Understanding adolescence as a period of social–affective engagement and goal flexibility

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Abstract | Research has demonstrated that extensive structural and functional brain development continues throughout adolescence. A popular notion emerging from this work states that a relative immaturity in frontal cortical neural systems could explain adolescents' high rates of risk-taking, substance use and other dangerous behaviours. However, developmental neuroimaging studies do not support a simple model of frontal cortical immaturity. Rather, growing evidence points to the importance of changes in social and affective processing, which begin around the onset of puberty, as crucial to understanding these adolescent vulnerabilities. These changes in social–affective processing also may confer some adaptive advantages, such as greater flexibility in adjusting one's intrinsic motivations and goal priorities amidst changing social contexts in adolescence.

Cognitive control
A set of neurocognitive processes that are important for achieving short- and long-term goals, particularly when individuals are required to adjust their thoughts and actions adaptively in response to changing environmental demands in order to achieve their goal.

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Adolescence, which is defined as the transition phase between childhood and adulthood, is a natural time of learning and adjustment, particularly in the setting of long-term goals and personal aspirations (BOX 1). It also is a time when youths are discovering how to navigate new, often compelling, social challenges and are adjusting to myriad physical, cognitive and emotional changes within themselves[1,2]. The onset of adolescence is characterized by the start of pubertal maturation, which typically begins between 9 and 12 years of age (usually 1–2 years earlier in girls than in boys). The onset of puberty creates a cascade of hormonal changes — including dramatic increases in the secretion of adrenal androgens, gonadal steroids and growth hormone (BOX 2). This surge in hormones has a central role within a larger set of biological changes in the process of achieving reproductive maturity. These changes include: rapid physical growth; sexually dimorphic alterations in facial structure, voice and body characteristics; metabolic changes; the activation of new drives and motivations; changes in sleep and circadian regulation; and a wide array of social, behavioural and emotional changes[3].

Although the beginning of adolescence is characterized by distinct and dramatic physiological changes, the end of adolescence has less clear biological boundaries. Attaining 'adulthood' involves changes in social roles and responsibilities, is partly culturally defined and typically extends into the early twenties[4] (BOX 1). This transition to becoming an independent and responsible adult is inherently intertwined with adjustments in personal goals and motivations — for example, developing priorities related to career, identity, friends, romantic partners, family, community and religious or philosophical beliefs. This developmental transition involves greater use of cognitive control skills, such as the use of top-down effortful control to modify attention, emotion and behaviour in service of long-term 'adult' goals. However, social and affective processes also have crucial roles in these maturational changes[5,6]. An adolescent's success in pursuing long-term academic, athletic or artistic goals, for example, typically requires motivation to practice the relevant skills and a desire to persevere through difficulties, and these motivations are shaped by social experiences and are inherently intertwined with individual feelings about the value and relative priority of the goal.

There has been growing interest in understanding the neural changes that underpin these complex developmental processes. This has led to exciting scientific advances at this nexus of cognitive neuroscience, social neuroscience and developmental science. Investigations into these neuromaturational changes also hold promise for addressing some of the high-impact negative health problems that emerge in adolescence, including increased rates of accidents, alcohol and drug use, teenage pregnancies, depression and suicide, and violence[7–9].

Box 1 | **Adolescence from an anthropological perspective**

There is a commonly cited myth that adolescence was 'invented' by industrial society to extend occupational training beyond childhood. However, some of the neurobehavioural changes seen in human adolescence, such as increases in exploratory tendencies and changes in reward processing, have been observed in many non-human species as they go through puberty (BOX 4). Moreover, as documented by the anthropologists Schlegel and Barry[155] in a study of 186 pre-industrial societies, virtually every human society (including hunter-gatherers and pastoralists) recognizes an 'adolescent' period as a stage that is distinct from childhood but during which individuals are not yet fully adult in status. Thus, it is not the existence of adolescence as a developmental stage that has changed in recent history but rather the timing and length of this developmental period. That is, historically puberty occurred at relatively older ages (for example, age of menarche at 15–16 years of age) and taking on adult status typically ensued within 2–4 years. In contemporary society, puberty often occurs at much earlier ages (the mean age of menarche in the United States is 12 years and early signs of puberty typically begin by 9–11 years of age), whereas the process of achieving full adult roles is often stretched into the mid-twenties. Thus, in modern society, 'adolescence' has been stretched to span a much longer interval of development.

In addition, the social structures of adolescents have undergone major changes in recent human history, as have key aspects of developing long-term goals. In contemporary society, adolescents spend most of their time in school with same-age peers or in other structured educational and training environments, where the primary goal is to prepare the adolescent for occupations in a distant and abstract future. In pre-industrial societies, however, adolescence functioned primarily as a period of social and reproductive development[155] or apprenticing to learn directly utilitarian skills.

The relationships between these changes in the length, timing, nature and goals of adolescence and the brain changes associated with adolescence are not yet understood. For example, some aspects of adolescent development (for example, social–affective changes at puberty) occur at earlier ages, whereas other developmental milestones (for example, taking on adult roles and responsibilities in society) occur at later ages, raising the question how this differential timing of these external factors (combined with earlier activation of pubertal changes in social and affective processing) affects the development of neural systems that are involved in social and emotional regulation and the self-regulation necessary for taking on fully adult roles.

In this Review, we briefly discuss some of the prevailing views on adolescent brain development. Next, we review neuroimaging studies of cognitive control, affective processing and social processing in adolescence. In addition, we discuss the pronounced social and affective changes in adolescence, including the importance of interactions between cognitive, affective and social processing during this period of development[10,11]. Last, we suggest a re-evaluation and extension of the prevailing models of adolescent brain development. We emphasize the lack of data supporting any simple view of frontal cortical immaturity as the explanation for adolescent vulnerabilities, and consider the growing evidence for specific social–affective changes that begin during pubertal development as conferring increased vulnerabilities in some adolescent contexts. We also highlight the need for a better understanding of the neuromaturational underpinnings to these social–affective changes, including the role of pubertal development, and the potential value of investigating how these changes may contribute to unique opportunities for learning and adaptation in adolescence.

Current views of adolescent brain development

Over the past decade, our understanding of the neural mechanisms that underlie changes in cognitive, affective and social development during adolescence has increased tremendously. As will be reviewed, there has also been intense interest in applying this advancing knowledge to help inform broad societal issues, such as adolescent health, education and legal policies. Several influential models of adolescent brain development have proposed that a maturational gap between cognitive control and affective processes (including reward and threat processing) may explain adolescent increases in risks for engaging in impulsive and dangerous behaviour (for example, see REFS 2,7,8). These models tend to emphasize the relatively faster maturation of subcortical affective brain areas in comparison to more slowly maturing frontal cortical brain areas as the reason why adolescents tend to make more emotional (that is, less rational) decisions, resulting in actions that do not sufficiently weigh consideration of long-term outcomes.

Despite the appeal of these models in explaining the high rates of dangerous and impulsive behaviour in adolescents, it also is important to evaluate the degree to which the available neuroimaging data support these models. A number of research groups have begun to suggest that there has been too much emphasis on frontal cortical immaturity as the reason why adolescents engage in risky behaviour, and they have begun to point increasingly towards a more nuanced understanding of interactions across cognitive, affective and social processing[12]. There also is a growing recognition that social contexts strongly influence how these neural systems develop and how adolescents make decisions.

Neuroimaging adolescent development

Structural MRI (BOX 3) and functional MRI (fMRI) have been used to study how changes in brain structure and activity, respectively, are associated with changes in behaviour during development. In the past decade, a large number of fMRI studies have been conducted in the domains of cognitive, emotional and social development. In these studies, the typical age range of the subjects is 8–25 years, which provides a good framework for the examination of broad changes that occur during adolescence. However, as mentioned above, there is considerable variability in the ages used, many studies have gaps in the measurement of different phases of adolescence (for example, comparing only early adolescent 8–12-year-olds with adults or only comparing mid-adolescent 13–17-year-olds with adults) and most studies have only tested for linear age-related changes rather than testing for models of adolescent-specific patterns of change (for example, U-shape or inverted U-shape patterns of development). Furthermore, age-related changes provide a rough proxy for adolescent phases but do not permit examination of puberty-specific effects, and most of these studies did not include an assessment of pubertal development. Nonetheless, there is now an impressive set of fMRI studies through which to consider the developing brain and its role in adolescence-specific transitions in cognitive, affective and social processing and their interactions. Below we review and discuss these studies in the context of a meta-analysis (FIG. 1a; Supplementary information S1 (table)).

Box 2 | **Sex hormones in adolescence**

Pubertal development is associated with numerous changes in the brain, with evidence that hormone levels and neural function mutually influence each other. The single most important step in the onset of puberty occurs when the hypothalamus begins to release substantial amounts of gonadotrophin-releasing hormone (GnRH) in a pulsatile manner during sleep. This pulsing of GnRH begins the re-awakening of the hypothalamic–pituitary–gonadal (HPG) axis, which is first active during prenatal and early postnatal life (sometimes referred to as the neonatal 'mini-puberty') and then is shut down by inhibitory inputs to the hypothalamus, remaining quiescent throughout childhood. Pulses of GnRH stimulate the pituitary to produce the hormones follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which in turn stimulate the ovaries and testis to produce the sex hormones oestrogen and testosterone, respectively. The mechanisms that trigger the re-awakening of pubertal GnRH pulsing are not fully understood, but they include interactions with neural systems involved in metabolic regulation, energy storage and sleep regulation. There has been rapid progress in understanding several aspects of the process over the past decade, including the importance of the hormone leptin (a protein manufactured in fat cells that has a key role in regulating energy intake, energy expenditure and appetite) and kisspeptins (a family of neuropeptides encoded by the *KISS1* (KiSS 1 metastasis-suppressor) gene that have been identified as the conduits for the effects of leptin actions on GnRH neurons in the hypothalamus).

A second neuroendocrine axis that forms a core aspect of pubertal maturation involves increases in growth hormone (GH) secretion from the pituitary, which has a crucial role in the rapid physical growth during this period. As with the gonadal hormones, this GH increase at puberty is also sleep-dependent. A third component of puberty involves increases in the secretion of a testosterone-like hormone from the adrenal glands called dehydroepiandrosterone (DHEA) — this process is the least well understood in terms of the neural systems that initiate and regulate it.

The main hormones that regulate the bodily changes and emergence of secondary sexual characteristics of puberty are testosterone, oestradiol and DHEA. The physical sex differences that emerge at puberty are in part attributable to differences in hormone levels (for example, higher oestradiol levels in girls and greater testosterone increases in boys) but also to differences in the distribution and types of hormone receptors in target tissues.

There is relatively limited knowledge of how these hormones influence adolescent brain development and specific behavioural, cognitive and affective changes during adolescence. Several research groups have begun to focus on the role of pubertal hormones on neurobehavioural changes in adolescence, with intriguing preliminary findings[3,83]. As discussed in those reviews[3,83], addressing these questions will require both conceptual and methodological advances. Animal experiments that examine neural and behavioural changes associated with specific aspects of pubertal maturation and clinical studies that examine neural changes in response to hormone treatments (for example, the administration of oestrogen to pre-adolescent girls with Turner syndrome[156]) can provide additional insights.

Functional MRI studies of cognitive control

It is well recognized that during adolescence, there is a steady increase in the ability to use cognitive control over thoughts and actions[13,14]. Cognitive control abilities start to emerge in early childhood and gradually improve over childhood and through adolescence[15,16]. These abilities and are often seen as a driving force behind cognitive development[17], and these increases in cognitive control abilities in adolescence mark a period of significant advancements in learning and successful adaptations to a wide variety of social contexts and cultural influences. For example, the ability to exert cognitive control over thoughts and actions is of crucial importance to success in most classroom settings — not only for the direct learning of skills such as reading, maths and the capacity to reason about abstract ideas but also at the level of behavioural control that supports sitting at a desk, avoiding distractions and doing homework.

Many developmental fMRI studies have been conducted in this domain, including investigations of basic cognitive control functions and more complex cognitive control functions in which different basic functions have to be combined. Although these functions are separable in their contributions to complex behaviour[18], they rely on overlapping areas in the lateral prefrontal cortex (PFC) and parietal cortex (also see REF. 19). However, the extent to which these brain areas are activated across development differs between studies and samples, as discussed below (FIG. 1a).

Basic cognitive control functions. Many studies of basic cognitive control functions, such as working memory, inhibition and interference, and task switching, have reported that regions involved in these functions in adults (including the lateral PFC and parietal cortex) become increasingly engaged during childhood and adolescence (FIG. 1a; Supplementary information S1 (table)). For example, in spatial and verbal working memory paradigms that contrast high working memory load with low working memory load, increases in activity in the ventral and dorsolateral PFC and parietal cortex have been reported when 7–12-year-olds were compared with adults; when 7–12-year-olds were compared with mid-adolescents (13–17 years) and adults; and for linear comparisons from the age of 7 years to adulthood[20–30]. Studies using response inhibition or interference suppression tasks report an age-related increase in activation in the inferior and middle frontal gyrus in 'go' versus 'no-go' trials when children and early adolescents (7–12 years) were compared with adults; when children and early adolescents (6–12 years) were compared with mid-adolescents (13–17 years) and adults; and for linear comparisons from the age of 7 years to adulthood[31–36]. In addition, several task switching studies have reported increased activation in the lateral PFC and parietal cortex in adults relative to children (ages 7–12 years) and adults versus mid-adolescents (ages 10–17 years or 13–18 years) in 'switch' versus 'repeat' trials[37–39]. These findings have been interpreted as indicating that areas of the PFC have a slow developmental trajectory and are

Box 3 | **Structural brain development in adolescence**

Numerous structural neuroimaging studies have demonstrated that adolescent development involves widespread changes in the brain. Longitudinal research examining changes in brain structure over time has shown that cortical white matter throughout the brain increases with age throughout childhood and adolescence. By contrast, cortical grey matter, which reflects neuronal density and the number of connections between neurons, follows an inverted-U shape over development, peaking at different ages depending on the region[157–159]. Within the cortex, grey matter reduction is most protracted for the dorsolateral prefrontal cortex and the temporoparietal junction; here, cortical grey matter loss continues until the early twenties[159,160]. The development of subcortical brain regions is also subject to both linear and nonlinear changes, such that some subcortical regions (such as the caudate and the putamen) linearly decrease in size throughout adolescence, whereas other subcortical regions (such as the amygdala and the hippocampus) show an increase in size at the onset of puberty, after which growth stabilizes in adolescence and adulthood[161]. These dynamics of structural brain development have been summarized in several excellent reviews (for example, see REF. 160).

not engaged to the same extent in children and adolescents as in adults[40].

However, many studies of the same basic cognitive control functions have found age-related decreases in frontal cortical activity in early adolescents compared with children and adults, mainly in the superior part of the lateral and medial PFC (FIG. 1a; Supplementary information S1 (table)). These decreases were found for different domains of working memory (in studies comparing ages 6–12 years, 13–17 years and adults)[41–43], for response inhibition (in studies comparing ages 6–12 years versus adults)[32,44–48] and in task switching (in studies comparing ages 8–13 years versus adults)[49,50]. These findings have been interpreted as indicating increased efficiency of these networks over time. However, it is difficult to confirm this interpretation because these decreases in activation are not always accompanied by performance differences.

Thus, although the parietal cortex seems to show a relatively consistent pattern of increased activation in cognitive control tasks with increasing age (except for one study that showed a decrease with increasing age[22]), studies of lateral and medial PFC show both increases and decreases in activation, depending on the task paradigm and the PFC subregion involved in the task (FIG. 1a). Moreover, mid-adolescence-specific increases (for ages 13–17 years relative to both 6–12 years and adults) have been reported for regions in the lateral PFC in working memory, inhibition and task switching tasks[39,41,47,51,52] (FIG. 1a; Supplementary information S1 (table)); such an inverted U-shaped relationship between age and activation could be due to increases in task engagement in adolescents compared to children and adults.

Taken together, it is difficult to reconcile how this degree of variability in neuroimaging findings in the development of basic cognitive control functions provides support for the model of 'frontal cortical immaturity' or the concept of 'linear advances in PFC development' across adolescence. Indeed, if such varied findings of increases or decreases in activation can be interpreted as consistent with the concept of frontal cortical immaturity, this would seem to render the model as virtually unfalsifiable. Our meta-analysis suggests that such a simple model of increased activation in the PFC is unlikely to account for the developmental transitions in basic cognitive control that take place during adolescence[53,54].

Complex cognitive control functions. Several recent studies have used approaches that involve more complex cognitive control tasks, such as performance monitoring, feedback learning and relational reasoning, which require a combination of basic cognitive control functions[18]. This approach can detect strategy differences between people in a particular task. These studies have revealed interesting developmental trajectories of PFC activation (Supplementary information S1 (table)). For example, performance monitoring studies (that is, studies involving error and feedback processing) that included early adolescent (ages 8–12 years), mid-adolescent (ages 13–17 years) and adult age groups did not confirm the strict frontal cortical immaturity view[55–59]. Instead, these studies report that the frontal cortical network was engaged to the same extent in participants of different age groups but under different experimental conditions. Specifically, in early adolescents, the PFC and parietal cortex were activated following positive performance feedback, whereas in adults, the same regions were activated to the same extent following negative feedback, with mid-adolescents showing a transition phase[57,58]. A similar nonlinear pattern was found in a relational reasoning task[60] in early adolescents, mid-adolescents and young adults (ages 11–30 years). When subjects were asked to combine and integrate different spatial dimensions (that is, relational integration), only mid-adolescents (14–18 years) showed increased activation in the anterior PFC. The authors interpreted this as reflecting a mid-adolescence-specific cognitive strategy to perform the task in an efficient way (see REFS 61–63 for other examples of relational reasoning studies). Indeed, the increased activation in mid-adolescence was associated with faster reaction times and increased accuracy. However, the exact relation between neural activation, task performance and strategy use is not well understood at this time.

Flexibility for recruiting cognitive control systems? The question then arises: what is the general pattern that emerges from fMRI studies on cognitive control? The data discussed so far provide evidence against the view that these brain regions simply come increasingly 'online' with advancing age through adolescence. Instead, the high degree of variability in the findings could reflect a less automatic and more flexible cognitive control system in adolescence. It is possible that the degree to which cognitive control processes are engaged or activated in adolescence are strongly influenced by the motivational salience of the context. Factors such as the presence of peers, task instructions, strategies and the affective appraisal of the value or priority of performing the task may have relatively large influences on the extent to which cognitive control systems are recruited in adolescence[53]. As will be discussed in later sections, there is growing recognition that social and affective factors are particularly important in influencing aspects of adolescent engagement. The ability to quickly shift priorities,

Relational reasoning
An essential component of fluid intelligence that requires a number of verbal or spatial dimensions to be considered simultaneously to reach a correct solution.

adjusting the degree of cortical activation in a given task or situation according to the social and motivational context could contribute to greater variability in cognitive control. However, this flexibility in making quick adjustments in the degree of engagement across changing contexts may be crucial to the ability of youths to learn about and adapt to rapidly changing adolescent social contexts. For example, adolescents are often the fast-adopters of social change — such as learning new trends in language, technology, music and fashion or when adapting to new cultures after immigration[64].

Interestingly, two longitudinal studies that followed adolescents (ages 8–23 years and 15–18 years) over a period of 3 years reported no age-related changes in activation in the frontoparietal network in a feedback-learning and working memory paradigm. Instead, changes in task performance in the same person measured at different ages correlated with changes in activation in the lateral PFC[65,66]. Furthermore, in a working memory training study, young adolescents (ages 11–13 years) showed increased activation in the lateral PFC after 6 weeks of practice, whereas before training these adolescents showed less activation in the lateral PFC compared to adults before training[67]. These findings support the idea that frontal cortical brain regions in adolescence are sensitive to context and that their activity can be enhanced by training. The training study[67] indicates that this flexibility of the frontal cortical network may be greater in adolescence than in adulthood, although further studies are needed to confirm these findings.

This proposed flexibility in frontal cortical networks in adolescence is further supported by studies on functional connectivity in the absence of a behavioural task (that is, resting state analyses). These studies have demonstrated that the main circuitry for cognitive control is already in place at the start of adolescence[68], but the strength of connectivity within this circuitry continues to undergo maturational changes across adolescence. For example, there is a tendency for short-range connections to become weaker with age, whereas long-range connections, which are important for integration across circuits, become stronger with age[69]. The authors of this study interpreted their findings as consistent with a model of developing tighter 'integration' of some regions into long-range networks over time, while segregating the short-range connections between other sets of regions into separate networks. Because the long-range connectivity patterns are still undergoing maturational strengthening, it is likely that some aspects of integrative cognitive control may be less automatic and more flexible during adolescence. As a result of weaker connectivity across these long-range integrating circuits, adolescents may be more vulnerable to variability in performance under high demands on attentional and decision-making networks in some situations (because the ability to integrate control is less automatic); however, these same qualities (less automatic responses) may also enable adolescents to respond in creative and adaptive ways. Most importantly, however, these findings suggest that adolescence is a crucial time of development during which specific learning (or training) experiences may actively sculpt final connectivity patterns in some of these long-range cognitive control networks (see REF. 70 for a training study on functional connectivity in adults supporting the view of adaptive change in the frontal cortical circuitry).

Taken together, findings from the few existing longitudinal and training studies (which are more powerful in detecting the trajectories of brain change than the more usual cross-sectional studies comparing individuals of different ages) highlight the complexities of disentangling specific developmental changes during adolescence. An important goal for future research will be to parse the developmental changes in brain activation that reflect four relatively different processes that could influence cognitive performance in adolescents: maturational changes in the fundamental capacity to perform a task; other task-relevant factors, such as degree of engagement, motivation and sensitivity to social and affective context; changes that reflect the direct effects of training; and developmental changes in the capacity for learning and training. As reviewed below, it appears that task performance (and perhaps some developmental learning effects) in adolescents may be particularly sensitive to social and affective influences.

Functional MRI studies of affective processing

Neural systems that underpin affective processing can be conceptualized not only as systems involved in emotions and motivation but also, more broadly, as a network of 'valuing' systems that are involved in learning about rewards and threats and in regulating 'approach' and 'avoidance' behaviours accordingly. During adolescent development, the most salient types of rewards and threats typically reside in the social domain (for example, being admired, accepted or rejected by peers and early romantic and sexual experiences). Accordingly, it is important to recognize the inherent overlap between affective and social processing in adolescence. However, to date, most studies in this area have focused on monetary rewards to examine how the ventral striatum, which is a subcortical brain region that is active when a person receives or expects a reward[71], responds to risks and rewards in adolescents compared to adults (FIG. 1b; Supplementary information S1 (table)).

Box 4 | **Animal research on puberty-specific changes in reward processing**

There is compelling evidence from animal models showing that changes in gonadal hormone levels in puberty induce a (second) organizational period to guide the remodelling of the adolescent brain in sex-specific ways[162,163]. Rodent studies have also shown a remodelling of the dopaminergic systems involved in reward and incentive processing in the peri-adolescent period. This remodelling involves an initial rise in dopamine receptor density, starting in pre-adolescence, and a subsequent reduction of dopamine receptor density in the striatum and prefrontal cortex[163] — a pattern that is more pronounced in males than females[163]. As a result, dopaminergic activity increases substantially in early adolescence and is higher during this period than earlier or later in development[163]. The developmental changes in reward processing in animals in these studies are similar to those emerging from the human functional MRI literature. Given the important role of dopamine in reward processing, the developmental changes in dopamine receptor levels may be linked to the increase in novelty seeking, exploratory behaviour and reward-seeking behaviour at puberty[164,165]. Thus, translational research focusing on the mechanisms that underpin pubertal changes in reward responses may provide important insights into human adolescent behaviour.

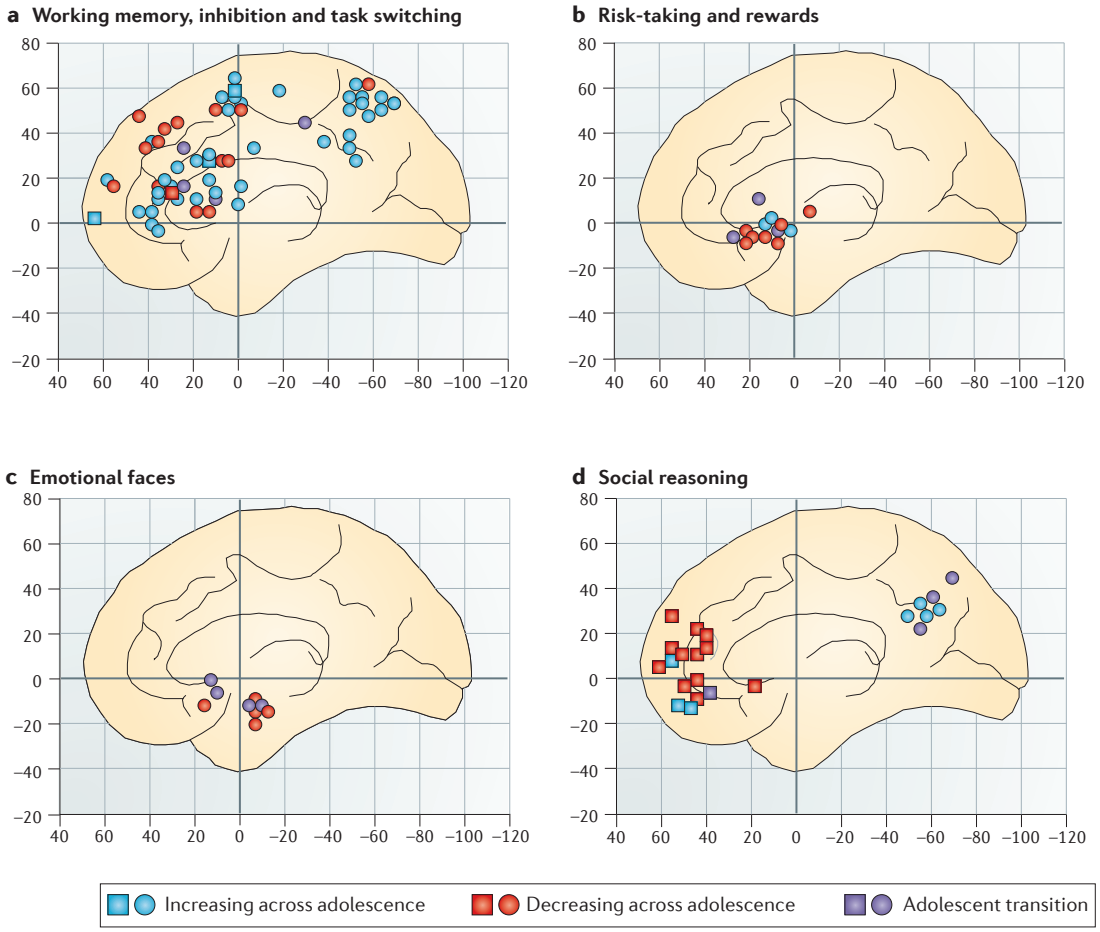

Figure 1 | **Meta-analysis of functional MRI studies in adolescents.** Results from a meta-analysis of a representative set of functional MRI studies, which were conducted between 2001 and 2011, of cognitive, affective and social processing in adolescents compared to other age groups. **a** | Frontoparietal and anterior cingulate cortex activation in working memory[20–30,41–43,52,65,167], inhibition[31–36,44–48,168] and interference suppression and task switching studies[35,37–39,49,50,78]. **b** | Striatum activation in reward processing studies[72–82,169]. **c** | Amygdala and striatum activation for face processing studies[89–94,96,100,170]. **d** | Anterior medial prefrontal cortex and temporoparietal junction activation in social–cognitive reasoning studies[107–113,115,116,127,128,130,171,172]. For illustrative purposes and for reasons of comparability, a slice of the mid-brain is shown ((x = 0), Montreal Neurological Institute coordinates) but the activations are displayed as circles when activation was in ventral and dorsolateral prefrontal cortex (x > +/– 20) or in superior frontal sulcus–frontal eye fields and parietal cortex (x > +/– 20), and as squares when activation was in the medial prefrontal cortex (x < +/– 20). The findings of the reviewed studies are summarized as 'increasing across adolescence' (light blue squares and circles), which indicates that the specific region is more engaged with increasing age; 'decreasing across adolescence' (red squares and circles), which indicates that the specific region is less engaged with increasing age; and 'adolescent transition' (purple squares and circles), which indicates that mid-adolescents process information differently from both children and adults. It should be noted that: first, the increases and decreases were dependent on the contrast used and therefore should be interpreted in this context (see REF. 173) and, second, not all studies used more than two age groups — a design that does not allow for an examination of transitions. Supplementary information S1 (table) provides an overview of all studies that were included in the meta-analysis, including the age range and sample size for each age group.

When receiving rewards, adolescents (ages 12–17 years) consistently show increased striatal activation relative to children (ages 7–12 years) and adults[72–80]. By contrast, adolescents tend to show less activation in the striatum than adults during reward expectation or anticipation (that is, when participants observe a cue that indicates a potential reward)[76,81,82]. The differential response to cues (reward anticipation) and actual receipt of rewards in adolescents may help to explain some of the inconsistencies with regard to ventral striatum activity in adolescents[83]. For example, the finding that underactivation (or no change) in ventral striatum activity is found during reward anticipation in adolescents may help to explain why some studies show no differences between adolescents and adults in risk-taking behaviour, despite pronounced neural differences during reward processing[73,84–86].

One way in which reward processing may influence decision-making is through the prediction error. Reward prediction error signals reflect the difference between the expected value of an action and the actual outcome of the action, and are encoded by phasic

activity in the mesolimbic dopamine system (including the ventral striatum). These prediction error signals appear to have a crucial role in the process of learning and adjusting behaviour to adapt to changing contexts or conditions. The first developmental study[56] of prediction error signals in children, adolescents and adults found that prediction error signals in the striatum were highest in adolescents, whereas decision-value signals in the medial PFC did not show a consistent developmental pattern. Results of a second developmental study of reinforcement learning did not implicate the prediction error signal directly but pointed to the connectivity between the ventral striatum and medial PFC as the source of developmental differences in how learning signals guide adolescent behaviour[87]. Interestingly, recent evidence has demonstrated that value-based decision processes are based on neural computations that use the subjective value of the expected reward[88], again implicating interactions between reward prediction at the level of the ventral striatum and higher-level, cortical processing of 'valuing', which is likely to incorporate more subjective aspects of valuing, such as the social or affective context. Taken together, these findings point to a promising line of investigation into the mechanisms by which subcortical value-based inputs may interact with cortical value-based inputs to signal motivational salience.

In addition to these studies of reward processing, a number of investigations have examined developmental changes in the response to threat stimuli. For example, increased activity in subcortical brain regions has been observed in adolescents in response to emotional faces (FIG. 1c). Several studies have reported enhanced activity in the amygdala, a region of the brain that is important for the processing of negative affect, in mid-adolescents (ages 12–18 years) compared with adults when looking at pictures of fearful faces[89–94] (see REFS 95–99 for studies that focused on other brain regions or younger children). Pictures displaying positive emotional (for example, happy) faces induced more activation in adolescents relative to adults in the ventral striatum — the area that is also more active in response to receiving rewards in mid-adolescents relative to adults[94,100]. Thus, it appears that mid-adolescence is associated with a more general intensification of affective processing, not only in the approach — or positive affect — domains (such as rewards and happy faces) but also for stimuli that may signal threat and avoidance (that is, fearful faces).

Together, these findings suggest that the neurodevelopmental changes in affective processing in approach and avoidance follow nonlinear developmental patterns, with a peak in subcortical brain activation in mid-adolescence. This pattern may underlie part of the intensification of emotional and motivational experiences in mid-adolescence, and this intensification of affect may create new challenges to emotional regulation and self-control[101]. Moreover, the increased activity in 'valuing' systems in adolescence may reflect a sensitive period for learning about sources of reward and threat, particularly in social domains.

Social–cognitive development
Changes in cognitive skills and knowledge that facilitate understanding social situations, such as mentalizing and perspective-taking abilities.

Social–affective development
Changes in motivational and emotional aspects of social processing (such as empathy, increases in the salience of obtaining status, admiration and affiliation from peers) and the development of affective skills that support social competence.

Mentalizing
The ability to infer mental states of others, such as one's intentions, beliefs and desires — a key dimension of social–cognitive development in adolescence.

Functional MRI studies of social development

The fundamental maturational task of adolescence is achieving adult social competence — that is, developing the knowledge and skills to be capable of functioning independently from parents or other responsible adults. Adolescents appear to be naturally motivated to want greater independence from their parents and to establish their individuality[102]. Adolescents are drawn to build and explore new social networks (that is, peer groups) and to increase prioritization around peer issues of belonging, acceptance and interests in romantic and sexual partners. Achieving success in these domains requires new social skills, social knowledge, affect regulation, adaptive coping skills and, in general, improved social competence[103].

There has been recent progress in understanding neural systems relevant to two dimensions of social development in adolescence: social–cognitive development, which concerns the knowledge and capacity to understand social situations, and social–affective development, which concerns the motivational and emotional aspects of social skills.

Social–cognitive development. There has been considerable progress in understanding the development of neural systems that underlie social–cognitive skills such as mentalizing[104]. Basic social detection and theory-of-mind develop in early childhood, whereas more complex social–cognitive skills, such as mentalizing and metacognition, mainly develop in adolescence. The development of complex social–cognitive skills is probably driven partly by environmental demands and experiences, such as the greater need to adapt to the peer group and newly emerging romantic interests. Such social–cognitive skills become increasingly important as adolescents learn to adapt to rapidly changing social environments, in which the opinions and evaluations of peers become increasingly salient.

Recently, researchers have identified a 'social brain network' — a network of brain regions, including the medial PFC and temporoparietal junction (TPJ) — that is important for mentalizing and perspective-taking[105] and that undergoes structural and functional changes during development[106]. Studies using mentalizing and social interaction paradigms have shown that specific regions in the social brain network contribute to the development of intention understanding in social reasoning in children and adolescents (see REF. 106 for a review). As highlighted in our meta-analysis (FIG. 1d), studies using social reasoning paradigms[107–114] and self-knowledge paradigms[115,116] have shown that the medial PFC is often more activated in adolescents (ages 9–18 years) compared to adults[106], whereas the TPJ is often less activated in adolescents (ages 10–17 years) compared to adults[106].

One of the main changes in the nature of social interactions in adolescence is the shift from self-oriented behaviour towards other-oriented (that is, pro-social) behaviour[117]. These changes enable the formation of more complex social relationships and are particularly important for functioning in peer groups — adolescents have a stronger motivation for peer acceptance compared with children and adults[118]. Social interaction paradigms

can be used to investigate neural activity associated with self-oriented thoughts and other-oriented thoughts and actions. Inspired by classic social utility models of decision-making, social psychologists have developed experimental 'games' in which two-person interactions are investigated in a laboratory setting. According to social utility models, social behaviour is generally motivated by self-gain and by concern for others[105]. The latter is essential for other-oriented behaviour and requires the ability to consider other people's feelings, thoughts, intentions and actions, therefore drawing heavily on theory-of-mind (that is, perspective-taking) abilities. Comparison of self-gain and other-gain is involved in social judgements of fairness and reciprocity, which in turn have important roles in the display of other-oriented behaviour. Therefore, these games provide a valid experimental context for studying these important aspects in the development of self- and other-oriented processes[105].

Two of the most commonly used games to study social decision-making in adults are the Ultimatum Game[119] (FIG. 2) and the Trust Game[120]. These games have proven to be highly useful for studying developmental differences in self- versus other-oriented thoughts[105]. Studies using these games have found that self-oriented thoughts decrease and other-oriented thoughts increase with age, with a transition phase around mid-adolescence (ages 12–16 years) during which other-oriented thoughts become more dominant than self-oriented thoughts. In addition, these studies showed that children and early adolescents (ages 9–12 years) have less understanding of other people's intentions when making or judging decisions and, with age, increasingly take the perspective of others into account[121–123]. A meta-analysis demonstrated that these games activate brain regions that are implicated in the different value computations of social interaction, such as the valuing of self-gain versus gains for others[124]. That is, the brain regions that are involved in social cognition (anterior medial PFC, TPJ and insula) are involved in judging fairness and in reciprocating trust, and activity in these regions depends on perspective-taking demands[125,126].

Age comparisons using these games have demonstrated that with increasing age, adolescents are increasingly responsive to the perspective of another player. Concurrent with this behavioural change, there was a gradual increase in activation in the TPJ (and the dorsolateral PFC) and a gradual decrease in activation in the anterior medial PFC across adolescence[123,127,128]. The increase in TPJ activation correlated with the perspective-taking behaviour, independently of age, confirming the role of this area in perspective-taking[128]. The overactivation in the anterior medial PFC and underactivation in the TPJ in adolescents relative to adults mentioned above could be interpreted as underlying the decrease in self-oriented thoughts and actions and the increase in other-oriented thoughts and actions, respectively, that occur across adolescent development.

It is important to recognize that some of these developmental changes in fairness and reciprocity appear to reflect changes in explicit social knowledge and understanding; however, some of these changes may involve implicit learning processes and rely on the development of social–affective skills. Indeed, considerations of self and other's outcomes appear to be influenced by the social environment of adolescents. For example, there is evidence that popular adolescents (that is, those frequently liked and seldom disliked by peers) generally help, share and cooperate with peers and score highly on measures of empathy and perspective-taking[129].

Social–affective development. There is growing understanding of the neural systems that underlie aspects of social–affective development in adolescence. For example, studies on empathy[130] and social acceptance and rejection[131–134] have reported differences in brain activity between children, adolescents and adults in brain areas involved in processing affect and social pain, including the temporal pole and the insula (Supplementary information S1 (table)).

One study[131] that examined, in different age groups (ages 8-10 years, 12–14 years, 16–17 years and adults), neural activation in response to social acceptance and rejection from peers found increased activation in the ventral anterior cingulate cortex (ACC) and striatum in each age group when a participant received feedback that a peer liked them compared to feedback indicating that a peer did not like them. This is consistent with the idea that social acceptance is salient across these age groups and continues to be salient in adulthood. Social rejection was associated with activation of the insula and dorsal ACC in all age groups, but only adults showed additional recruitment of the dorsolateral PFC, which may indicate a better capacity to regulate rejection, although this was not tested using behavioural measures. In a study using the Cyberball game to elicit feelings of rejection, early adolescents (ages 10–12 years) showed more activation in the subgenual ACC during rejection than adults[135]. Activity in this region was associated with greater rejection-related distress in youths in a different Cyberball study[136]. Activity in the insula (which was also associated with greater rejection-related distress)[136] was reduced in individuals who have many friends in daily life (in the 2 years before the fMRI scan)[137], suggesting that young adolescents who had developed strong friendship networks were less sensitive to social rejection. Finally, this same research group also showed that increased subgenual ACC and medial PFC activity to social exclusion in the 12–13-year-olds predicted increased depressive symptoms in the year following the Cyberball study[138].

Taken together, these findings show promising approaches to investigating the development of social–affective processing in adolescence; however, they also raise a number of questions. One particularly thorny set of issues focuses on questions about the direction of effects. For example, some changes in neural activation in response to social and affective stimuli may depend on new patterns of social learning and experience in adolescence (such as greater reaction to social rejection secondary to affective learning that is simply more likely to occur during this period of development). By contrast, changes in the neural systems that underpin the motivational

Self-oriented thoughts
Concern for outcomes that benefit one's own gains, such as in economic exchange when benefits for self and benefits for others are often conflicting.

Other-oriented thoughts
Concern for outcomes that benefit others, even when this is at the expense of gains for self, such as when evaluating what is fair for two parties.

Trust Game
Two-person interaction game that requires perspective-taking and relies on feelings of fairness and concern for others.

salience of peer rejection may undergo maturational changes that render the systems biologically more reactive. It also seems likely that bidirectional effects could occur (maturational changes that fundamentally alter the motivational salience or reactivity that also interact with learning experiences that are more likely to occur in adolescence). Such bidirectional interactions could contribute to spiralling effects over time, such as sensitivity to rejection and a pattern of negative experiences leading to the development of depression in adolescence. Studies of high-risk and clinical samples followed over time will be needed to test these hypotheses.

There is also a need to focus on the specific role of puberty as a neurodevelopmental mechanism that may contribute to the increase in motivational salience of social learning relevant to depression. For example, there is evidence that the increased risk for depression in adolescence is linked to the increase in gonadal hormone levels[139]. Given the finding that neural activity during social rejection at ages 12–13 years predicted later depression, this suggests that pubertal hormones may influence social–affective development, perhaps by increasing the affective salience (and vulnerability to long-term consequences) of social rejection.

Puberty and social–affective changes

There is growing evidence that some of the social and affective changes that occur in adolescence are linked

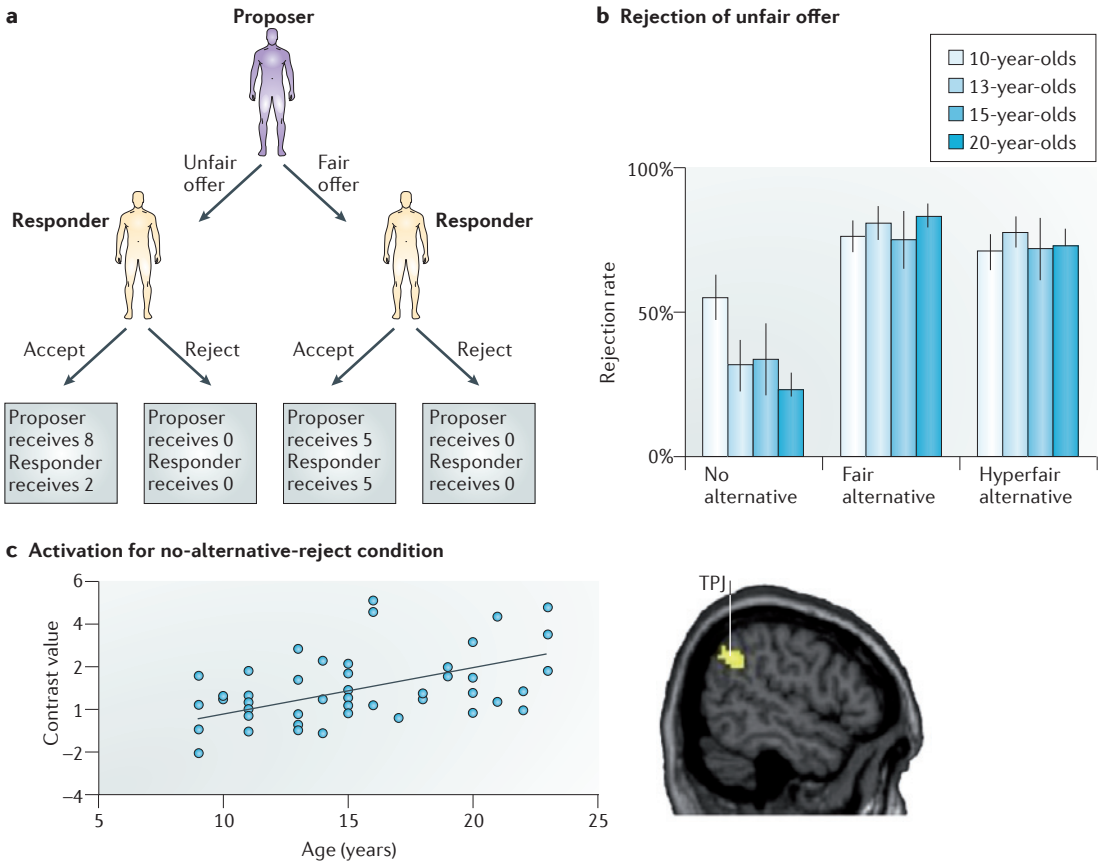

Figure 2 | **Interactive decision-making paradigms to examine social reasoning.** **a** | An example of the Ultimatum Game (UG) — a two-person interaction game that requires perspective-taking and relies on feelings of fairness. The game involves a proposer and a responder. The proposer can divide a fixed amount of money between the two players, and the responder decides whether to accept or reject the offer. When the offer is accepted, both players receive the stake according to the offer. When the responder rejects the offer, both players receive nothing. **b** | To vary perspective-taking demands on the responder, studies have made use of the mini-UG, in which the proposer is given two money-dividing options by the computer. One option is always an unfair division (8 for proposer, 2 for responder), and depending on the experimental condition, the second option can be unfair as well ('no alternative for proposer condition'), a fair split ('fair alternative condition') or a split that gives the advantage to the responder ('hyperfair alternative condition'). Results from behavioural tests show that in the mini-UG, responders take into consideration the options that the proposer had[121,127]. That is, unfair offers are mostly rejected when the alternative was fair or hyperfair but are more often accepted when the alternative was also unfair (in other words, the proposer could not help it but was restricted by the offers from the computer). Developmental studies have shown that in the no-alternative condition, which relies most on perspective-taking skills of the responder, there was an age-related decrease in rejection, indicating that the ability to understand the perspective of the first player increases with age. **c** | This increase was accompanied by increased activation in the temporoparietal junction (TPJ)[127].

to the onset of puberty[1–3,83,140]. Studies have focused on the role of the onset of puberty in the social re-orientation towards peers[10], in changes in neural processing of reward[141] and as shifting the balance of affective processing (with relatively more reward versus threat processing) interacting with cognitive control[2,101] in adolescents. Despite considerable evidence that puberty is linked to the increases in sensation-seeking and some aspects of risk-taking that occur in adolescence[3,9,83], there is little understanding of the specific hormonal changes that influence the development of those neural systems involved in motivational or emotional tendencies towards sensation-seeking behaviour. More generally, relatively few studies have investigated the role of puberty versus the role of age per se or the role of specific hormones in these behavioural changes.

We believe there are several reasons why it is important to investigate the role of hormonal changes in puberty at the interface between social and affective processing. For example, there is growing evidence that increases in risk-taking in adolescence emerge after the increase in sensation-seeking associated with puberty and occur primarily in affective salient social contexts. That is, adolescents show greater risk-taking than adults or children primarily when they are with peers (or believe they are being observed by peers), and such 'peer' effects are evident in both real-life and laboratory studies of risk-taking[77,142]. Greater risk-taking in adolescence has also been reported in emotionally charged (or 'hot') situations, but no adolescent increases in risk-taking occur in low-affect (or 'cool') contexts in the same experimental task[143]. On the basis of these and other findings (as discussed below), we propose that changes in gonadal hormone levels at puberty contribute to adolescent risk-taking through two interacting effects, namely by increasing the motivational salience of acquiring social status and by increasing the tendency to seek novel and high-intensity affective experiences — particularly in social contexts that create opportunities to gain peer admiration.

Moving forward: new heuristic models

On the basis of the findings reviewed above, we highlight what we regard as two important challenges facing the field regarding the prevailing models of adolescent brain development. First, the prevailing models are typically used to address broad issues of clinical relevance and social policy in ways that emphasize frontal cortical immaturity (or a maturational 'gap' in cognitive control) to explain the emergence of risky, impulsive and dangerous behaviours in adolescents. As described above, neuroimaging studies in adolescents do not support these aspects of the prevailing models. Rather, the data point to an adolescent flexibility in cognitive engagement, depending on the social and motivational context. The exciting challenge is to better understand how these incentives exert such strong influences on adolescents' engagement, decisions and behaviour — not only in ways that create vulnerabilities towards unhealthy incentives but also in ways that create unique opportunities for learning, adaptation and positive motivations relevant to health, education and social development in adolescence.

Second, the prevailing models are based on cognitive neuroscience studies that have relied primarily on cross-sectional comparisons between samples of 'adolescents' and 'children' and/or 'adults', and these groups have typically been defined by widely varying age ranges across different studies and laboratories. As a result, the current understanding of the maturational processes that underlie adolescent development is limited. One important example is the need to better understand the role of pubertal maturation on specific neurodevelopmental processes. We believe that this challenge will entail addressing not only methodological issues (for example, conducting studies designed to disentangle age and pubertal effects) but also conceptual issues (for example, refining models to address the role of specific hormones on specific aspects of social and affective development).

Below, we offer suggestions on how these challenges can be tackled and present a model of adolescent brain development that includes a focus on the role of puberty (FIG. 3). Our model proposes that the combination of flexibility in PFC recruitment and changes in social–affective processing can create vulnerabilities to engaging in negative behaviours in some incentive situations but is generally adaptive and developmentally appropriate to the tasks and learning demands of adolescence. There are two key aspects to this model. The first focuses on social–affective engagement and goal flexibility; and the second focuses on the role of pubertal hormones in social–affective engagement.

Social–affective engagement and goal flexibility. As described above, there is growing evidence that adolescence is a developmental period during which the degree of cognitive engagement is relatively flexible, depending on the social and motivational salience of a goal. This flexibility (and sensitivity to social and affective influences) may confer greater vulnerabilities for adolescents to act in ways that appear impulsive and immature, such as placing greater motivational value on gaining peer admiration for a daring action than considering the risks and long-term health consequences of that behaviour. However, this capacity to quickly shift goal priorities may also enable adolescents to effectively engage cognitive systems in situations in which they are highly motivated to do so and in ways that facilitate learning, problem-solving and the use of divergent creative abilities[144]. Indeed, emerging evidence from animal studies supports the idea that juveniles can outperform adults in some complex cognitive tasks (BOX 5).

Our model also is consistent with the idea that adolescence is an important period for developing cognitive control skills through training and experience. When adolescents are motivated, their capacity to engage can result in quick mastery of complex tasks. Consider, for example, a tedious and precision-demanding task such as using cell phone text messaging to communicate with peers — individuals who have learned these skills in adolescence typically reach a higher level of mastery than those who have learned as adults.

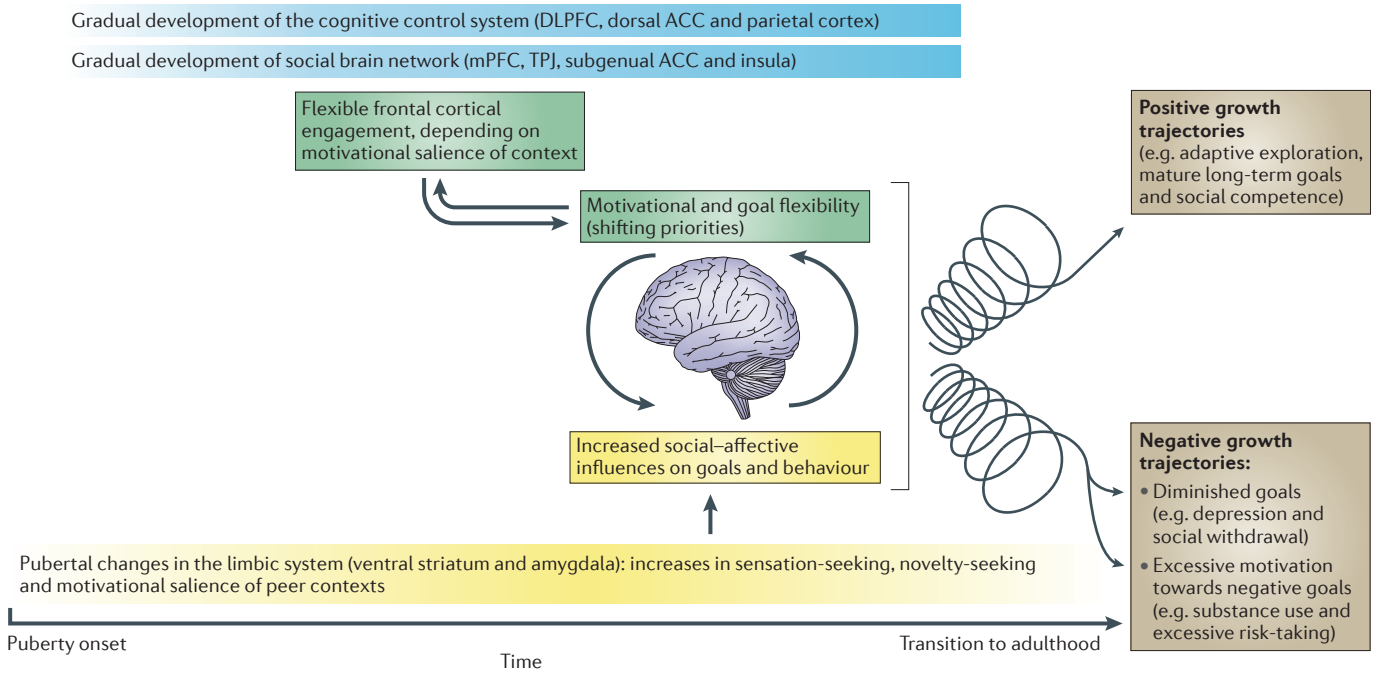

Figure 3 | **A model of adolescent brain development.** This figure illustrates a proposed model of adolescent brain development that begins with changes in social and affective processing (yellow boxes) associated with the onset of puberty. Specifically, rapid increases in hormone levels at the onset of puberty influence the development of limbic circuits, probably by inducing changes in the ventral striatum and amygdala (these regions have a pre-eminent role within the broader corticostriatal circuitry, which enables affect-laden stimuli to influence goals and behaviour). These pubertal changes contribute to increases in novelty-seeking, sensation-seeking and a tendency to process status-relevant social stimuli (for example, receiving attention and admiration from peers) as having increased motivational salience. Although these social and affective changes begin early (near the onset of puberty), they appear to peak in mid-adolescence and continue to influence behaviour, decisions and learning throughout several years of adolescent experiences (indicated by the colour gradient in the bottom yellow box). These social and affective influences interact with a broader set of changes in cognitive control and social cognitive development (blue boxes), which includes the acquisition of social and cognitive control skills that develop gradually across adolescence. These interactions between social–affective processing systems and cognitive control systems contribute to flexibility in the engagement of frontal cortical systems in adolescents, depending on the motivational salience of the context. In many contexts, these changes lead to increased social motivation and tendencies to explore, take risks and try new things — particularly when such bold behaviours may bring admiration from peers. An important feature of this model is the prediction that this increase in social–affective engagement not only influences incentives and behaviour in the moment (for example, choosing a specific bold but risky action to impress peers) but also influences motivational learning and patterns of behaviour over longer intervals (depicted by spirals). Specifically, over time, these tendencies to quickly shift priorities according to social incentives can contribute to healthy exploration and risk-taking behaviours, which promote social and emotional learning and the development of skills and knowledge that underpin adult social competence. However, these same tendencies can also lead to negative spirals, such as when risk-taking and motivational learning processes respond to unhealthy incentives, such as drug and alcohol abuse or dangerous thrill-seeking. Another version of a negative spiral as a consequence of increased flexibility in adjusting goals and heightened sensitivity to social evaluation may be perceived failure in receiving admiration from peers, leading to disengagement from social goals, as seen in adolescent depression. The model proposes that changes in social–affective processing in combination with flexible prefrontal cortex (PFC) recruitment is generally adaptive and developmentally appropriate to the tasks and learning demands of adolescence, but in some situations — perhaps through interactions between individual risk factors and risk environments — can contribute to negative consequences. ACC, anterior cingulate cortex; DLPFC, dorsolateral PFC; mPFC, medial PFC; TPJ, temporoparietal junction.

This flexibility of cognitive control may also confer adaptive advantages for learning to navigate the often unpredictable social challenges of adolescence. The increased tendencies towards novelty-seeking and greater social–affective engagement might naturally nudge motivational tendencies towards the exploration of peer and romantic contexts. This may promote behavioural exploration in ways that create risks and vulnerabilities but also in ways that contribute to learning and developing new social–cognitive and social–affective skills. As described earlier, the fundamental task of adolescence is to achieve mature levels of social competence. The requisite skills require a great deal of practice, learning and refinement — particularly in the realms of self-control and affect regulation in socially charged situations. Natural tendencies to approach, explore and experiment with these often frightening, but sometimes thrilling, peer and romantic social situations — and to quickly engage

Box 5 | **An example of motivational flexibility in adolescent mice**

A study examined learning and decision-making in adolescent (or juvenile) (26–27-day-old) and adult (60–70-day-old) mice in a two-choice and four-choice odour-based foraging task[166]. The mice learned to discriminate different odours and learned which one was associated with a reward. Subsequently, the reward was paired with a different odour, and the reversal phase of the task assessed how fast the juvenile and adult mice learned this new association. The adolescent mice learned the four-choice discrimination and reversal faster than adult mice, with shorter choice latencies and more focused search strategies, suggestive of increased behavioural flexibility. The authors interpreted these findings as suggesting that adolescent mice are optimized to make flexible decisions in uncertain and unstable environments, which are likely to be encountered during adolescence.

frontal cortical systems in flexible ways — may promote key aspects of learning and social–affective development in adolescence.

The role of hormones on social–affective development. There has been growing interest in the cognitive, affective and social effects of puberty-related changes in the levels of several hormones, including oestradiol (which affects prefrontal functioning[145]), oxytocin (which influences social bonding and social motivation[146]), and adrenal androgens (dehydroepiandrosterone or dehydroepiandrosterone sulphate) and testosterone (which influence the motivation to attain and maintain social status[147–149]). Among these, we believe that the social effects of testosterone are particularly relevant to understanding some key changes in adolescence. Animal and human studies have shown that testosterone influences neural systems that regulate reward and social motivation. For example, in juvenile animals, testosterone has a crucial role in rough-and-tumble play, which serves as an important preparatory precursor to competition for dominance, territory maintenance and access to mates. Specifically, testosterone acts to direct attention and enhance approach to threatening social situations[150]. Data from human studies — including behavioural studies in which testosterone was administered to adults, experimental economic studies and functional neuroimaging studies — have provided compelling evidence for the role of testosterone as a social hormone[147–149]. Together, these findings indicate that testosterone promotes the search for and maintenance of social status, and that testosterone alters the appraisal of threats and rewards — particularly when these are relevant to social status[147,148]. A recent fMRI study in adults[151] showed that testosterone appears to cause a functional decoupling of amygdala and ventral PFC activity. The studies conducted in adults may be relevant to models of adolescent brain development because there is growing evidence for pubertal changes in ventral PFC, including the emergence of sex-differences at puberty[11].

To date, few studies have directly investigated how testosterone influences adolescent development. Preliminary findings from fMRI studies suggest that testosterone levels correlate with maturational changes in reward processing in adolescent boys and girls[152,153]. Structural MRI studies have shown associations between circulating testosterone levels and cortical thickness in the left inferior parietal lobule, middle temporal gyrus, calcarine sulcus and right lingual gyrus, which are all regions known to be high in androgen receptors. Of note, however, the fMRI findings show similar testosterone effects on male and female reward processing, whereas the structural findings showed sex differences, with testosterone being associated with grey matter thinning in girls but with grey matter thickening in boys[154].

There is a need for a better understanding of the effects of testosterone (and other hormones) on behaviour and brain function during human adolescent development. The evidence for the role of testosterone in social motivation (in animal studies and studies in adult humans) raises compelling questions about the role of testosterone in social–affective changes during adolescence. For example, if the pubertal surge in testosterone levels amplifies the motivational salience of social status (in both boys and girls), adolescents may show a general increase in the motivation to be admired. The specific types of behaviour (and reward learning) that result from this increased motivation could vary widely across cultural contexts. Thus, in a culture that admires bold, assertive behaviour in boys but not in girls, different adolescent experiences in boys versus girls may sculpt motivational learning in fundamentally different ways through patterns of adolescent experience. Similarly, in a Tibetan Buddhist monastery, where adolescent boys may be competing for social status by demonstrating the greatest kindness and compassion, the testosterone-amplified desire to be admired might promote a very different pattern of motivational learning in boys than in other societies. These examples highlight the importance of interactions between biology and social context in the refinement of neural circuitry in adolescence.

Conclusions and future directions

As highlighted in this Review, some of the most compelling questions about the adolescent window of maturation focus on the affective dimension of motivations and goals. This includes mechanistic questions about hormone-specific effects in early adolescence that contribute to the intensification of feelings related to social valuation. Progress in understanding these mechanistic questions may provide insights into the unique opportunities for motivational learning in adolescence. For example, how do social and affective learning in adolescence contribute to the development of individual differences in motivational priorities, such as enduring heartfelt goals? It seems clear that these learning processes involve implicit and affective aspects of developing one's values and attitudes as well as the explicit cognitive processes of setting priorities. For example, individual differences in the tendencies to be kind, honest and loyal in a romantic relationship may have as much to do with one's feelings about these values as with consciously weighed decisions about the consequences of such behaviours. Another example concerns acquired intrinsic motivations in adolescence. Progress in identifying the neurodevelopmental underpinnings of these acquired motivations are relevant to understanding the development of healthy versions of inspired passions as well as vulnerabilities for developing unhealthy versions

of acquired motivations, such as drug and alcohol use and reckless versions of thrill-seeking.

It seems likely that during several phases of development across the lifespan, neural systems in the PFC may have some 'experience-expectant' qualities — that is, they may have windows of development during which the brain 'expects' or is biologically prepared for learning. These qualities enable adaptive adjustments that are relevant to the challenges and opportunities that tended to occur at that phase of development during our evolutionary history. Accordingly, the social challenges and changes facing adolescents (throughout human history[155]) may have favoured a slightly different cognitive style (more flexible, exploratory and sensitive to social–affective influences) compared with adults. This notion argues against the idea that the adult brain is the optimal or 'normal' functional system and that differences during adolescent development represent 'deficits'.

As we have described in this Review, there is a compelling need for studies that advance, refine and test key features of this heuristic model at the level of the underlying neural changes, in large part because these questions have such relevance to early intervention and prevention for a wide range of adolescent-onset health problems, as well as broad implications for health, education, juvenile justice and social policies aimed at youths.

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Competing interests statement
The authors declare no competing financial interests.

FURTHER INFORMATION
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