PERSPECTIVE

Importance of investing in adolescence from a developmental science perspective

Ronald E. Dahl[1], Nicholas B. Allen[2], Linda Wilbrecht[3] & Ahna Ballonoff Suleiman[4]

This review summarizes the case for investing in adolescence as a period of rapid growth, learning, adaptation, and formational neurobiological development. Adolescence is a dynamic maturational period during which young lives can pivot rapidly—in both negative and positive directions. Scientific progress in understanding adolescent development provides actionable insights into windows of opportunity during which policies can have a positive impact on developmental trajectories relating to health, education, and social and economic success. Given current global changes and challenges that affect adolescents, there is a compelling need to leverage these advances in developmental science to inform strategic investments in adolescent health.

It is well-recognized that the first few years of life represent a sensitive period for growth, early learning and brain maturation[1]. As a result, the scientific understanding of the formational effects of early experience has had a pronounced impact on global policies and practices[2,3]. Recent scientific advances are now contributing to the growing recognition that adolescence is a second period of rapid growth and foundational learning associated with distinct neuro-maturational changes[4,5]. There is great potential for leveraging these advances to inform strategies for investing resources during this pivotal time in the life course[6,7].

Notably, the global stakes for choosing to invest in adolescence are increasing. Global demographics reveal a disproportionate surge in the number of adolescents in the world, including an unprecedented expansion of adolescents in low-income regions. More than a billion adolescents are now coming of age among an increasing array of social changes and global challenges. The revolutionary changes in information technology that are sweeping across the globe are having the greatest impact on adolescents. Adolescents are often the early adopters of new technology in ways that can intensify vulnerabilities (for example, exploitation and radicalization) as well as opportunities (education, social connection, innovation and learning). These accelerating technological and social changes heighten the importance of understanding how (and when) to intervene to prevent harmful effects and to promote health.

In this review, we present a developmental science perspective on adolescence as a distinct maturational period that begins with the onset of puberty. Developmental science is the study of the patterns and processes of biological, cognitive and behavioural changes that occur as an organism grows and matures. Here, we summarize our current understanding of developmental processes that occur during and after puberty. We describe some of the distinctive aspects of learning in adolescence that are thought to support acquisition of the culturally embodied knowledge, skills and self-regulatory capacities that are needed for adolescents to become independent and to integrate into adult society. We explore how a nuanced understanding of the distinctive features of this developmental period may inform intervention and policy, especially the developmental changes in learning and exploration that are amplified during adolescence. Specifically, we highlight the role that pubertal hormones may have in enhancing the motivational importance of status, prestige and sex as notable drivers of social learning and identity development during adolescence. Finally,

we discuss the exciting potential of using insights from developmental science to inform intervention and policy—particularly in light of current global challenges.

Puberty initiates a distinct developmental period

Adolescence encompasses the numerous developmental changes and foundational learning experiences that occur during the transition from childhood to the attainment of adulthood. This transition begins with the onset of puberty—a biological process that drives sexual maturation, typically starting by age 10 in girls and by age 12 in boys (Fig. 1). Puberty begins with changes in the brain, which initiate a cascade of transformational changes in the body that include rapid acceleration in physical growth (pubertal growth spurt), metabolic changes, changes in sleep and circadian regulation, and sexual maturation (that is, sex-specific changes in facial structure, voice, muscle and fat distribution, body hair distributions, changes in skin and glandular secretions, and breast, genital, adrenal and gonadal development)[8]. Hormones released from the gonads and adrenals, in turn, affect the brain, altering cognitive, emotional and motivational processes (It is important to note that although puberty is often thought of as a developmental process that is sexually differentiated, testosterone and oestrogens can be found in the brain and blood of both males and females with variable, and sometimes overlapping, concentrations.).

Developmental changes during adolescence also include structural and functional changes in the brain—particularly neural systems involved in cognitive, emotional, social and motivational processes[4,9,10]. These neural changes are associated with behavioural changes such as increases in sensation-seeking and a re-orientation of attention and motivation (towards peers, social evaluation, status and prestige, and sexual and romantic interests)[11,12]. Adolescent development also involves profound changes in social contexts, social roles and social responsibilities[13]. Importantly, there are complex interactions between and among these levels of change. Indeed, learning and brain development are inextricably intertwined throughout this period as learning affects brain development, and maturational changes in the brain in turn affect learning and motivation.

The end point of adolescence is considerably more difficult to define scientifically. Becoming an adult cannot simply be equated to a measure of physical maturation, such as attaining final adult height or reproductive maturity. There have also been some recent attempts to define

[1]School of Public Health, Institute for Human Development, University of California, Berkeley, California, USA. [2]Department of Psychology, University of Oregon, Eugene, Oregon, USA. [3]Department of Psychology, Helen Wills Neuroscience Institute, University of California, Berkeley, California, USA. [4]Institute for Human Development, University of California, Berkeley, California, USA.
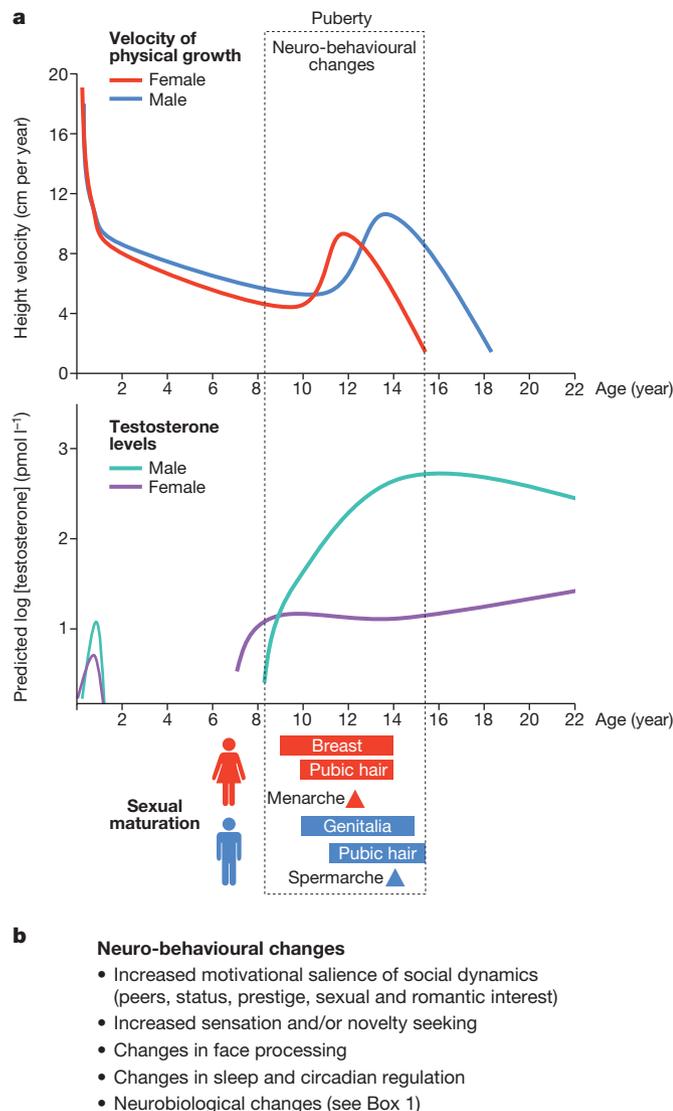
Figure 1 | Puberty initiates a period of rapid growth and multi-level dynamic change. a, The red and blue solid lines (height velocity in cm per year as a function of age in girls and boys) show that growth is very rapid in infancy and then slows during childhood. Growth rates accelerate at the onset of puberty and then decelerate at later stages of puberty. This dynamic pubertal growth spurt begins about 18 months earlier in girls than in boys—and is part of a large collection of physical manifestations of sexual maturation (which in girls includes breast and genital development, pubic and axillary hair and menarche, and in boys includes genital development, pubic, axillary and facial hair). The red and blue lines represent testosterone levels (log(pmol l^{-1})) as an example of one of several hormones that contribute to these pubertal changes. **b**, Other physical changes include sexually dimorphic changes in facial architecture, changes in skin and sebaceous glands (for example, acne and body odour) and deepening of the voice in boys. Pubertal maturation also influences neuro-behavioural development, particularly social, emotional and motivational processes, such as the well-recognized increases in sensation-seeking, and a re-orientation of attention and motivational salience towards peers, social evaluation, status and prestige, and sexual and romantic interests. Pubertal maturation also influences (and is influenced by) the rapidly changing social contexts in which adolescent learning and development are occurring. Taken together these multi-level changes (and their bidirectional interactions) create a dynamic period of growth, development, learning and adaptation. Understanding these dynamic developmental processes can inform targets (and developmental timing) for early intervention, prevention and policy.

the end of adolescence in terms of cognitive and affective processes[14]. However, 'adulthood' is inherently intertwined with taking on certain social roles, and importantly, having the knowledge, skills and social competence to succeed in these roles. It also involves societal recognition that the individual has the rights (and responsibilities) to exercise these roles. As a pragmatic matter, modern societies typically confer adult rights and responsibilities based on age. However, this is at best an approximate way to estimate maturation—especially during adolescence when punctuated growth processes can result in markedly different maturational development between individuals of the same age. Moreover, laws can vary widely (within and across countries) regarding which age is used to designate specific adult rights, roles or responsibilities (for example, the legal age for driving a car, voting in an election, marriage, serving in the armed forces, being sanctioned as an adult for committing crimes, using alcohol, cigarettes or other drugs, making personal decisions about health or owning a gun)[15]. Typically, these legal frameworks are primarily informed by cultural (and sometimes religious) values, rather than evidence about the developmental effects of exposure to particular learning experiences and independent decision making at different stages of development[16].

Learning, development and maturation in adolescence

Adolescent development builds on considerable childhood learning, and allows adolescents to acquire a new level of knowledge, skills and cultural competence to successfully transition to an independent adult role. During adolescence, we gain cognitive, affective and self-regulatory abilities that allow us to adaptively pursue new goals and priorities that can be increasingly abstract and extend far into the future[4,17]. We gain more nuanced understanding of the workings of adult society, which involves learning to reason about abstract concepts and future consequences, and creating a more mature understanding of self, others and the complexities of adult social relationships[17–21]. We also acquire skills to navigate a growing range of novel, uncertain and emotionally charged social situations (including a new level of cognitive, social, emotional and self-regulatory capacities[22]) and to apply these skills to an increasingly complex set of social relationships with peers, adults and societal institutions.

In addition, during adolescence, we must also adapt to fundamentally new aspects of our own emerging identity[23], which includes learning how to relate to the world, and ourselves, as a suddenly and (often) mystifyingly sexual being[24]. We must discover in a new way—through an elaborate series of trials and errors, successes and failures, and with growing independence—who we are. That is, we must develop (within a family, cultural and social context) an adult identity, with our own heartfelt goals, values and priorities.

As supported by a large number of studies, this developmental trajectory from childhood to emerging adulthood is fraught with a multitude of risks and vulnerabilities. These contribute to a marked increase in risk of death and disability through adolescent accidents, suicide, violence, depression, alcohol and substance use, sexually transmitted diseases, unwanted pregnancies, as well as the establishment of a wide range of health-related behavioural risk factors (such as smoking, drinking, substance use, unhealthy eating and sedentary behaviour) that will contribute to health consequences in later life[25]. Pivotal changes in educational trajectories during adolescence have increasingly important lifetime consequences, with educational attainment impacting career options and economic success[15].

The rapidly changing world of adolescence

We are currently witnessing pronounced and historically unprecedented changes in the demography and lifestyle of adolescents[15]. In 2015, the estimated global population of adolescents aged 10–19 years was 1.2 billion, which is approximately 16% of the world's population[26]. The vast majority of the world's adolescents—approximately 90%—live in low- and middle-income countries, in which the barriers to achieving positive health and well-being are often the most complex and challenging. As such, nations that are already being challenged to

meet the educational and health needs of adolescents are likely to need increased resources to address these issues in the near future.

Technological innovations, especially in mobile computing (for example, smartphones) and online social networks, are transforming the daily lives of adolescents[27–29]. Today's adolescents in middle- and high-income countries are 'digital natives'—individuals who have never experienced the world before the internet. The social capabilities of internet-enabled devices tap into core adolescent motivations in powerful ways. Adolescents are particularly motivated to explore peer relationships, and social media provide almost ubiquitous access to these interactions[29]. Moreover, it provides these opportunities in ways that are particularly appealing to adolescents—relatively free of the reach of parental monitoring[30]. This creates unprecedented opportunities for positive social connection and support (for example, the isolated teen who finds a community of like-minded individuals online), but it also intensifies adolescents' exposure to negative social encounters (for example, ostracism, bullying, sexual exploitation and violent radicalization). Adolescents' emerging interests in sex and sexuality are now met with an almost unlimited supply of freely available highly explicit pornography. Importantly, these technologies can also add to the 'digital divide', in which social inequalities between those adolescents growing up in high-resource contexts (in which parents, teachers and social influences help to scaffold adolescents' learning and use of technology) and those growing up in impoverished contexts (who may be more vulnerable to the negative effects) are exacerbated[31].

Other factors are also rapidly altering the lives of adolescents. Today, adolescents enter puberty earlier, and take on independent adult roles (for example, finishing formal education and entering the workforce, living apart from their family of origin, becoming fully financially independent) later than they did in the past centuries, making adolescence a longer period of life than it has been previously[32].

Economically, adolescents increasingly take on the role of active consumers, with their own disposable cash and credit accounts making them independently responsible for purchasing decisions[33]. As a result, adolescents are now the direct target of marketing efforts (including marketing of financial products) that no longer need to be filtered through parental control. Although many of these secular changes are particularly pronounced for adolescents living in high-income countries, the environment in low- and middle-income countries is rapidly changing to reproduce these phenomena, often in contexts in which there is less education and regulation to buffer their potentially deleterious effects (for example, the rapid changes in point of sale advertising for alcohol, tobacco and unhealthy snack foods[34]).

Given the importance of successful adolescent development for adult attainment of social, educational and financial success, achieving these goals will require policy initiatives and investments aimed at adolescents. A recent study has found evidence for high returns from such investments[7]. However, there is marked variation between countries, with returns expected to be greatest in low-income countries. A range of interventions, including policies targeting physical, mental and sexual health, road traffic injuries, child marriage, and increasing the extent and quality of secondary schooling, are all predicted to be associated with especially high benefit to cost ratios[7]. Accordingly, there have been many calls for comprehensive and increasing investments in adolescent health and wellbeing in both national and international policy[15,35,36].

We support these proposals to invest in the lives of adolescents, and moreover assert that in order to have the most positive impact, such investments must be guided by science. To ensure that policies are not too diffuse, they should also be carefully targeted to the epochs in which these policies may have the greatest impact.

Informing strategic investment in adolescence
Maturational periods of rapid growth and change can create opportunities for pivotal influences on developmental trajectories. This

principle can be illustrated by rates in physical growth (see Fig. 1). For example, it is easy to anticipate the probable impact of experiencing a severe famine during a period of accelerated growth. Given the extra nutritional and metabolic demands of rapid growth, it makes sense that being an infant or being in the middle of a pubertal growth spurt during a period of malnutrition could have particularly deleterious long-term effects. Indeed, analyses of data from the famine during the Nigerian Civil war[37] and from the famine in Cambodia (1975–1979)[38] show that experiencing famine as an adolescent resulted in more pronounced stunting of adult height than does exposure to famine during other life stages. Another study has shown that being in early adolescence during historical periods of adverse experiences, such as war or famine, is particularly associated with a shortened life expectancy[39].

However, periods of rapid growth and maturational change can also create opportunities. For example, establishing healthy bone density during the adolescent growth spurt (by getting enough calcium, vitamin D and exercise) can be protective against developing osteoporosis in later life[40]. Similarly, adolescence creates an opportunity to normalize the risk trajectory of developing polycystic ovarian syndrome during adulthood among females with very low birth weight, through insulin sensitization (via metformin treatment) when administered during pubertal maturation[41].

These examples highlight a general principle about modifiable inflection points along developmental trajectories. We believe that there are parallels in adolescent development in cognitive, affective, social and motivational domains, which could provide opportunities to modify developmental trajectories in behavioural, educational and mental health outcomes. Peri-pubertal changes in learning and motivation and in the neural systems that underlie these changes may provide these opportunities.

Brain development and changes in learning
Both human and animal models have provided evidence for distinctive neurodevelopmental changes during adolescence (see Box 1). Most notably, the grey matter in higher-order brain regions becomes thinner and prunes synapses during adolescence[42–44]. However, some specific brain connections are formed primarily in early to mid-adolescence, which may potentiate new forms of motivation and and/or new learning. For example, dopaminergic[45] and amygdala neurons[46,47] increasingly innervate the frontal cortices, and the frontal cortex shows striking changes in top-down innervation of the amygdala[48]. There is a strengthening of functional connectivity between cortical regions implicated in cognitive control and the basal ganglia (relative to more affective regions), altering the ratio of cognitive versus affective inputs in a region that serves as an mediator of value-based decision-making[49]. Finally, gains in special inhibitory synapses may enable bursts of neuroplasticity[10,50,51], which may function to transiently enhance learning from experience in a sensitive period (Box 1).

Mid- to late adolescence is also a period of more global refinement and stabilization for the brain. Although many of these processes start much earlier in development, mid- to late adolescence is particularly associated with slowing in the rate of thinning in the grey matter regions implicated in higher cognition[52], decline in the outgrowth of new cortical synapses[47,53], and decreases in the total density of synapses on pyramidal neurons[43,44]. Also, myelination increases[54,55] and perineuronal nets accumulate in the extracellular space around some neurons[50,56]. Together, these processes are thought to bring greater stabilization and efficiency that may enhance function but could potentially limit further change[50,56–58].
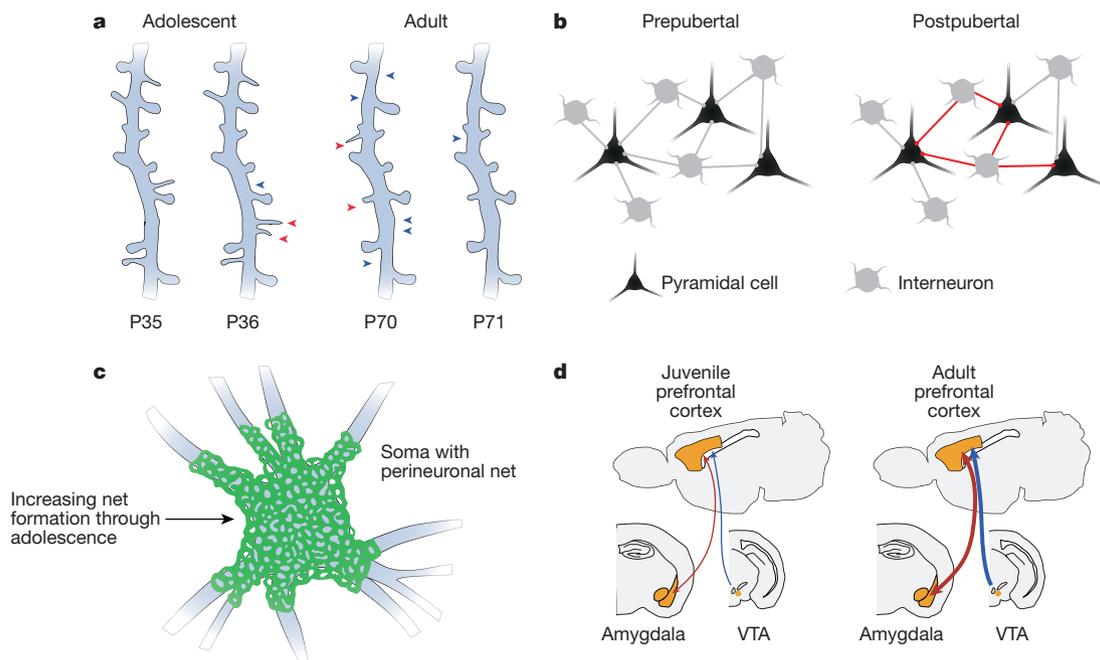
Overall, these diverse changes across brain systems in adolescence result in a series of shifts in how the brain attends to, integrates and retains information[6,59]. This means that changes in the brain during adolescence not only shape behaviour, but also learning—in ways that could have a lifelong impact. Across development, our capacity for learning does not just gradually (and monolithically) increase, but rather learning and motivation change in nonlinear ways, and can show

Changes in the adolescent brain at the level of circuits, cells and synapses.

The mammalian brain is remodelled during adolescence, particularly in associative cortical regions. Studies of human brains and animal models have shown that pruning of cortical synapses, as well as gaining of select new synapses in the neocortex, occurs during adolescence. These changes may reflect loss of juvenile forms of plasticity as well as potentially adolescent-specific sensitive periods. Whereas some of these changes have been shown to be puberty-dependent, others are thought to be puberty-independent. Shifts in pubertal timing could potentially alter the sequence and/or phase overlap of different maturational events.

In **a**, a schematic of a dendritic segment is shown at four time points, illustrating both the pruning and stabilization of spines (protrusions where synapses can form) that occur during adolescence. The first two time points are 24 h apart in early adolescence, whereas the second two are 24 h apart in early adulthood. When comparing adolescent time points to the adult time points, a decrease in spine density can be observed (lost spines are indicated by blue arrowheads). In addition, at the younger age, it has been shown that a greater fraction of the spines are lost or gained (red arrowheads) over 24 h, compared to the adult brain. These transient spines are thought to reflect the dendrite 'sampling' of the local space for potential new synaptic connections. As spine gains and losses become more infrequent, opportunities for rewiring and neuroplasticity are thought to lessen. Thus, during adolescence when dendritic spines become less dense and more stable, experience-dependent learning may be solidified, connectivity may become more efficient, and plasticity may become more limited. It remains debated whether spine changes are related to gonadal hormone effects at puberty[42,116]. In **b**, the schematic shows the increased inhibitory neurotransmission on to frontal cortical pyramidal neurons that occurs after puberty (indicated by red lines). This increase in a special form of neurotransmission has been shown to be organized by ovarian hormones at puberty in female mice[51]. The image in **b** is based on data from refs 10, 51. Changes in inhibition are thought to regulate the balance of excitation and inhibition and could initiate a transient sensitive period for plasticity[50]. A schematic of a perineuronal net surrounding the soma of a neuron is shown in **c**. Perineuronal nets increasingly form during adolescence in the neocortex[58] and amygdala[56], particularly around inhibitory neurons. These changes may limit plasticity and potentially sensitive periods across the brain[56,58] and in multiple species[57]. The schematic in **d** shows cross-sections of the rodent brain that highlight new long-range connections, which continue to form during adolescence. This is notable, because pruning of connectivity generally predominates in this phase (as in **a**). The arrows indicate increasing innervation of the prefrontal cortex by amygdala inputs[46,47] (red) and dopaminergic inputs from the ventral tegmental area (VTA)[45,69] (blue) during the adolescent transition. The schematic also shows that top-down prefrontal cortex innervation of the amygdala (red) undergoes marked growth during adolescence[48]. Human imaging studies have shown that similar prefrontal–amygdala remodelling may be occurring in human brains[117]. It has been shown that the increase in dopaminergic innervation of the prefrontal cortex, does not show sex-specific changes at pubertal milestones[118] but the role of amygdala connectivity during puberty has not been tested, to our knowledge.

a   Adolescent   Adult

P35   P36   P70   P71

b   Prepubertal   Postpubertal

Pyramidal cell   Interneuron

c   Increasing net formation through adolescence   Soma with perineuronal net

d   Juvenile prefrontal cortex   Adult prefrontal cortex

Amygdala   VTA   Amygdala   VTA

qualitative as well as quantitative shifts. If we focus on highly specific forms of learning using carefully designed tasks, we can observe that some forms of learning are 'better' (meaning more accurate or more efficient) for adolescents[60–63], whereas other forms are 'better' for adults, or children[64–66].

There is considerable complexity in the science of learning during adolescence. Nevertheless, during early to mid-adolescence, there appears to be evidence of distinctive enhancements in: (1) exploration[64], sensation seeking and sensitivity to novelty[61,67–69];

(2) learning from situations in which information needs to be integrated over time from multiple experiences with imperfect (probabilistic) feedback[60,62,68] (a process that may be especially important for acquiring social, emotional and cultural competence, which cannot be easily mastered by memorizing rules or simply reasoning one's way through complex, rapidly changing social situations);(3) learning from negative feedback or about negative associations[62,68]; and (4) learning from social information obtained from peer interactions (both positive and negative)[4,70].

In particular, processing of social information and feedback may undergo distinctive developmental changes in adolescence. Reviews have previously described adolescence as a period of 'social reorientation'[4,9,12,71], which includes increases in sensitivity to social evaluation and the importance of social status and popularity[18]. The social reorientation of adolescents is thought to be associated with changes in neural systems that are involved in the development of social cognition[72]—especially affective responses to social acceptance and social rejection[73,74]—and neural changes that are thought to enhance the motivational importance of engaging with peers[75], which may motivate behaviour and serve to enhance learning. (While acknowledging this increasing importance of peer relationships, the quality of family relationships continues to have an important influence on adolescent development and health, and provides a compelling example of bidirectional influences between social and biological development. See Box 2.)

The role of the late maturation of the prefrontal cortex in these shifts in learning is probably multifaceted, supporting not only gains in function but also weakening contributions from other systems[49,60]. The role of pubertal hormones in adolescent brain and behavioural changes is also not yet fully characterized[10], but it is likely that puberty-dependent and puberty-independent components and processes are intermingled[69]. Gonadal hormones have long been recognized to have a role in subcortical development[5], but there is also evidence that pubertal processes play a critical part in neocortical maturation[69,76–78] and shifts in learning[51].

Animal models and sensitive periods for learning

It may be informative to consider the social learning that occurs during adolescence as the product of a potential sensitive period. Over time, evolutionary influences have shaped each species' development in order to regulate the timing of different forms of learning. Sensitive periods for learning are timed to when important information is available and most useful to the adaptive development of the organism[79–81]. Humans and laboratory animals have been found to share similar early sensitive periods in sensory regions, such as in binocular visual regions for which there is a critical balance in the input from two eyes[50]. Humans also have multiple early sensitive periods for the acquisition of language[79,82]. There may be additional undiscovered sensitive periods for human cognitive, affective, and, importantly, social development that could be leveraged to enhance the impact of interventions. We can use sensitive periods for learning and social behaviour in other species as a guide. Here we focus on the biology of the sensitive periods that may be associated with puberty onset.

Human social learning during adolescence may share some parallels with sensitive periods for the acquisition of song learning in song birds. The timing of song learning in songbirds differs between species and involves imprinting on a song model (a 'tutor') through social interactions[79]. Some birds learn their song from their father and go through puberty in the first 90 days of life[79]. Others time their learning (and gonadal hormone and receptor fluctuations) to allow song plasticity during different periods[79,83,84], for example, when they arrive in a new territory and should imitate the songs of their new neighbours[79,85]. Gonadal hormones are thought to regulate the neurobiology of song learning by altering both motor flexibility and the salience of social cues. Changes in salience are thought to ensure appropriate selection of the song to be copied (that is, the correct species, time and context)[86–89] and selection of an appropriate mate[86–91].

In mammals, frontal neocortical areas, which have a critical role in higher cognition, self-regulation and social behaviours, develop late—from the time of pubertal milestones and into early adulthood[10,45–47,77]. In laboratory mice, the onset of puberty has been found to rapidly alter frontal cortex neurobiology, changing inhibitory neurotransmission mechanisms that have previously been identified as key regulators of sensitive periods in the neocortex[10,51] (see Box 1). Changes in frontal

---

BOX 2

The role of parenting in adolescent social learning, health and brain development

Despite the strong cultural belief that the importance of parental contributions wanes compared to the input of peers during adolescence, empirical research has demonstrated that parenting is a strong determinant of adolescent health and well-being during this period of life, often more so than peer processes[119,120]. Moreover, recent empirical research has suggested that parenting processes during adolescence provide a compelling example of bidirectional relationships between environmental learning and/or experiences and biological development, potentially generating cascading effects of either vulnerability or resilience. For example, individual differences in adolescent brain development are associated with adolescents' behaviour during parent–child interactions[121], suggesting that neurobiology may influence interpersonal behaviour in family contexts. However, early adolescent parent–child relationships also prospectively predict patterns of future adolescent brain development[122], and brain function has been shown to serve a mediating link between family relationships and future psychopathology[123]. Finally, the quality of the parent–child relationship during early adolescence has been shown to buffer some of the potentially deleterious effects of low socio-economic status earlier in life on adolescent brain development[124]. Family processes during early adolescence are therefore potentially influenced by, and influence, both neurobiological development and functional outcomes. Of particular note is the potential role of family relationships as modifiable aspects of developmental processes during a maturational window of dynamic change. Greater precision in understanding the specific maturational changes (such as pubertal maturational changes in social information processing, and motivational salience) could provide insights into developmental timing, targets, and processes that have critical roles in these mutually interacting developmental processes in ways that inform leverage points for adolescent-focused public policy and clinical interventions. For example, although recent meta-analytic reviews have supported the role of parental intervention in the prevention of anxiety and depression[125], effect sizes are small, and few of these approaches have been informed by an explicitly developmental science perspective on the timing and targets of these interventions.

---

cortex inhibitory neurotransmission can also be connected to changes in learning[10,92], suggesting a causal link between puberty and adolescent shifts in learning.

In rats, the adolescent period is characterized by social learning, such as rough-and-tumble play and learning about sexual encounters. Interestingly, male rats need exposure to testosterone during adolescence in order to display rapid learning from sexual experience, and do not recover this learning if testosterone is replaced in adulthood[5,93]. Thus, in rodents, as in birdsong, we can see a repeated pattern, in which developmental signals (specifically, here, involving a change in gonadal hormone signalling) may prime the brain's ability to learn during an adolescent sensitive period when (1) the information is available in the environment and (2) developmentally appropriate. When the temporal intersection of these processes is prevented, which can occur when a developing adolescent is deprived of critical learning opportunities, the trajectory towards developing the capacities that are required to take up independent adult roles can be derailed or disrupted[5,79,93].

Developmental timing, investments and interventions

If comparable sensitive period processes occur in association with pubertal maturation in humans, this could inform developmental timing and targets for interventions. For example, if pubertal hormones underpin distinct changes in social learning, leveraging these insights by designing interventions that target this window of opportunity could have large positive effects on developmental trajectories.

The sharp rise in testosterone at the onset of puberty in both boys and girls is associated with shifts in social and affective information processing[67,94–96] and increased prioritization of social-status feedback[94]. A recent review of decades of research into the behavioural effects of testosterone in animals and humans has concluded that testosterone increases 'motivation to gain social status'[97]. Consistent with this conclusion, testosterone administration can increase status-enhancing behaviours in both prosocial and antisocial ways[98]. In humans, the process of earning prestige may shape behaviour in a manner that is separate from gaining status through aggressive dominance[99]. The specific types of learning—and criteria for earning prestige—relevant to social success are highly variable. Importantly, these are not only, or even primarily, determined by our biology.

A unique feature of our species, and potentially a distinct leverage point for intervention, is the role of human culture in shaping social learning relevant to prestige and admiration. Cultural values for prestige vary widely. For example, a Tibetan Buddhist community that confers the highest prestige on kindness and compassion will create different social learning opportunities for admiration-seeking adolescents than a warrior society or a highly materialistic culture. Developmental science cannot yet fully explain how and when these values are learned and maintained at the neural level. However, there appears to be promising evidence supporting these as potential leverage points for positive change during adolescence.

When designing interventions, it is important to note that adolescents are not simply passive learners conforming to adult values. Complaints about the rebellious contempt of adolescents towards adult authority go back to the time of Socrates. Although adolescents are strongly influenced by family and cultural values, they are also naturally seeking greater autonomy and independence. Dutifully acquiring knowledge and skills from accomplished adults represents one path for gaining status and prestige. An alternative pathway is to discover novel approaches or simply an innovative twist or refinement that leads to success. These tendencies are evident today as adolescents worldwide are early adopters of expertise with new technology (as well as frequent contributions to the leading edge of the latest trends in music, fashion and innovative use of language).

From this perspective, adolescence can be considered an inflection point for pivotal changes in human development in a very broad sense. Adolescent risk taking, together with status seeking (both of which are often maligned), may actually have contributed to unique group level capacities to exploit and preserve serendipitous innovations throughout human history. An extended (adolescent) developmental period of exploratory social learning—when an individual is also highly sensitive to social evaluation and the motivational importance of earned prestige through valued contribution—could have had a critical role in humans' remarkable capacity for rapid expansion, adoption and refinement of innovation through human culture. We speculate that interventions, which support and provide social scaffolding for healthy pro-social versions of innovation and success during this sensitive window of social learning and adolescent identity development, could potentially have large positive impacts on health and education.

Policy and intervention

The developmental science of adolescence is advancing rapidly, and we have only reviewed a small proportion of the field. We have selected work that illustrates the growing understanding of adolescence as a period of critical investment opportunity because of the specific types of learning that are potentiated during this period of development. In addition to scientific advances in understanding, the enormous potential for growth and positive development, we have also focused on areas of scientific progress that are providing insights into opportunities for specific policies and interventions. The emerging evidence points towards investments that place a strong emphasis on creating mastery learning experiences that maximize social learning and enhance status and autonomy at a key time in an individual's development of social identity and competence.

Translating our understanding of developmental processes to target specific outcomes will, of course, require careful attention to contextual norms around sex, gender and culture. As an example, let us further explore how an enhanced understanding of adolescent sensitivity to social evaluation and the motivational importance of earning prestige might create a window of opportunity for positive social learning experience to address gender inequalities. Consider, for example, the harmful social learning experiences for girls coming into adolescence in a social context that admires bold, courageous behaviour in boys, but disapproves of these qualities in girls. By contrast, girls who attend schools or clubs in which prestige and admiration signals are comparable across genders could have very different social learning experiences[100]. Given that puberty in girls typically starts between 10 and 12 years of age, this may be a particularly important time to promote gender equality by providing opportunities for girls to discover, through experiential learning, that they can excel and gain admiration and prestige for their bold successes (at an age when they are also typically bigger, stronger and more socially competent than boys of the same age). A formative learning experience during this key developmental window is likely to also positively influence the well-established gender differences in rates of mental disorders, which typically emerge during adolescence and which are also likely to be related to differences in the social experiences of girls and boys during these formative periods in early adolescence[101,102].

The perspective we present on prestige learning also provides a novel approach to risk taking tendencies in adolescence—often considered the *sine qua non* of unhealthy adolescent behavioural tendencies. Research has shown that adolescents often find risk-taking behaviours reinforcing, and moreover, that such behaviours can enhance their social reputation[103,104]. Indeed, courage is a quality that is admired almost uniformly across human cultural contexts, and showing courage in ways that are aligned to cultural values is a powerful route to earning prestige. As promoted through positive youth development frameworks, having pro-social opportunities to demonstrate courage—through sports, drama, civic engagement or supporting social justice—are likely to have enhanced positive effects during this developmental period[105]. Such experiences may not only prevent antisocial and self-injurious paths, but may also promote healthy trajectories and identity development. Moreover, the tendency to take risks—especially if it creates gains in status or prestige—now affects adolescents in new ways, as they can post videos of daring acts or innovative creation online and get thousands of 'likes' from all over the world. Social media amplify the social reinforcement associated with risk-taking behaviour.

Regarding more traditional approaches to prevention and early intervention for health problems in adolescence, a previous review[106] has focused on the relative failure of many traditional behavioural interventions during adolescence, because well-intentioned efforts to instruct adolescents to make positive changes to improve their health often indirectly (or directly) imply that adolescents require adult expertise and are unable to make the right choices on their own. Interventions that honour adolescents' sensitivity to status and respect appear to more effectively capture adolescent attention and motivation and can result in improved behavioural outcomes[106]. These same developmental science-based insights have implications for education policy—especially for students aged 10–14. The importance of student-driven learning (autonomy), collaborative learning (social engagement in learning) and school and classroom climates that honour adolescent sensitivities to status, respect and purpose, are likely to have powerful positive effects on learning—particularly in this formative period[106].

Table 1 | Examples of matching intervention strategies to developmental changes during adolescence

Developmental changes	Intervention strategies
Period of rapid physical growth and increased metabolic demands	• Mitigate risk of famine and malnutrition[38] • Establish a healthy bone density through optimal calcium and vitamin D intake and exercise[40]
Increased tendency to explore, seek novelty and excitement	• Create opportunities for positive risk taking that results in healthy, positive, productive, high arousal learning[103,104] • Provide context for self-directed, discovery/exploratory learning
Pubertal changes in sleep and circadian regulation	• Couple later school start times with prevention and intervention efforts to improve and regularize sleep[113] • Provide sleep interventions to youth at increased risk for mental-health problems[114]
Motivation for status, prestige and respect	• Design health promotion and behavioural interventions in ways that honour adolescents' sensitivity to autonomy, respect and prestige[106] • Train adult teachers/facilitators to treat adolescents with respect and appropriately enhance autonomy[115]
Motivation for social learning	• Leverage social relationships to reinforce positive behaviour[94,98] • Support adolescents in processing social information and understanding social experiences • Structure learning experiences to include, rather than ignore, social context[70,72] • Enhance collaborative social learning in education settings[19]
Identity development and heartfelt goals	• Introduce positive role models and mentors who exemplify feeling-based values and inspired goals[23] • Create mastery curve learning opportunities that gradually become more challenging

Applying a developmental science perspective to strategic investment and intervention requires consideration of a number of principles. Firstly, developmental epidemiology[107] can provide information on which opportunities and/or problems arise during different life stages, and can, therefore, provide suggestions regarding appropriate, developmentally informed prevention and intervention targets. Secondly, there should be an understanding of an underlying developmental process that results in greater sensitivity to interventions at this stage of life[106,108]. Finally, the process must be modifiable though educational, clinical, public health, policy or other interventions and have protective effects. In this sense, the developmental perspective can contribute not only to precision medicine[109] and precision public health[110], but also to precision public policy, by identifying ways to target investment and intervention for maximum benefit. Bearing in mind these three principles, Table 1 presents examples of developmental processes that putatively show sensitive periods during adolescence, along with examples of developmentally informed investment and intervention strategies. These are, however, only examples of potential opportunities. Other potential targets could include substance misuse, mental health, parenting, sexual and romantic relationships, nutrition, physical activity and use of digital technologies, to name a few.

As developmental science progresses to provide a more mechanistic understanding of developmental processes, it will lead to greater precision in understanding developmental risk factors and identifying the timing, mechanistic targets and best contexts to improve adolescent trajectories. This area of research is challenging, as it requires the evaluation of the differential effects of similar learning interventions across multiple developmental phases. However, some promising examples of such studies have been published[111,112]. Ultimately, the full integration of adolescent developmental science, intervention science and public policy will require a comprehensive evidence base that thoroughly evaluates which kinds of interventions can be improved upon through optimal matching to specific developmental windows of opportunity.

Outlook

The developmental science of adolescence is providing new insights into windows of opportunity during which we can have especially strong positive impacts on trajectories of health, education, social and economic success across the lifespan. This emerging science points towards adolescence as a time of enhanced growth and a sensitive period for learning—one in which adolescents' sensitivity to belonging, feeling valued and respected and finding a way to make a valued contribution (that is, to earn prestige and admiration) is also linked to adolescents' search for meaning and larger purpose. This social and affective learning can shape the development of 'heartfelt' goals and priorities, such as those associated with experiences of inspiration,

creativity and innovation. Given current global changes, and the specific challenges affecting adolescents, there is a compelling need to understand the potential for strategic investments in adolescents to unleash this potential. From a global perspective, strategic investment of very limited resources, and the potential acceleration of economic inequalities and amplification of vulnerabilities and opportunities by the information technology revolution, makes the integration of insights from developmental science into public policy even more compelling. The stakes of investing in adolescents are rapidly increasing—especially if we are going to create sustainable growth, address climate change and reduce social inequalities—all problems that are critical for the achievement of the United Nations sustainable development goals. Strategic and developmentally informed investments in adolescents could contribute to a positive impact on the adolescents themselves, their future lives as leaders in adult society, and the next generation to whom they will be parents[7,15].

1. Shonkoff, J. P. & Garner, A. S. The lifelong effects of early childhood adversity and toxic stress. *Pediatrics* **129**, e232–e246 (2012).
2. Black, M. M. & Hurley, K. M. Investment in early childhood development. *Lancet* **384**, 1244–1245 (2014).
3. Shonkoff, J. P., Radner, J. M. & Foote, N. Expanding the evidence base to drive more productive early childhood investment. *Lancet* **389**, 14–16 (2017).
4. Crone, E. A. & Dahl, R. E. Understanding adolescence as a period of social–affective engagement and goal flexibility. *Nat. Rev. Neurosci.* **13**, 636–650 (2012).
   This review of neuroimaging data presents a model of pubertal changes in social and affective processing, and how these may support the greater flexibility in motivations and priorities needed to navigate the changing social contexts of adolescence.
5. Schulz, K. M. & Sisk, C. L. The organizing actions of adolescent gonadal steroid hormones on brain and behavioral development. *Neurosci. Biobehav. Rev.* **70**, 148–158 (2016).
   This study reviews the organizational effects of gonadal hormones on brain and behaviour, and presents a 'wedge-shaped' model of decreasing sensitivity to gonadal hormonal effects with age.
6. Lee, F. S. et al. Adolescent mental health—opportunity and obligation. *Science* **346**, 547–549 (2014).
7. Sheehan, P. et al. Building the foundations for sustainable development: a case for global investment in the capabilities of adolescents. *Lancet* **390**, 1792–1806 (2017).
   This study estimates returns for investments in adolescents in low-income, lower-middle income, and upper-middle income countries, and concludes that investments in health and education could generate high economic and social returns.
8. Patton, G. C. & Viner, R. Pubertal transitions in health. *Lancet* **369**, 1130–1139 (2007).
9. Nelson, E. E., Jarcho, J. M. & Guyer, A. E. Social re-orientation and brain development: An expanded and updated view. *Dev. Cogn. Neurosci.* **17**, 118–127 (2016).
10. Piekarski, D. J. et al. Does puberty mark a transition in sensitive periods for plasticity in the associative neocortex? *Brain Res.* **1654**, 123–144 (2017).

11. De Lorme, K., Bell, M. R. & Sisk, C. L. The teenage brain: social reorientation and the adolescent brain—the role of gonadal hormones in the male Syrian hamster. *Curr. Dir. Psychol. Sci.* **22,** 128–133 (2013).

12. van den Bos, W. Neural mechanisms of social reorientation across adolescence. *J. Neurosci.* **33,** 13581–13582 (2013).

13. Crockett, L. J. & Crouter, A. C. *Pathways through Adolescence: Individual Development in Relation to Social Contexts* (Lawrence Erlbaum, 1994).

14. Cohen, A. O. et al. When is an adolescent an adult? Assessing cognitive control in emotional and nonemotional contexts. *Psychol. Sci.* **27,** 549–562 (2016).

15. Patton, G. C. et al. Our future: a *Lancet* commission on adolescent health and wellbeing. *Lancet* **387,** 2423–2478 (2016).
    This comprehensive report describes how unprecedented global forces are shaping the health and wellbeing of the largest generation of adolescents in human history.

16. Cohen, A. O., Bonnie, R. J., Taylor-Thompson, K. & Casey, B.J. When does a juvenile become an adult: implications for law and policy. *Temp. Law Rev.* **88,** 769–788 (2015).

17. Davey, C. G., Yücel, M. & Allen, N. B. The emergence of depression in adolescence: development of the prefrontal cortex and the representation of reward. *Neurosci. Biobehav. Rev.* **32,** 1–19 (2008).

18. Blakemore, S.-J. & Mills, K. L. Is adolescence a sensitive period for sociocultural processing? *Annu. Rev. Psychol.* **65,** 187–207 (2014).
    This study describes how brain regions involved in social processing and behaviour undergo both structural changes and functional reorganization during the second decade of life, possibly reflecting a sensitive period for adapting to one's social environment.

19. Blakemore, S. J. & Choudhury, S. Development of the adolescent brain: implications for executive function and social cognition. *J. Child Psychol. Psychiatry* **47,** 296–312 (2006).

20. Dumontheil, I. Development of abstract thinking during childhood and adolescence: the role of rostrolateral prefrontal cortex. *Dev. Cogn. Neurosci.* **10,** 57–76 (2014).

21. de Water, E., Cillessen, A. H. & Scheres, A. Distinct age-related differences in temporal discounting and risk taking in adolescents and young adults. *Child Dev.* **85,** 1881–1897 (2014).

22. Gestsdottir, S., Bowers, E., von Eye, A., Napolitano, C. M. & Lerner, R. M. Intentional self regulation in middle adolescence: the emerging role of loss-based selection in positive youth development. *J. Youth Adolesc.* **39,** 764–782 (2010).

23. Schwartz, S. J. & Petrova, M. Fostering healthy identity development in adolescence. *Nat. Hum. Behav.* https://doi.org/10.1038/s41562-017-0283-2 (2018).

24. Suleiman, A. B., Galván, A., Harden, K. P. & Dahl, R. E. Becoming a sexual being: the 'elephant in the room' of adolescent brain development. *Dev. Cogn. Neurosci.* **25,** 209–220 (2017).
    This review explores the role of puberty in the social, emotional and cognitive maturation processes necessary for reproductive success, and the role of sex and romance as important developmental dimensions of health and well-being in adolescence.

25. Dahl, R. E. Adolescent brain development: a period of vulnerabilities and opportunities. Keynote address. *Ann. NY Acad. Sci.* **1021,** 1–22 (2004).

26. United Nations. *World Population Prospects, the 2012 Revision.* https://esa.un.org/unpd/wpp/ (UNDESA, 2013).

27. Bell, V., Bishop, D. V. & Przybylski, A. K. The debate over digital technology and young people. *Br. Med. J.* **351,** h3064 (2015).

28. Madden, M., Lenhart, A., Duggan, M., Cortesi, S. & Gasser, U. *Teens and Technology 2013* http://www.pewinternet.org/2013/03/13/teens-and-technology-2013/ (2016).

29. Spies Shapiro, L. A. & Margolin, G. Growing up wired: social networking sites and adolescent psychosocial development. *Clin. Child Fam. Psychol. Rev.* **17,** 1–18 (2014).

30. Smetana, J. G., Metzger, A., Gettman, D. C. & Campione-Barr, N. Disclosure and secrecy in adolescent–parent relationships. *Child Dev.* **77,** 201–217 (2006).

31. Notten, N., Peter, J., Kraaykamp, G. & Valkenburg, P. M. Research note: digital divide across borders—a cross-national study of adolescents' use of digital technologies. *Eur. Sociol. Rev.* **25,** 551–560 (2009).

32. Worthman, C. M. & Trang, K. Dynamics of body time, social time and life history at adolescence. *Nature* https://doi.org/10.1038/nature25750 (2018).

33. Palan, K. M., Gentina, E. & Muratore, l. Adolescent consumption autonomy: a cross-cultural examination. *J. Bus. Res.* **63,** 1342–1348 (2010).

34. Stuckler, D., McKee, M., Ebrahim, S. & Basu, S. Manufacturing epidemics: the role of global producers in increased consumption of unhealthy commodities including processed foods, alcohol, and tobacco. *PLoS Med.* **9,** e1001235 (2012).

35. McCarthy, K. B. M. & Hall, K. *Investing when it Counts: Reviewing the Evidence and Charting a Course of Research and Action for Very Young Adolescents* (Population Council, 2016).
    This report reviews the literature and presents a compelling case that investing in very young adolescents (ages 10–14) is important, as this is a pivotal time in the life course.

36. World Health Organization. Global Accelerated Action for the Health of Adolescents (AA-HA!): guidance to support country implementation. http://www.who.int/maternal_child_adolescent/topics/adolescence/framework-accelerated-action/en/ (WHO, 2017).

37. Akresh, R., Bhalotra, S., Leone, M. & Osili, U. O. War and stature: growing up during the Nigerian Civil War. *Am. Econ. Rev.* **102,** 273–277 (2012).

38. Holmqvist, G. & Pereira. A. Famines and stunting: Are adolescents the hardest hit? https://blogs.unicef.org/evidence-for-action/famines-and-stunting-are-adolescents-the-hardest-hit/ (Unicef, 2017).

39. Falconi, A., Gemmill, A., Dahl, R. E. & Catalano, R. Adolescent experience predicts longevity: evidence from historical epidemiology. *J. Dev. Orig. Health Dis.* **5,** 171–177 (2014).

40. Bonjour, J. P., Theintz, G., Buchs, B., Slosman, D. & Rizzoli, R. Critical years and stages of puberty for spinal and femoral bone mass accumulation during adolescence. *J. Clin. Endocrinol. Metab.* **73,** 555–563 (1991).

41. Mericq, V. et al. Long-term metabolic risk among children born premature or small for gestational age. *Nat. Rev. Endocrinol.* **13,** 50–62 (2017).

42. Drzewiecki, C. M., Willing, J. & Juraska, J. M. Synaptic number changes in the medial prefrontal cortex across adolescence in male and female rats: a role for pubertal onset. *Synapse* **70,** 361–368 (2016).

43. Petanjek, Z. et al. Extraordinary neoteny of synaptic spines in the human prefrontal cortex. *Proc. Natl Acad. Sci. USA* **108,** 13281–13286 (2011).

44. Rakic, P., Bourgeois, J. P. & Goldman-Rakic, P. S. Synaptic development of the cerebral cortex: implications for learning, memory, and mental illness. *Prog. Brain Res.* **102,** 227–243 (1994).

45. Benes, F. M., Vincent, S. L., Molloy, R. & Khan, Y. Increased interaction of dopamine-immunoreactive varicosities with GABA neurons of rat medial prefrontal cortex occurs during the postweanling period. *Synapse* **23,** 237–245 (1996).

46. Cunningham, M. G., Bhattacharyya, S. & Benes, F. M. Amygdalo-cortical sprouting continues into early adulthood: implications for the development of normal and abnormal function during adolescence. *J. Comp. Neurol.* **453,** 116–130 (2002).

47. Johnson, C. M. et al. Long-range orbitofrontal and amygdala axons show divergent patterns of maturation in the frontal cortex across adolescence. *Dev. Cogn. Neurosci.* **18,** 113–120 (2016).

48. Arruda-Carvalho, M., Wu, W. C., Cummings, K. A. & Clem, R. L. Optogenetic examination of prefrontal–amygdala synaptic development. *J. Neurosci.* **37,** 2976–2985 (2017).

49. Larsen, B., Verstynen, T. D., Yeh, F. C. & Luna, B. Developmental changes in the integration of affective and cognitive corticostriatal pathways are associated with reward-driven behavior. *Cereb. Cortex* https://doi.org/10.1093/cercor/bhx162 (2017).

50. Hensch, T. K. Critical period plasticity in local cortical circuits. *Nat. Rev. Neurosci.* **6,** 877–888 (2005).

51. Piekarski, D. J., Boivin, J. R. & Wilbrecht, L. Ovarian hormones organize the maturation of inhibitory neurotransmission in the frontal cortex at puberty onset in female mice. *Curr. Biol.* **27,** 1735–1745 (2017).
    This study provides evidence for organizational effects of ovarian hormones on the maturation of inhibitory neurotransmission in the cingulate cortex in mice, and provides experimental evidence for puberty-linked changes in learning.

52. Tamnes, C. K. et al. Development of the cerebral cortex across adolescence: a multisample study of inter-related longitudinal changes in cortical volume, surface area, and thickness. *J. Neurosci.* **37,** 3402–3412 (2017).

53. Zuo, Y., Lin, A., Chang, P. & Gan, W. B. Development of long-term dendritic spine stability in diverse regions of cerebral cortex. *Neuron* **46,** 181–189 (2005).

54. Baum, G. L. et al. Modular segregation of structural brain networks supports the development of executive function in youth. *Curr. Biol.* **27,** 1561–1572 (2017).

55. Paus, T. Growth of white matter in the adolescent brain: myelin or axon? *Brain Cogn.* **72,** 26–35 (2010).

56. Gogolla, N., Caroni, P., Lüthi, A. & Herry, C. Perineuronal nets protect fear memories from erasure. *Science* **325,** 1258–1261 (2009).

57. Balmer, T. S., Carels, V. M., Frisch, J. L. & Nick, T. A. Modulation of perineuronal nets and parvalbumin with developmental song learning. *J. Neurosci.* **29,** 12878–12885 (2009).

58. Lee, H. H. C. et al. Genetic Otx2 mis-localization delays critical period plasticity across brain regions. *Mol. Psychiatry* **22,** 680–688 (2017).

59. Guskjolen, A., Josselyn, S. A. & Frankland, P. W. Age-dependent changes in spatial memory retention and flexibility in mice. *Neurobiol. Learn. Mem.* **143,** 59–66 (2017).

60. Davidow, J. Y., Foerde, K., Galván, A. & Shohamy, D. An Upside to reward sensitivity: the hippocampus supports enhanced reinforcement learning in adolescence. *Neuron* **92,** 93–99 (2016).

61. Johnson, C. & Wilbrecht, L. Juvenile mice show greater flexibility in multiple choice reversal learning than adults. *Dev. Cogn. Neurosci.* **1,** 540–551 (2011).

62. van den Bos, W., Cohen, M. X., Kahnt, T. & Crone, E. A. Striatum–medial prefrontal cortex connectivity predicts developmental changes in reinforcement learning. *Cereb. Cortex* **22,** 1247–1255 (2012).

63. van der Schaaf, M. E., Warmerdam, E., Crone, E. A. & Cools, R. Distinct linear and non-linear trajectories of reward and punishment reversal learning during development: relevance for dopamine's role in adolescent decision making. *Dev. Cogn. Neurosci.* **1,** 578–590 (2011).

64. Gopnik, A. et al. Changes in cognitive flexibility and hypothesis search across human life history from childhood to adolescence to adulthood. *Proc. Natl Acad. Sci. USA* **114,** 7892–7899 (2017).

65. Lucas, C. G., Bridgers, S., Griffiths, T. L. & Gopnik, A. When children are better (or at least more open-minded) learners than adults: developmental differences in learning the forms of causal relationships. *Cognition* **131,** 284–299 (2014).

66. Walker, C. M., Bridgers, S. & Gopnik, A. The early emergence and puzzling decline of relational reasoning: effects of knowledge and search on inferring abstract concepts. *Cognition* **156**, 30–40 (2016).

67. Braams, B. R., van Duijvenvoorde, A. C., Peper, J. S. & Crone, E. A. Longitudinal changes in adolescent risk-taking: a comprehensive study of neural responses to rewards, pubertal development, and risk-taking behavior. *J. Neurosci.* **35**, 7226–7238 (2015).

68. Hauser, T. U., Iannaccone, R., Walitza, S., Brandeis, D. & Brem, S. Cognitive flexibility in adolescence: neural and behavioral mechanisms of reward prediction error processing in adaptive decision making during development. *Neuroimage* **104**, 347–354 (2015).

69. Walker, D. M. *et al.* Adolescence and reward: making sense of neural and behavioral changes amid the chaos. *J. Neurosci.* **37**, 10855–10866 (2017). **This study describes the role pubertal hormones have in the development of adolescent social and reward-related behaviours with a focus on sex differences, the medial prefrontal cortex, mesocorticolimbic dopamine and amygdala in rodents.**

70. Pfeifer, J. H. *et al.* Longitudinal change in the neural bases of adolescent social self-evaluations: effects of age and pubertal development. *J. Neurosci.* **33**, 7415–7419 (2013).

71. Nelson, E. E., Leibenluft, E., McClure, E. B. & Pine, D. S. The social re-orientation of adolescence: a neuroscience perspective on the process and its relation to psychopathology. *Psychol. Med.* **35**, 163–174 (2005).

72. Goddings, A. L., Burnett Heyes, S., Bird, G., Viner, R. M. & Blakemore, S. J. The relationship between puberty and social emotion processing. *Dev. Sci.* **15**, 801–811 (2012).

73. Somerville, L. H. *et al.* The medial prefrontal cortex and the emergence of self-conscious emotion in adolescence. *Psychol. Sci.* **24**, 1554–1562 (2013).

74. Stroud, L. R. *et al.* Stress response and the adolescent transition: performance versus peer rejection stressors. *Dev. Psychopathol.* **21**, 47–68 (2009).

75. Rosen, M. L. *et al.* Salience network response to changes in emotional expressions of others is heightened during early adolescence: relevance for social functioning. *Dev. Sci.* https://doi.org/10.1111/desc.12571 (2017).

76. Herting, M. M. & Sowell, E. R. Puberty and structural brain development in humans. *Front. Neuroendocrinol.* **44**, 122–137 (2017).

77. Juraska, J. M. & Willing, J. Pubertal onset as a critical transition for neural development and cognition. *Brain Res.* **1654**, 87–94 (2017).

78. Sisk, C. L. Hormone-dependent adolescent organization of socio-sexual behaviors in mammals. *Curr. Opin. Neurobiol.* **38**, 63–68 (2016).

79. Doupe, A. J. & Kuhl, P. K. Birdsong and human speech: common themes and mechanisms. *Annu. Rev. Neurosci.* **22**, 567–631 (1999).

80. Fawcett, T. W. & Frankenhuis, W. E. Adaptive explanations for sensitive windows in development. *Front. Zool.* **12**, S3 (2015).

81. Insel, T. R. & Fernald, R. D. How the brain processes social information: searching for the social brain. *Annu. Rev. Neurosci.* **27**, 697–722 (2004).

82. Werker, J. F. & Hensch, T. K. Critical periods in speech perception: new directions. *Annu. Rev. Psychol.* **66**, 173–196 (2015).

83. Alvarez-Buylla, A. & Kirn, J. R. Birth, migration, incorporation, and death of vocal control neurons in adult songbirds. *J. Neurobiol.* **33**, 585–601 (1997).

84. Kirn, J., O'Loughlin, B., Kasparian, S. & Nottebohm, F. Cell death and neuronal recruitment in the high vocal center of adult male canaries are temporally related to changes in song. *Proc. Natl Acad. Sci. USA* **91**, 7844–7848 (1994).

85. Templeton, C. N. *et al.* Immediate and long-term effects of testosterone on song plasticity and learning in juvenile song sparrows. *Behav. Processes* **90**, 254–260 (2012).

86. Bottjer, S. W. & Johnson, F. Circuits, hormones, and learning: vocal behavior in songbirds. *J. Neurobiol.* **33**, 602–618 (1997).

87. Marler, P., Peters, S., Ball, G. F., Dufty, A. M. Jr & Wingfield, J. C. The role of sex steroids in the acquisition and production of birdsong. *Nature* **336**, 770–772 (1988).

88. Marler, P., Peters, S. & Wingfield, J. Correlations between song acquisition, song production, and plasma levels of testosterone and estradiol in sparrows. *J. Neurobiol.* **18**, 531–548 (1987).

89. Remage-Healey, L., Dong, S. M., Chao, A. & Schlinger, B. A. Sex-specific, rapid neuroestrogen fluctuations and neurophysiological actions in the songbird auditory forebrain. *J. Neurophysiol.* **107**, 1621–1631 (2012).

90. Matragrano, L. L., LeBlanc, M. M., Chitrapu, A., Blanton, Z. E. & Maney, D. L. Testosterone alters genomic responses to song and monoaminergic innervation of auditory areas in a seasonally breeding songbird. *Dev. Neurobiol.* **73**, 455–468 (2013).

91. Matragrano, L. L. *et al.* Estradiol-dependent modulation of serotonergic markers in auditory areas of a seasonally breeding songbird. *Behav. Neurosci.* **126**, 110–122 (2012).

92. Cho, K. K. *et al.* Gamma rhythms link prefrontal interneuron dysfunction with cognitive inflexibility in $Dlx5/6^{+/-}$ mice. *Neuron* **85**, 1332–1343 (2015).

93. De Lorme, K. C. & Sisk, C. L. The organizational effects of pubertal testosterone on sexual proficiency in adult male Syrian hamsters. *Physiol. Behav.* **165**, 273–277 (2016).

94. Cardoos, S. L. *et al.* Social status strategy in early adolescent girls: testosterone and value-based decision making. *Psychoneuroendocrinology* **81**, 14–21 (2017).

95. Spielberg, J. M., Olino, T. M., Forbes, E. E. & Dahl, R. E. Exciting fear in adolescence: does pubertal development alter threat processing? *Dev. Cogn. Neurosci.* **8**, 86–95 (2014).

96. Tyborowska, A., Volman, I., Smeekens, S., Toni, I. & Roelofs, K. Testosterone during puberty shifts emotional control from pulvinar to anterior prefrontal cortex. *J. Neurosci.* **36**, 6156–6164 (2016).

97. Bos, P. A., Panksepp, J., Bluthé, R. M. & van Honk, J. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. *Front. Neuroendocrinol.* **33**, 17–35 (2012).

98. Dreher, J. C. *et al.* Testosterone causes both prosocial and antisocial status-enhancing behaviors in human males. *Proc. Natl Acad. Sci. USA* **113**, 11633–11638 (2016).

99. Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A. & Henrich, J. Two ways to the top: evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *J. Pers. Soc. Psychol.* **104**, 103–125 (2013).

100. Chandra-Mouli, V. *et al.* Implications of the global early adolescent study's formative research findings for action and for research. *J. Adolesc. Health* **61**, S5–S9 (2017).

101. Allen, N. B., Latham, M. D., Barrett, A., Sheeber, L. & Davis, B. in *Comprehensive Women's Mental Health* (eds Castle, D. & Abel, J.) 65–80 (Cambridge Univ. Press, 2016).

102. Avenevoli, S., Swendsen, J., He, J.-P., Burstein, M. & Merikangas, K. R. Major depression in the national comorbidity survey–adolescent supplement: prevalence, correlates, and treatment. *J. Am. Acad. Child Adolesc. Psychiatry* **54**, 37–44 (2015).

103. Maggs, J. L., Almeida, D. M. & Galambos, N. L. Risky business: the paradoxical meaning of problem behavior for young adolescents. *J. Early Adolesc.* **15**, 344–362 (1995).

104. Silbereisen, R. K. & Reitzle, M. in *Self-Regulatory Behaviour and Risk Taking: Causes and Consequences* (eds Lipsitt, L. P. & Mitnick, L. L.) 199–217 (Ablex, 1991).

105. Catalano, R. F., Hawkins, J. D., Berglund, M. L., Pollard, J. A. & Arthur, M. W. Prevention science and positive youth development: competitive or cooperative frameworks? *J. Adolesc. Health* **31**, 230–239 (2002).

106. Yeager, D. S., Dahl, R. E. & Dweck, C. S. Why interventions to influence adolescent behavior often fail but could succeed. *Perspect. Psychol. Sci.* **13**, 101–122 (2018). **This study provides a developmental perspective as to why traditional preventative school-based interventions work less well for adolescents, and reviews examples of promising approaches that take into account adolescents' enhanced desire to feel respected and be accorded status.**

107. Costello, E. J. & Angold, A. in *Developmental Psychopathology* 3rd edn (ed. Cicchetti, D.) 1–35 (John Wiley & Sons, 2016).

108. Suleiman, A. B. & Dahl, R. E. Leveraging neuroscience to inform adolescent health: The need for an innovative transdisciplinary developmental science of adolescence. *J. Adolesc. Health* **60**, 240–248 (2017).

109. Collins, F. S. & Varmus, H. A new initiative on precision medicine. *N. Engl. J. Med.* **372**, 793–795 (2015).

110. Khoury, M. J., Iademarco, M. F. & Riley, W. T. Precision public health for the era of precision medicine. *Am. J. Prev. Med.* **50**, 398–401 (2016).

111. Knoll, L. J. *et al.* A window of opportunity for cognitive training in adolescence. *Psychol. Sci.* **27**, 1620–1631 (2016).

112. Knoll, L. J., Leung, J. T., Foulkes, L. & Blakemore, S. J. Age-related differences in social influence on risk perception depend on the direction of influence. *J. Adolesc.* **60**, 53–63 (2017).

113. Minges, K. E. & Redeker, N. S. Delayed school start times and adolescent sleep: A systematic review of the experimental evidence. *Sleep Med. Rev.* **28**, 86–95 (2016).

114. Freeman, D. *et al.* The effects of improving sleep on mental health (OASIS): a randomised controlled trial with mediation analysis. *Lancet Psychiatry* **4**, 749–758 (2017).

115. Okonofua, J. A., Paunesku, D. & Walton, G. M. Brief intervention to encourage empathic discipline cuts suspension rates in half among adolescents. *Proc. Natl Acad. Sci. USA* **113**, 5221–5226 (2016).

116. Anderson, S. A., Classey, J. D., Condé, F., Lund, J. S. & Lewis, D. A. Synchronous development of pyramidal neuron dendritic spines and parvalbumin-immunoreactive chandelier neuron axon terminals in layer III of monkey prefrontal cortex. *Neuroscience* **67**, 7–22 (1995).

117. Gabard-Durnam, L. J. *et al.* The development of human amygdala functional connectivity at rest from 4 to 23 years: a cross-sectional study. *Neuroimage* **95**, 193–207 (2014).

118. Willing, J., Cortes, L. R., Brodsky, J. M., Kim, T. & Juraska, J. M. Innervation of the medial prefrontal cortex by tyrosine hydroxylase immunoreactive fibers during adolescence in male and female rats. *Dev. Psychobiol.* **59**, 583–589 (2017).

119. Morris, A. S., Criss, M. M., Silk, J. S. & Houltberg, B. J. The impact of parenting on emotion regulation during childhood and adolescence. *Child Dev. Perspect.* **11**, 233–238 (2017).

120. Schwartz, O. S., Sheeber, L. B., Dudgeon, P. & Allen, N. B. Emotion socialization within the family environment and adolescent depression. *Clin. Psychol. Rev.* **32**, 447–453 (2012).

121. Whittle, S. *et al.* Prefrontal and amygdala volumes are related to adolescents' affective behaviors during parent–adolescent interactions. *Proc. Natl Acad. Sci. USA* **105**, 3652–3657 (2008).

122. Whittle, S. *et al.* Observed measures of negative parenting predict brain development during adolescence. *PLoS ONE* **11**, e0147774 (2016).

123. Callaghan, B. L. *et al.* Amygdala resting connectivity mediates association between maternal aggression and adolescent major depression: a 7-year longitudinal study. *J. Am. Acad. Child Adolesc. Psychiatry* **56**, 983–991 (2017).

124. Whittle, S. *et al.* Role of positive parenting in the association between neighborhood social disadvantage and brain development across adolescence. *JAMA Psychiatry* **74**, 824–832 (2017).

125. Yap, M. B. *et al.* Parents in prevention: a meta-analysis of randomized controlled trials of parenting interventions to prevent internalizing problems in children from birth to age 18. *Clin. Psychol. Rev.* **50,** 138–158 (2016).
126. Richards, B. A. *et al.* Patterns across multiple memories are identified over time. *Nat. Neurosci.* **17,** 981–986 (2014).
127. Tompary, A. & Davachi, L. Consolidation Promotes the emergence of representational overlap in the hippocampus and medial prefrontal cortex. *Neuron* **96,** 228–241 (2017).