels of cognition (Piaget's formal operations stage). The fourth event is peak height velocity. For the Kikuyu girls, PHV occurs about 2 years later than for the London girls. Indeed Kikuyu girls achieve each adolescent event later than English girls, varying from a few months delay in the case of reaching the B2 stage to a 2.6-year delay in menarche (13.2 years for London and 16.8 years for Kikuyu).

For many Kikuyu girls, the fifth biocultural event is clitoridectomy, which removes the tip of the clitoris. About 40% of girls underwent this operation, at the time that Carol Worthman undertook this research in 1979 and 1980. Clitoridectomy takes place just after PHV, at about breast stage 3, and just before menarche. The operation is a rite of passage. In various forms, adolescent rites of passage are found in all societies, although particular individuals may or may not participate in them. Rites of passage are symbolic activities, generally understood to have social functions, but which also have biological sequelae. Kikuyu clitoridectomy is timed so that it precedes the onset of sexual activity and marriage which follow menarche. London girls may experience some adolescent rites of passage after PHV, such as Anglican Confirmation, the school prom, a first job, and other events that may be less well defined and less traumatic than clitoridectomy.

The sixth event is menarche, which is taken as a sign of impending sexual maturation in all cultures. In many cultures, menarche often precipitates intensified instruction about sexual behaviors and the practice of these behaviors.

For both London and Kikuyu boys, the first two biocultural events are enlargement of the testes (G2), and a rise in serum concentration of luteinizing hormone. The third event is a rise in the serum concentration of testosterone, which precipitates a cascade of physical and behavioral changes. The fourth event is pubic hair development (PH2). As was the case for the girls, English boys experience each of these events, on average, at an earlier age than Kikuyu boys. The overall delay for all adolescent events for Kikuyu boys tends to be about 1 year.

For the Kikuyu, the fifth biocultural event is separation, a rite of passage requiring the adolescent boys to leave their nuclear family household and begin living in an age-graded adolescent male household. The separation to the 'boys' house' is closely correlated with age at first nocturnal emission or ejaculation. Separation takes place at about the same age that girls undergo clitoridectomy. The sixth event is peak height velocity. At PHV boys achieve about 92% of total adult height, which is taken in many human cultures as an indicator of entry into early adulthood. The spurt in muscle mass (PMV) of boys follows PHV by about 2 years (Figure 5). This means that between PHV and PMV boys are not capable of performing physical tasks of adult men. In most cultures, boys at this stage of development are often considered to be biologically and socially immature, and still in need of much training and education.

The seventh biocultural event for Kikuyu adolescents is circumcision, which is done to all young men and marks their entry into final training for adulthood. Circumcision is timed to occur along with the spurt in muscle mass. London boys do not undergo a circumcision rite of passage, but within that same year they usually graduate from secondary school. That event, which London girls also experience, is a rite of passage in most industrialized societies and often marks entry into the social and economic world of adults.

From these examples we may see that the adolescence, as defined as the time span of the adolescent growth spurt, is a biologically and socially significant event for both sexes. The order of adolescent events, however, is different for each sex. The reasons for the variation between boys and girls seem to be related with the way each sex prepares for mating (sexual selection) and parenting (natural selection).

Why Do Girls Have Adolescence?

In human societies, adolescent girls gain knowledge of sexuality and reproduction because they look mature sexually, and are treated as such, several years before they actually become fertile. The adolescent growth spurt serves as a signal of maturation. Early in the spurt girls develop pubic hair and fat deposits on breasts, buttocks, and thighs. They appear to be maturing sexually. About a year after peak height velocity, girls experience menarche, an unambiguous external signal of internal reproductive system development. However, most girls experience 1–3 years of anovulatory menstrual cycles after menarche. Nevertheless, the dramatic changes of adolescence stimulate both the girls and the adults around them to participate in adult social, sexual, and economic behavior. For the postmenarchial adolescent girl, this participation may be 'low risk' in terms of pregnancy.

Some girls, of course, may become pregnant and there are other social and psychological risks of adolescent sexual behavior. Teenage mothers and their infants are at risk because of the reproductive and emotional immaturity of the mother. This often leads to a low-birth-weight infant, premature birth, and high blood pressure in the mother. The likelihood of these risks declines and the chance of successful pregnancy and birth increases markedly after age 15 years and reaches its nadir after age 18 years. Due to these biological and social risks, most human societies carefully regulate, according to age and sex, the onset and type of sexual behavior that is permitted by adolescents.

Another evolutionary reason for the delay between menarche and adulthood in girls is that human female fertility tracks the growth of the pelvis. Marquisa LaVelle Moerman reported in 1982 that the crucial variable for successful first birth is size of the pelvic inlet, the bony opening of the birth canal. Moerman measured pelvic X-rays from a sample of healthy, well-nourished American girls who achieved menarche between 12 and 13 years. These girls did not attain adult pelvic inlet size until 17–18 years of age. Quite unexpectedly, the adolescent growth spurt, which occurs before menarche, does not influence the size of the pelvis in the same way as the rest of the skeleton. Rather, the female pelvis has its own slow pattern of growth, which continues for several years after adult stature is achieved.

Why the pelvis follows this unusual pattern of growth is not clearly understood. Perhaps another human attribute, bipedal walking, is a factor. The evolution of bipedalism is known to have changed the shape of the human pelvis from the basic ape-like shape. Apes have a cylindrical-shaped pelvis, but humans have a bowl-shaped pelvis. The human shape is more efficient for bipedal locomotion but less efficient for reproduction because it restricts the size of the birth canal. It may take human women longer than an ape to grow a large enough pelvis to achieve full reproductive maturity. That time of waiting provides adolescent girls with many opportunities to practice and learn important adult behaviors that lead to increased reproductive fitness in later life. Cross-cultural studies of reproductive behavior show that human societies acknowledge (consciously or not) this special pattern of pelvic growth. The age at marriage, and first childbirth, clusters around 19 years for women from such diverse cultures as the Kikuyu of Kenya, Mayans of Guatemala, Copper Eskimos of Canada, and the United States from the colonial period to the 1950s.

Why Do Boys Have Adolescence?

The adolescent development of boys is quite different from that of girls. Boys become fertile well before they assume the size and the physical characteristics of men. Analysis of urine samples from boys 11–16 years old show that they begin producing sperm at a median age of 13.4 years. Yet cross-cultural evidence indicates that few boys successfully father children until they are into their third decade of life. In the United States, for example, only 3.09% of live-born infants in 1990 were fathered by men under 20 years of age. In Portugal, for years 1990, 1994, and 1999, the percentage of fathers under 20 years of age was always below 3%. In 2001, Portugal stopped presenting results concerning the percentage of fathers below 20 because there were too few of them. Among the traditional Kikuyu of East Africa, men do not marry and become fathers until about age 25 years, although they become sexually active after their circumcision rite at around age 18.

The explanation for the lag between sperm production and fatherhood is not likely to be a simple one of sperm performance, such as not having the endurance to swim to an egg cell in the woman's fallopian tubes. More likely is the fact that the average boy of 13.4 years is only beginning his adolescent growth spurt (Figure 1). Growth researchers have documented that in terms of physical appearance, physiological status, psychosocial development, and economic productivity, the 13-year-old boy is still more a juvenile than an adult. Anthropologists working in many diverse cultural settings report that few women (and more important from a cross-cultural perspective, few prospective in-laws) view the teenage boy as a biologically, economically, and socially viable husband and father.

The delay between sperm production and reproductive maturity is not wasted time in either a biological or social sense. The obvious and the subtle psychophysiological effects of testosterone and other androgen hormones that are released after gonadal maturation may 'prime' boys to be receptive to their future roles as men. Alternatively, it is possible that physical changes provoked by the endocrines provide a social stimulus toward adult behaviors. Whatever the case, early in adolescence, sociosexual feelings including guilt, anxiety, pleasure, and pride intensify. At the same time, adolescent boys become more interested in adult activities, adjust their attitude to parental figures, and think and act more independently. In short, they begin to behave like men.

However – and this is where the survival advantage may lie – they still look like boys. One might say that a healthy, well-nourished 13.5-year-old human male, at a median height of 160 cm (62 in.) 'pretends' to be more childlike than he really is. Because their adolescent growth spurt occurs late in sexual development, young males can practice behaving like adults before they are actually the size of an adult and perceived as mature by other adults. The sociosexual antics of young adolescent boys are often considered to be more humorous than serious. Yet, they provide the experience to fine-tune their sexual and social roles before their lives or those of their offspring depend on them. For example, competition between men for women favors the older, more experienced man. Because such competition may be fatal, the childlike appearance of the immature but hormonally and socially primed adolescent male may be life-saving as well as educational.

Genetic and Environmental Influences on Puberty

In 2009 Ken K. Ong and colleagues reported that a region on human chromosome 6 called *LIN28B* is the first specific region of the human genome associated with the timing of puberty. Each copy of the major allele for *LIN28B* is associated with 0.12 years earlier menarche. This same genome region is linked with earlier breast development in girls, earlier voice breaking and pubic hair development in boys, a faster tempo of height growth in girls and boys, and shorter adult height in women and men. Earlier puberty often results in shorter adult stature due to the completion of skeletal maturation at a younger age.

Prior to the discovery of *LIN28B*, there were many less direct indications of genetic influences on the timing of puberty. Studies of parents and offspring and twin studies contrasting monozygotic (identical) versus dizygotic (fraternal) twins showed that the greater the genetic similarity between people the more similar they were in terms of pubertal events. Medical disorders with a genetic basis influence the age at puberty and even its absence. These findings pertain to individuals and family members, or to pathological medical conditions. While these are important contributions to the biology of puberty, they tell us little about the wide variation within and between human populations in the timing of puberty and the duration of adolescence.

The study of secular trends in human growth and development tell us more about population variation in puberty. In human biology, the phrase 'secular trends' refers to changes in the mean size, shape, or rate of maturation of the members of a population from one generation to the next. Such trends can be positive (e.g., increasing size or decreasing the age at puberty) or negative (decreasing size or increasing the age at puberty). The word 'secular' has two meanings: (1) worldly, especially pertaining to the material, nonspiritual world, and (2) just once in an age, indicating a relatively long span of time. Secular trends in human biology are aptly named because the factors influencing these trends are related to the material conditions of life and these conditions do act on human growth over long spans of time.

Secular trends in growth and maturation are some of the best examples of the effect of the environment on growth. Increases in stature and reductions in the age of menarche have taken place during the past century and a half in virtually all affluent countries and more recently in many developing countries. In North America and Western Europe, the adult height increases average about 0.6 cm per decade and the decline in the age at menarche averages about 1 or 2 months per decade. An example of the secular trend in Sweden is shown in Figure 6.

Sometimes the changes are greater. For example, in Poland age at menarche declined from 1955 to 1978 by about 4.15 months per decade for girls living in villages and towns. For city girls, the decline was 3 months per decade. Despite the greater rate of decline for village and town girls, the city girls have always had the earliest mean age at menarche. In 1955 the mean ages were 14.3 years in villages, 13.9 in towns, and 13.4 in cities. In 1978 these mean ages were 13.5, 13.1, and 12.9 years, respectively. Polish researchers attribute the differences between locales to the lower quality of nutrition and health care, and greater physical labor, in towns and villages compared with cities. The overall decline in age at menarche in all locales attests to improvements in the quality of life in all three areas with time.

Even negative secular trends are best explained by environmental factors. Between 1978 and 1988, Poland suffered considerable political and economic turmoil. The age at menarche in all regions increased by an average of 1.7 months during the decade. Such reversals in secular trends are common during times of deterioration in the biological and socioeconomic environment. By 2008 the political and economic climate had improved and the mean age of menarche for urban girls declined again to 12.4 years.

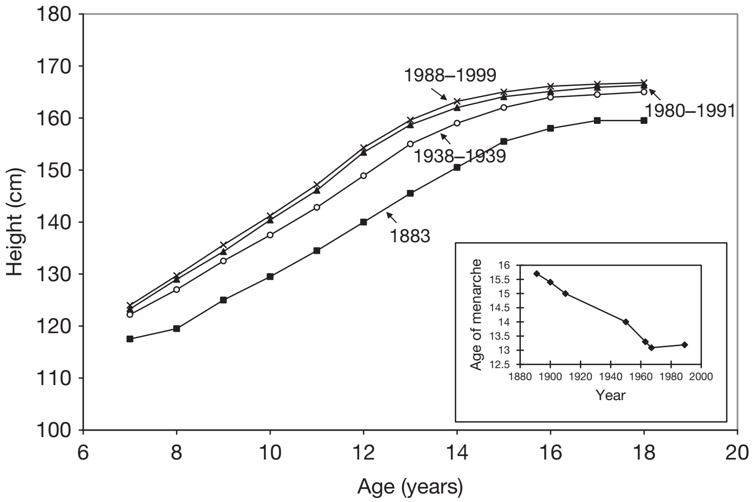

Figure 6 Secular trends in height and age of menarche (inset) in Swedish girls since the 1880s. Height has increased and age of first menstruation has decreased. Courtesy of Prof. Sara Stinson, Queens College, New York.

Several studies find that earlier puberty is related to smaller size at birth and rapid growth between birth and 2 years of age. Other research shows that persistent overweight due to excess body fat throughout the childhood and juvenile stages is associated with earlier puberty. These studies suggest that nutritional balance from the prenatal to the juvenile stages is an important regulator of the tempo of growth and pubertal development. Psychosocial stress caused by restrictive or abusive parenting, poverty, and racism also is linked with earlier puberty in otherwise well-nourished groups of girls. A specific example is the earlier average age of breast development and menarche in African American girls compared with European American girls. On average, African American girls have more body fat, are of lower socioeconomic status, and have greater exposure to racism. These observations are somewhat counterintuitive to the findings of the secular trend studies, which show that better environments lead to earlier menarche. Researchers in this area are actively trying to understand these relationships. There are several other environmental factors that influence the timing of puberty, including artificial lighting and adoption of infants and children from developing nations by parents from wealthy nations. An important area of research is the link between precocious or delayed puberty and exposure to endocrine disruptors, such as estrogen-like compounds in industrial pollutants (PCBs and PBBs), cosmetics, food, and drugs.

Risks of Puberty and Adolescence

The evolution of any new structure, function, or stage of development may bring about many biosocial benefits; however, it also incurs risks. Human puberty and adolescence comes with its own set of specific risks. Among the most common and serious of these are psychiatric and behavioral disorders. The onset of such problems tends to peak during adolescence. Most mammalian species terminate all brain growth well before sexual maturation, but human adolescents show enlargement and pruning of some brain regions leading to structural changes in the cerebral cortex. Some scholars hypothesize that the increase in brain-related disorders may derive from these cortical changes, which affect the adolescent brain's sensitivity to reward.

The reward system of the brain may lead adolescents toward risk-taking behavior. One perspective on this is expressed by Laurence Steinberg who in 2004 wrote of

> . . . a disjunction between novelty and sensation seeking (both of which increase dramatically at puberty) and the development of self-regulatory competence (which does not fully mature until early adulthood). This disjunction is biologically driven, normative, and unlikely to be remedied through educational interventions . . . .

A less biologically deterministic perspective on risk-taking is expressed by Dan Romer who in 2010 wrote that

> Individual differences in impulsivity underlie a good deal of the risk taking that is observed during adolescence . . . However, early interventions appear able to reduce the severity and impact of these traits by increasing control over behavior and persistence toward valued goals . . . .

Whether inherently biological or shaped by social intervention adolescence is a time of life with a high level of risk for certain diseases, of the mind and the body, and greater mortality. The later is often due to exposure to ritualized violence, such as serving as combatants in warfare, or being exposed to inherently dangerous but socially normative behaviors, such as automobile driving, alcohol consumption, cigarette smoking, and sex, without appropriate instruction and regulation by the society.

Conclusions

In this article, we have taken a biocultural approach to the study of human puberty and adolescence. We reviewed the pattern of human postnatal growth and development – the stages of infancy, childhood, juvenile, adolescence – and set these basic principles in their evolutionary context. Puberty as a physiological and sociocultural event was defined. Adolescence was defined as the time span from puberty to adulthood. Several hypotheses were discussed concerning how the new life stages of the human life cycle represent feeding and reproductive specializations, which secondarily allow for the human style of learning and cultural behavior.

The biocultural perspective of human development focuses on the constant interaction taking place during all phases of human development, both between genes and hormones within the body and with the sociocultural environment that surrounds the body. Research from anthropology, developmental psychology, endocrinology, primate behavior, and human biology shows how the biocultural perspective enhances our understanding of human development.

See also: Initiation Ceremonies and Rites of Passage.

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