

REVIEW ARTICLE

Brain Development During Adolescence

Neuroscientific Insights Into This Developmental Period

Kerstin Konrad, Christine Firk, Peter J. Uhlhaas

SUMMARY

Background: Adolescence is the phase of life between late childhood and adulthood. Typically, adolescents seek diversion, new experiences, and strong emotions, sometimes putting their health at serious risk. In Germany, for example, 62% of all deaths among persons aged 15 to 20 are due to traumatic injuries. Neuroscientific explanations have been proposed for typical adolescent behavior; with these explanations in mind, one can derive appropriate ways of dealing with adolescents.

Method: We selectively review pertinent articles retrieved from the PubMed database about the structural and functional development of the brain in adolescence.

Results: New findings in developmental psychology and neuroscience reveal that a fundamental reorganization of the brain takes place in adolescence. In postnatal brain development, the maximum density of gray matter is reached first in the primary sensorimotor cortex, and the prefrontal cortex matures last. Subcortical brain areas, especially the limbic system and the reward system, develop earlier, so that there is an imbalance during adolescence between the more mature subcortical areas and less mature prefrontal areas. This may account for typical adolescent behavior patterns, including risk-taking.

Conclusion: The high plasticity of the adolescent brain permits environmental influences to exert particularly strong effects on cortical circuitry. While this makes intellectual and emotional development possible, it also opens the door to potentially harmful influences.

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Adolescence is the phase of life between late childhood and adulthood. It is a time not only of physical maturation, but also of mental and emotional development into an independent, responsible adult. The major developmental tasks of adolescence include the establishment and nurturing of intimate relationships and the development of identity, future perspectives, independence, self-confidence, self-control, and social skills (1).

Heightened risk-taking behavior

Many adolescents and young adults are prone to take risks and enjoy having extreme emotions (2, 3). This is reflected in statistics showing that risky behavior in adolescence is linked with an elevated risk to health (4). In Germany, for example, 62% of all deaths among persons aged 15 to 20 are due to traumatic injuries. The most common causes of death are motor vehicle accidents, other accidents, violence, and self-injury (5). The high mortality is attributable to drunk driving, driving without a seatbelt, carrying weapons, substance abuse, and unprotected sexual intercourse (4).

Boys and girls in comparison

As can be seen in the *Table*, boys and girls engage in risky behavior at similar frequencies. In recent years, for example, the prevalence of smoking among boys and girls has become nearly equal, although some qualitative differences remain: Boys smoke more cigarettes, and they also more commonly smoke “harder” tobacco products such as cigars, black tobacco, and unfiltered cigarettes. Boys and girls also drink different alcoholic beverages: Boys tend to drink beer and hard liquor, while girls tend to drink wine, sparkling wine, etc. Boys drink alcohol more frequently and in larger amounts. They also consume illegal drugs more commonly than girls. Boys are more prone to accidents, and they take more risks when driving. Girls, on the other hand, are more likely to engage in health-endangering behavior in the area of nutrition (e.g., dieting, eating disorders).

Method

This review concerns new neurobiological insights into typical adolescent behavior and their implications for the best ways to deal with adolescents. We studied these issues with a selective search for relevant publications in German library catalogues, in the PubMed database using

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TABLE

Risky behavior among German adolescents, in percent

Behavioral domains	Boys	Girls	Age range
Substance abuse			KiGGS* ¹ : 11–17 years
Current smoking	20.5	20.3	
Regular alcohol use	38.6	22.2	
Current cannabis use	9.2	6.2	
Current use of other illegal drugs	<0.5	<0.5	
Delinquency			BELLA* ² : 7–17 years
Aggressive and dissocial behavior	7.9	7.2	
Violence			KiGGS* ³ : 11–17 years
Commission of violent acts	19.6	9.9	
Being the victim of violent acts	5.2	3.9	
Both of the above	7.6	3.6	
Sexual behavior			BZgA* ⁴ : 14–17 years
Sexual intercourse at or before age 14	14	12	
Too early sexual intercourse in own estimation	38	22	
No protection the first time	15	9	
Sexual intercourse or other sexual conduct against one's will	3	13	
Mental abnormalities			BELLA* ³ : 7–17 years
Depression	5.4	5.3	
Anxiety	10.1	10.0	
Attention deficit hyperactivity disorder (ADHD)	2.9	1.4	
Scholastic problems			Shell Youth Study* ⁵ : 12–21 years
Ever at risk for repeating a grade	28	24	
Repeated a grade	20	14	
Physical inactivity			KiGGS* ⁶ : 11–17 years KiGGS* ⁷ : 11–17 years
Physically active less than once per week	10.1	21.5	
3 or more hours of television watching per day	22.1	23.6	
Nutrition			KiGGS* ⁸ : 14–17 years
Overweight	9.0	8.1	
Obese	8.2	8.9	
Markedly underweight	2.4	1.4	

¹Lampert and Thamm 2007 (e9); ²Ravens-Sieberer et al. 2007 (e11); ³Schlack and Hölling 2007 (e10); ⁴BZgA 2006 (e12); ⁵Shell Deutschland Holding (e13); ⁶Lampert et al. 2007 (e14); ⁷Lampert et al. 2007 (e15); ⁸Kurth and Schaffrath Rosario 2007 (e16). KiGGS, German Health Interview and Examination Survey for Children and Adolescents; BELLA, BELLA Study (mental health module within KiGGS), BZgA, German Federal Centre for Health Education. From (39) Bühler A: Risikoverhalten in der Jugend. In: Uhlhaas PJ, Konrad K (eds): Strukturelle Hirnentwicklung in der Adoleszenz. Stuttgart: Kohlhammer 2011; 189–205. Reprinted with the kind permission of Kohlhammer, Stuttgart

the search terms “adolescence/puberty,” “brain/neural,” and “development.” Cited publications were also considered. Special attention was paid to human neuro-imaging studies.

Background

Until just a few years ago, there was a general assumption in developmental psychology and neuroscience that major changes in the architecture and functioning of the brain were limited to the prenatal period and the first five or six years of life. (For a historical overview, see [6].) In the meantime, however, new scientific discoveries have compelled a revision of this assumption.

Large-scale longitudinal studies have shown that a basic reorganization of the brain occurs during adolescence (7). Many synapses are eliminated (8) while, at the same time, there is an increase in white matter (9, 10), and there are changes in neurotransmitter systems

as well (11, e1, e2). Thus, the anatomical and physiological maturation processes that take place in adolescence are much more dynamic than originally thought. It can be concluded that a reorganization of cortical circuits takes place in adolescence and is reflected in the changes in cognitive functioning and affect regulation that are typical of this period of life (12).

Interestingly, this pattern of human brain development differs from that of nonhuman primates. Although, for example, rhesus monkeys and chimpanzees (like human beings) are born with immature brains, all cortical brain areas in macaques mature at the same rate (13). In man, autopsy studies have shown that synaptogenesis reaches a maximum in the visual and auditory cortices a few months after birth, while synapses are formed much more slowly in the prefrontal cortex. Thus, over the course of human evolution, there was a switch from a synchronous to a

heterochronous pattern of cortical development (8). This protracted developmental process presumably facilitates the development of specifically human skills, especially those acquired through embedding in a highly stimulating sociocultural environment, e.g., by schooling, music, verbal communication, and social interaction (14) (Figure 1).

The current understanding of brain development in adolescence

Brain structure

The brain is fully grown relatively soon after birth, in the sense that the cerebral cortex soon reaches its maximal volume. Nonetheless, important structural maturation processes continue to occur in adolescence, as structural imaging studies have shown (15, e3–e5). In the brain, the gray matter matures from back to front, so to speak: The maximum density of gray matter is reached first in the primary sensorimotor cortex and last in higher association areas such as the dorsolateral prefrontal cortex, the inferior parietal gyrus, and the superior temporal gyrus. This means that, in particular, brain areas such as the prefrontal cortex—which subserves higher cognitive functions such as behavioral control, planning, and assessing the risk of decisions—mature later than the cortical areas associated with sensory and motor tasks (16) (Figure 2).

Autopsy findings suggest that these gray matter changes are due to synaptic pruning (17). Many synapses are formed in childhood that are later removed in adolescence. This occurs in an experience-dependent way, i.e., the synapses that survive are the ones that are more often “in use.” There are also other cellular mechanisms that might account for gray matter changes in this phase of life, e.g., a reduction in the number of glial cells and an increase of myelination (18).

As the gray matter decreases in volume, the white matter increases in volume. The white matter is composed of myelinated axons that conduct neural information rapidly. The volume of white matter increases continually from childhood into early adulthood (19). This expansion is presumed to be due, in large part, to the progressive myelination of axons by oligodendrocytes (10). Myelination tends to proceed from inferior to superior brain areas, and from posterior to anterior.

Brain function

The anatomical reorganization processes of the adolescent brain that are described above are associated with profound emotional and cognitive changes. In particular, there is progressive development of executive functions, i.e., cognitive processes that control thought and behavior and thereby allow the individual to adapt flexibly to new, complex situational tasks (20). In adolescence, at the same time that these basic cognitive skills are developing, there are also changes in social-affective abilities such as face recognition, the so-called theory of mind (i.e., the ability to put oneself mentally in another’s place), and empathy (21).

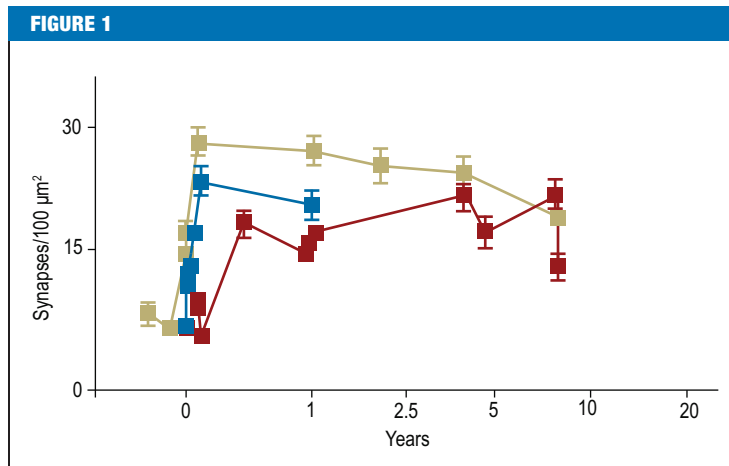
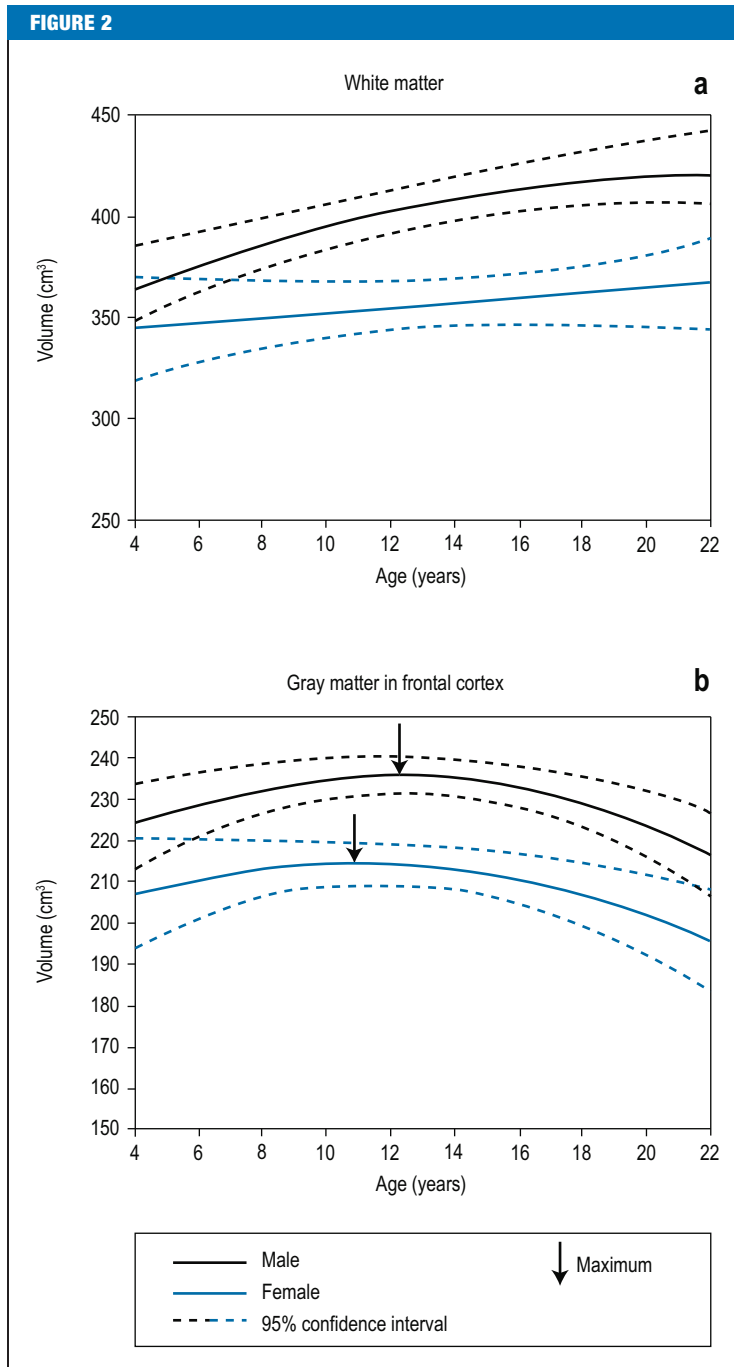


FIGURE 1 The development of the prefrontal cortex is protracted in man compared to other primates. The Figure shows the synaptic density per 100 μm² in the prefrontal cortex as a function of age in man (red), chimpanzees (blue), and rhesus macaques (olive green) (error bar = 95% confidence interval). From (40) Lui et al.: Extension of cortical synaptic development distinguishes humans from chimpanzees and macaques. *Genome Research* 2012; 22: 611–22. Reprinted with the kind permission of Cold Spring Harbor Laboratory Press, New York

At the neural level, functional imaging studies of brain development have shown that children and adolescents often have a broader, less focal activation pattern than adults, and that the effective recruitment of neural resources increases with age, so that neural activity decreases in brain regions other than those that are relevant to the task at hand (22). It is not yet clear to what extent this pattern of neural development is due to experience-dependent or biologically determined influences. Imaging studies have also shown that adolescents have heightened activity in limbic areas in emotional situations: For example, Galvan et al. (23) found that the anticipation of a reward is associated with a more marked activation in the nucleus accumbens in adolescents than in children and adults. Interestingly, these researchers also found a positive correlation between activation in the nucleus accumbens and the adolescents’ individual risk-taking tendency (24).

Moreover, both structural and functional imaging studies have shown that the prefrontal cortex becomes more strongly linked to sensory and subcortical structures during adolescence (25, 26, e6). This implies a greater influence of frontal brain regions on cognitive and affective processes. The development of cognitive and affective neural circuits should not be regarded as the sole determinant of structural neurobiological maturation; rather, there appears to be a strong interaction of genetic factors with environmental demands. For example, affect regulation and the brain structures subserving it are influenced by the parent-child interaction (27).

Further findings showing that a profound reorganization of neural circuitry takes place in adolescence are derived from electrophysiological studies, including



Development of the white matter and gray matter of the frontal cortex over a human lifetime; separate curves for each sex. From (7) Giedd JN, et al.: Brain development during childhood and adolescence: a longitudinal MRI study. *Nature Neuroscience* 1999; 2: 861–3. Reprinted with the kind permission of Nature Publishing Group, London

electroencephalographic (EEG) studies of changes in high-frequency and synchronous brain waves (28). Brain development in adolescence is associated with a decline of oscillatory activity at rest in the delta (0–3 Hz) and theta (4–7 Hz) bands, and an increase in the alpha (8–12 Hz) and beta bands (13–30 Hz). With task-dependent oscillations, the precision of synchronization of oscillatory activity in the theta, alpha, and beta bands increases. The late development of synchronized oscillations in adolescence is closely linked to structural (anatomical) maturation processes as well as to fundamental changes in neurotransmitter systems, which have been intensively researched in the past few years.

A neurobiological explanatory model for typical adolescent behavior

One of the more influential neurobiological models to explain typical adolescent behavior was developed by the group of Casey in New York (29, e7) (Figure 3).

The main premise of this model, based on neuroanatomical findings and data from functional imaging studies (23, 24, 30, 31), is that adolescence is a period of neural imbalance caused by the relatively early maturation of subcortical brain areas and the relatively delayed maturation of prefrontal control areas (Figure 3), with the result that, in emotional situations, the more mature limbic and reward systems gain the upper hand, so to speak, over the still relatively immature prefrontal control system. This should not be taken to imply that adolescents are by nature unable to make rational decisions. Rather, in situations that are particularly emotionally laden (e.g., in the presence of other adolescents or when there is the prospect of a reward), the probability rises that rewards and emotions will affect behavior more strongly than rational decision-making processes (23, 24, 32). This model has been tested in a series of experimental studies (Box).

It has been found, for example, that adolescents can assess the risk of certain behaviors just as well as adults can when asked about them in a questionnaire. On the other hand, ecologically valid behavioral tests clearly show that adolescents make more risky decisions in groups than they do when alone (33). The reason is presumably that, at this age, the benefit of risky behavior—the social approbation of peers—is rated much more highly than the risk itself. This may be associated with the nonlinear maturation pattern of the prefrontal and limbic brain areas. In accordance with this model, research on preventive programs has shown that programs based on imparting knowledge about risks are less effective than those focusing on individual benefits and on the training of social competence and resistance (34).

It is intriguing to ask what functional benefit, if any, might accrue to the individual from this temporary imbalance between cortical and subcortical brain structures. From the evolutionary perspective, adolescence is the developmental period in which a young person acquires independence. This process is not unique to

the human species; increased novelty-seeking and increased social interactions with other individuals of the same age can be observed in many other species as well (35). Risky behavior among adolescents can be seen as the product of a biological dysequilibrium between the search for diversion and new experiences (“sensation seeking”) on the one hand, and as yet immature self-regulatory capabilities on the other (2); its purpose may be to enable adolescents to break away from the familial security zone, so that they can, for example, find a partner outside their primary family. Immaturity of the prefrontal cortex seems to favor certain types of learning and flexibility (1).

In fact, over the lifetime of an individual, there are probably multiple developmental windows in which the brain is particularly well prepared for certain types of learning experience. From the evolutionary perspective, the cognitive style typical of adolescence, which is especially sensitive to social-affective stimuli and flexible in the assignment of goal priorities, may be optimally suited to the social developmental tasks facing the adolescent. This also implies that the adult brain cannot be considered the optimal functional system in an absolute sense, and that adolescence should not be considered a state of deficient brain performance.

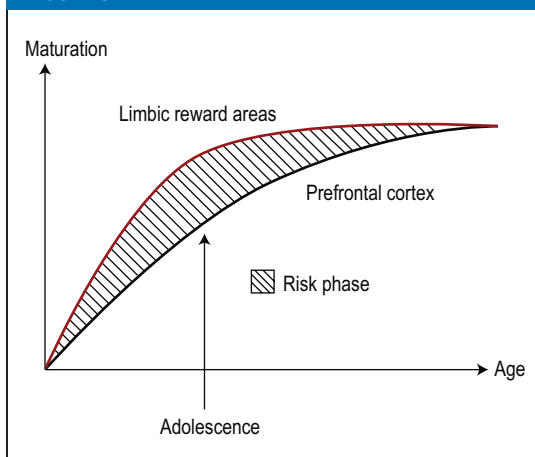
The influence of pubertal hormones on adolescent brain development

The maturation of the reproductive system during puberty is associated with rising concentrations of the gonadal steroid hormones. The brain has a high density of steroid receptors, and it is thus plausible that the sex hormones exert an effect on neural networks in adolescence. Sisk and Foster (36, e8) have proposed that a second wave of cerebral restructuring occurs in adolescence, building on an earlier, perinatal phase of sexual differentiation. According to this model, the hormones of puberty affect the further structuring of the adolescent brain, so that a permanent reorganization of the brain results, with the effect that neural networks are sensitized to activating hormonal effects. The rising concentrations of pubertal hormones have different effects on the developing hypothalamic-pituitary-adrenal (HPA) axis in boys and girls: The rise in androgens in boys apparently inhibits the hypothalamic secretion of corticotropin-releasing hormone (CRH), while estrogens in girls regulate the HPA axis upward. Estrogens may make girls more susceptible to stress, while androgens make boys more resilient to it (37).

Overview

Until now, research on early childhood has received the most attention from the scientific community and the media. Recent findings show, however, that the continuing psychological and biological changes of adolescence exert a powerful influence on cerebral structure and function. The brain of the adolescent goes through a new phase of plasticity in which environmental factors can have major, lasting effects on cortical circuitry. This opens up new opportunities for

FIGURE 3

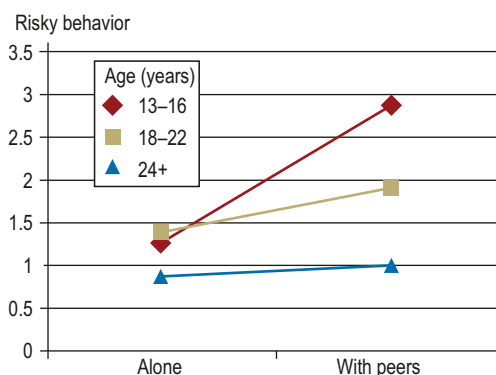


Nonlinear maturation processes of subcortical and prefrontal brain areas lead to an imbalance of neural networks in adolescence. Modified from (12) Casey BJ, Jones RM, Hare TA: The adolescent brain. *Annals of the New York Academy of Sciences* 2008; 1124: 111–26. Reprinted with the kind permission of John Wiley and Sons

BOX

The influence of peers on risky behavior

Researchers recruited persons in three age groups (13 to 16 years, 18 to 22 years, and over 24 years) to study whether the influence of contemporaries (peers) on risky decisions depended on the age of the probands. Participants were put in a type of driving simulator in which they had to drive as far as possible until a traffic light turned red



and a wall appeared. If the car was not stopped soon enough, it crashed into the wall, and the driver lost points. The participants were either alone or in groups of three persons in the simulator. The 13- to 16-year-olds were found to be more likely to make risky decisions than the participants in the other age groups, but only in the presence of their peers. Adult driving behavior was independent of the presence or absence of peers (33).

education. For example, for the very reason that adolescents are so readily influenced by emotions, they stand to profit from learning experiences taking place in a positive emotional context that are intentionally designed to train emotional regulation. Given that risky behavior in adolescence has a neurobiological basis, attempts to suppress such behavior completely seem bound to fail. It would be more reasonable to enable adolescents to have emotional experiences in a safe environment, and to increase the social rewards associated with non-risky behaviors through regulatory legislation (e.g., prohibition of certain kinds of advertising) and the provision of emotionally positive models. For instance, the teenage lead character in a television soap opera might decide to opt out of a hard-drinking contest organized by friends.

Moreover, the protracted period of neural plasticity in adolescence also makes adolescents more vulnerable to harmful environmental influences, e.g., drugs. The findings of animal experiments and human studies suggest, for example, that the use of cannabis in adolescence can cause permanent cognitive changes and structural changes in the brain that are more extensive than those seen in adult cannabis users (38).

Future research on brain development should, therefore, address the important matter of environmental influences on the function and organization of the brain.

Until now, cognitive neuroscience has not adequately analyzed the influence of social and cultural context on cognitive and affective processes and their development. Thus, our current understanding that adolescence is a decisive phase in brain maturation, and that brain maturation processes may be operative up to the age of twenty, or even beyond, also has important implications for educational and social policy. Any decisions affecting the development of children and adolescents should take the neurobiological facts into

account. Major current issues of this type include the question of legalizing cannabis consumption and the applicability of juvenile delinquency law in adolescence.

Conflict of interest statement

Prof. Konrad has received lecture honoraria from the Medice, Lilly, and Novartis companies and research support (outside funding) from Vifor Pharma Ltd.

The other authors state that no conflict of interest exists.

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KEY MESSAGES

- In adolescence, a fundamental reorganization of the brain takes place that continues into the beginning of the third decade of life.
- Adolescent brain development is characterized by an imbalance between the limbic and reward systems, which mature earlier, and the not yet fully mature prefrontal control system. This imbalance may be the neural substrate for the typical emotional reactive style of adolescence, and it may promote risky behavior.
- Typical adolescent behavior is the basis for the development of autonomy in adolescents and promotes their emancipation from the primary family.
- The hormones of puberty affect the further sex-specific restructuring of the adolescent brain.
- The reorganization of the adolescent brain renders it particularly susceptible to environmental influences, both positive and negative.

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