REVIEW

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Decision-making in the adolescent brain

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Adolescence is characterized by making risky decisions. Early lesion and neuroimaging studies in adults pointed to the ventromedial prefrontal cortex and related structures as having a key role in decision-making. More recent studies have fractionated decision-making processes into its various components, including the representation of value, response selection (including inter-temporal choice and cognitive control), associative learning, and affective and social aspects. These different aspects of decision-making have been the focus of investigation in recent studies of the adolescent brain. Evidence points to a dissociation between the relatively slow, linear development of impulse control and response inhibition during adolescence versus the nonlinear development of the reward system, which is often hyper-responsive to rewards in adolescence. This suggests that decision-making in adolescence may be particularly modulated by emotion and social factors, for example, when adolescents are with peers or in other affective ('hot') contexts.

Almost 400 years ago, Shakespeare portrayed adolescents as follows: "I would there were no age between ten and three-and-twenty, or that youth would sleep out the rest; for there is nothing in the between but getting wenches with child, wronging the ancientry, stealing, fighting." This quote, from *The Winter's Tale,* depicts adolescents as making risky decisions, a characteristic that is associated with this age group today. Adolescence is defined as the period of life that starts with the biological changes of puberty and ends at the time at which the individual attains a stable, independent role in society[1]. During this period, decisions become increasingly independent of adults, and instead peers become more influential. Risky decisions made during adolescence can have serious consequences: the leading cause of death in adolescence is accidents, which are often the result of risky decisions, for example, dangerous driving and experimentation with alcohol and drugs[2]. It is thus important to understand the neurocognitive processes that underlie decision-making in adolescence. Decision-making cognition depends on the interaction of several component processes, including the representation of value, response selection (including inhibitory control), learning and socio-emotional factors. We consider the development in adolescence of each of these processes, in the context of what has been established from studies of adult decision-making.

Impulsivity and inhibitory control

The heightened risk-taking and impulsivity observed in adolescence has been partly attributed to the slow development of the brain regions necessary for cognitive control, subsuming response selection, top-down control and inhibitory processes, and including prefrontal cortex (PFC). The human PFC undergoes particularly protracted structural development: the development of gray matter volume follows an inverted U-shaped trajectory, peaking in early adolescence[3–5] and then declining slowly throughout adolescence and early adulthood[6,7], possibly reflecting the decrease in synaptic density that occurs during this period of development[8] (**Fig. 1**).

In adults, paradigms that involve inhibition of a prepotent response, such as 'go/no-go' and 'stop-signal reaction time' tasks (**Fig. 2**), engage frontal regions including the anterior cingulate cortex (ACC) and lateral PFC[9,10]. Performance tends to improve between childhood and late adolescence on a variety of inhibitory control paradigms, including go/no-go, Stroop, stop-signal and antisaccade tasks[11]. In parallel, PFC activity during inhibitory control tasks changes during adolescence in a direction that seems to depend on the particular task used and the PFC subregion involved[12,13]. Early studies pointed to higher PFC activity during inhibitory paradigms such as the anti-saccade task in adolescents relative to adults[14]. In contrast, a common finding from other impulse-control paradigms is developmental 'frontalization', that is, gradually increasing PFC activity during inhibition tasks between early adolescence and adulthood[15,16]. Some studies have reported a 'diffuse to focal' developmental pattern of PFC activity, that is, a decline in the extent of activated regions in control tasks across adolescence[17]. Thus, there are inconsistencies in the results from the developmental fMRI (functional magnetic resonance imaging) studies of impulse control. The development of PFC responses during impulse control tasks is evidently complex and seems to depend on the specific task being used and the specific region within the PFC involved in the task.

Intertemporal choice

In addition to the slow development of impulse control, adolescents also show a preference for decisions that provide an immediate reward. In a widely used scenario, a participant is given the choice between a small, immediate reward and a large, delayed one. This reward, for adult humans, could be money (for example, $10 now or $30 in a month); for human children, sweets (for example, one sweet now or two in 15 minutes); or for rodents, food, (for example, one food pellet now, or four in 60 seconds). In all cases, the probability of choice behavior for the larger reward is a hyperbolic function of its delay ('temporal discounting of reward'[18]). There is also consistent individual variation in the propensity to discount value, with some

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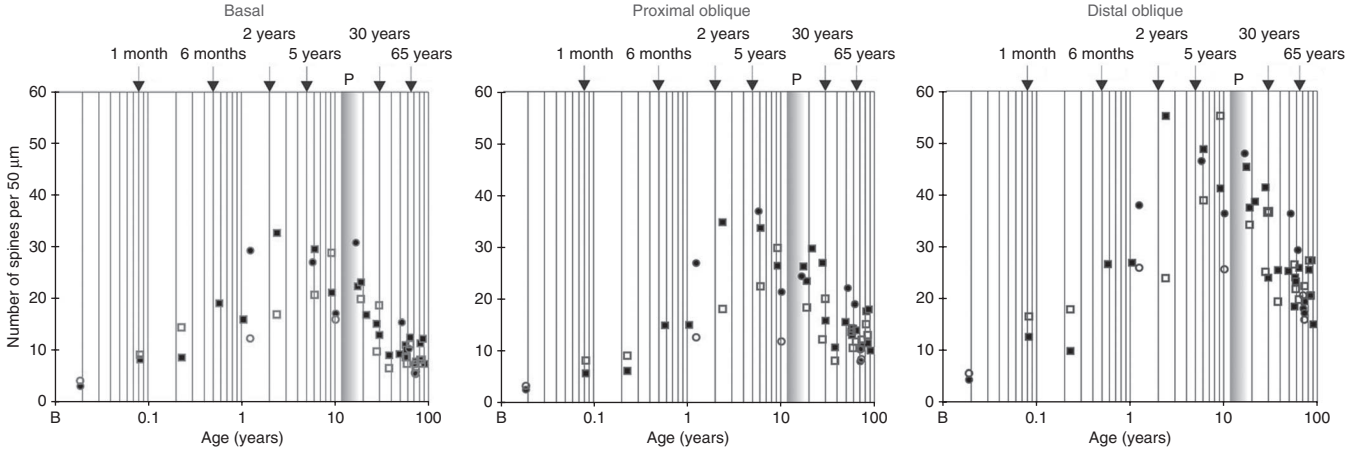

Figure 1 Synaptic development in the human brain. Graphs represent numbers of dendritic spines per 50-µm dendrite segment on basal dendrites after the first bifurcation (left); apical proximal oblique dendrites originating within 100 µm from the apical main shaft (center); and apical distal oblique dendrites originating within the second 100-µm segment from the apical main shaft (right) of layer IIIc (filled symbols) and layer V (open symbols) pyramidal cells in the dorsolateral prefrontal cortex. Squares represent males; circles represent females. The age in postnatal years is shown on a logarithmic scale. Puberty is marked by the shaded bar. B, birth (fourth postnatal day); P, puberty. Reproduced with permission from ref. 8.

individuals adopting the more 'impulsive' response styles of selecting the more immediate option. The classic study by Mischel illustrated the predictive power of such a paradigm in showing that discounting tendencies of 4-year-old children predicted their future real-life behavior as adolescents[19] as well as aspects of their brain activity in their mid-forties[20]. In adults, a 'reward system' (**Fig. 3**) including the ventral striatum and ventromedial PFC (vmPFC) is activated by decisions involving immediately available monetary rewards[21,22]. As impulse control gradually improves in adolescence, the temporal discounting of monetary reward decreases between 6 and 17 years of age[23]. The age-dependent reduction in the tendency to make impulsive choices with immediate reward has been associated with a linear increase in activity in left vmPFC and a decrease in the ventral striatum and other regions between 11 and 31 years of age[24].

Human decision-making cannot always be explained by the rational principles of economic theory. This theory prescribes that choice behavior is determined by utility theory, which states that decisions are made rationally on the basis of selecting the highest objective expected value or expected subjective utility of the options available[25,26]. Instead, the context (or 'frame') and individual unconscious response biases counteract rational choices and lead to more complex models of decision-making processes[27]. Particularly important are emotional factors; hence the term 'hot' (high arousal, emotional) as distinct from 'cold' (low arousal, non-emotional) decision-making. Also, the value of response options' outcomes appears to be computed along several dimensions: the magnitude and probability of the expected gain or loss (positive versus negative outcome) as well as the delay or expended effort between choosing an option and its consequences. Most of these dimensions of value are well represented in single unit activity of the adult primate prefrontal cortex and appear to converge on the ACC, which perhaps mediates response selection[28].

In decisions involving risk, adult humans generally prefer to avoid losses than to acquire gains ('loss aversion'[29]). This leads to a preference for certain gains compared to uncertain, risky ones—for example, a certain gain of $5 rather than a 0.5 probability of winning $10 ('risk aversion'). In contrast, adults generally prefer the risky option of an uncertain loss (for example, of $10 at a probability of 0.5) against a certain loss of $5, this asymmetry of heuristic biases produced by the positive and negative 'frames' predicted by the 'prospect theory'[30]. An influential fMRI study showed that blood oxygenation level–dependent (BOLD) signal in the ventral striatum varied according to the framing of an outcome[31], which is consistent with evidence from studies in rodents on the role of the ventral striatum in reward-related processes[32–34].

Early appreciation of the role of emotional processes in decision-making cognition came from the pioneering neuropsychological studies of decision-making on the Iowa Gambling Task (IGT) after damage to the vmPFC, which captured the catastrophic decision-making of

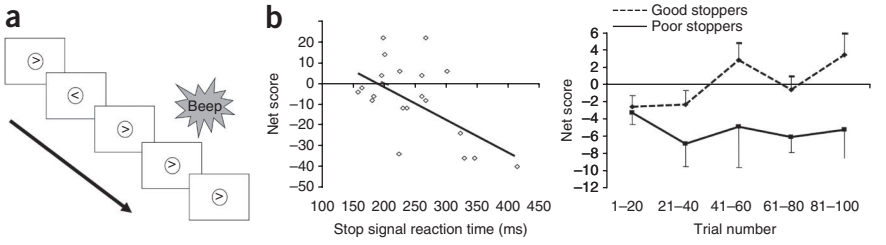

Figure 2 Relationship between response inhibitory control and decision-making in humans with large frontal lesions. (**a**) Stop-signal task. Participants respond as quickly as possible to a visual discriminative 'go stimulus' (for example, respond left or respond right). On a proportion of trials a brief 'stop signal' (auditory or visual; 'beep') is presented that indicates the subject must not respond, that is, they should cancel the initiated action. The stop signal is offset with a variable delay after the go signal; a stop signal reaction time independent of the 'go' reaction time can be computed from the response time distributions. (**b**) Relationship between performance on the IGT (*y* axis) and stop-signal task (*x* axis) in patients with right lateral frontal damage. Left, performance on the IGT, separating patients according to their performance on the stop signal reaction time task into 'good' and 'poor' stoppers in the stop-signal task. Right, net score collapsed over 100 trials for poor stoppers (<200 ms, $n = 5$), who exhibited relatively impaired performance on the IGT compared with the good stoppers (>300 ms, $n = 7$). Error bars, s.e.m. There was a significant difference between the two groups ($F_{1,10} = 10.3$, $P = 0.009$), driven by learning in the patients with right lateral PFC lesion versus no learning in poor stoppers. (Clark, L. & Robbins, T.W., previously unpublished analysis of data reported in refs. 48,95).

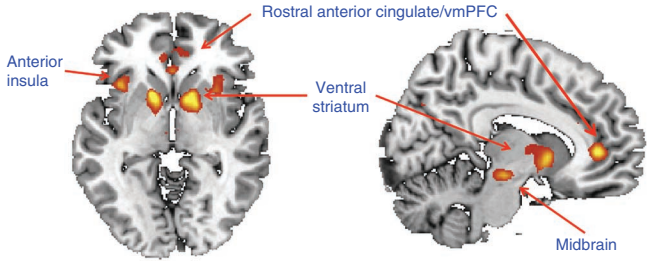

Figure 3 Major components of the human reward brain circuitry. The ventral striatum (including the nucleus accumbens and the ventral putamen) and the rostral anterior cingulate/vmPFC, derived from an fMRI study of human volunteers using a simulated slot machine[96]. Transverse section shows BOLD activation for the overall reward (small monetary wins) minus neutral outcome (non-wins) contrast, thresholded at $P < 0.05$ corrected for multiple comparisons. Also depicted (right) in sagittal section is a midbrain activation, which is presumed to contribute ascending dopamine neurons from the ventral tegmental area to the ventral striatum and vmPFC and from the substantia nigra to the dorsal striatum. Reproduced with permission from L. Clark.

patients with vmPFC lesions in everyday life[35]. The IGT requires participants to choose among four packs of cards, each associated with different profiles of monetary gain and loss. Some packs are apparently lucrative but eventually result in catastrophic loss. Other packs are 'steady earners', with small wins hardly ever being penalized by even smaller losses. Healthy adults tend to sample the risky packs initially but then tend to settle on the safer options. Patients with vmPFC damage tend to persist with the risky (and initially ambiguous) packs[35]. The somatic-marker account of this deficit suggests that the patients with vmPFC damage cannot retrieve from memory the emotional consequences of their prior decisions, which is possibly mediated in part via the insular cortex[36].

A number of studies have shown that although judgments about probability and value seem to be mature by mid-adolescence[37,38], the use of this information to guide decisions in 'hot' contexts, characterized by high emotion or arousal, is still developing[39]. In one study, adolescents (aged 13–19) and adults (aged 20 and over) played a card game in which cards could be turned over as long as gains were encountered, but as soon as participants received a loss, the trial terminated[40]. Adolescents exhibited sub-optimal decision-making, not taking into account value and probability information when making decisions in a 'hot' but not a 'cold' version of the task. Similarly, a peak in reward sensitivity in mid/late adolescence (14–21 years) has been found on a modified version of the IGT[41]. Adolescents were worse than adults at avoiding the disadvantageous decks of cards, with a linear increase in 'loss aversion' with age. In contrast, the tendency to play increasingly from the advantageous decks followed an inverted U shape, peaking in mid/late adolescence. Thus, adolescents' behavior seems to be biased toward potentially rewarding approach behavior, even when this behavior may have negative consequences.

Learning and prediction errors

Additional consideration of the complex cognitive requirements of the IGT emphasizes the importance of past experience (and hence learning) for decision-making, in particular the mismatch between expected and obtained outcomes. This mismatch is termed a 'prediction error' and is the basis of both Pavlovian and instrumental learning (reinforcement theory). The discovery of neuronal correlates of prediction errors in terms of fast phasic firing of midbrain dopamine cells[42] implicates dopamine in reinforcement learning and advances earlier notions that mesolimbic dopamine (innervating nucleus accumbens and amygdala) formed part of a reward system[43]. Aversive as well as appetitive prediction errors may also contribute to decision-making and may depend on different neurochemical coding involving serotonin[44].

The rigid decision-making of patients with vmPFC lesions may reflect a learning deficit. Impairments in reversal learning, such that responses do not adjust plastically to changing contingencies, occur after vmPFC lesions in humans[45] and other animals[46]. As in the case of impulsive behavior, perseveration could also arise from a deficit in cognitive control. Indeed deficits in IGT performance in patients with large frontal lesions can be correlated with impairments in inhibitory control, as measured by performance on the stop-signal reaction time task[47,48] (**Fig. 2**). In healthy adult volunteers, performance on an emotional variant of the stop-signal reaction time task was also correlated with risky choices on the IGT[49].

The decision-making deficit of patients with vmPFC lesions may also result from a conscious preference for risk[50]. It is difficult to isolate this element of decision-making on the IGT, but it is more feasible in another decision-making task, the Cambridge Gamble Task (CGT), which presents several decisions between options with different outcome probabilities in a visual format that does not depend on learning[51] (**Fig. 4**). Participants are asked to gamble a proportion of their earned points on each decision. Patients with large orbitofrontal (including the vmPFC) lesions[52] exhibit increased betting, indicative of enhanced risky behavior. This pattern was not caused simply by impulsive responding, through lapses in cognitive control[53]. The CGT involves making decisions under risk, whereas the IGT initially involves making decisions where the probabilities of outcomes are unknown (ambiguity). Risky versus ambiguous decisions may implicate different circuits that include the posterior parietal cortex versus lateral orbitofrontal cortex (OFC), respectively[54,55], although both types of decision also activate the reward system equivalently[56]. The involvement of parietal cortex in risky decision-making is consistent with discoveries of single units in the lateral inferior parietal cortex, which modulate performance of tasks involving simple perceptual-to-motor transformations according to the probability and magnitude of a reward[57].

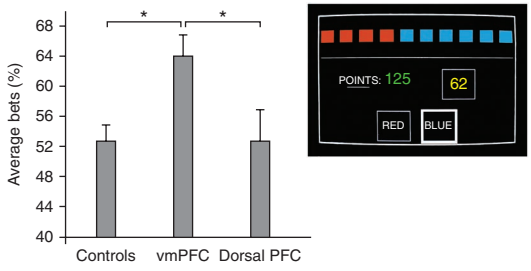

Figure 4 Performance on the CGT. A screen shot of the CGT (right). Patients decide which box to select to find a reward token, on the basis of explicitly defined risk probabilities. They are allowed to gamble a proportion of their earned points on this decision, which they will gain if correct and lose from their accumulated 'pot', if incorrect. The bets are presented in both ascending and descending orders, controlling for motor impulsivity[53]. Plotted are average bets across groups: patients with vmPFC lesions ($n = 20$), by comparison to healthy controls ($n = 41$) and to controls with primarily dorsal PFC damage ($n = 12$), showed significantly elevated betting collapsed over odds ratios, irrespective of tendencies to impulsive behavior. (*$P < 0.01$, one-way ANOVA). Based on data first published in ref. 53. Error bars, s.e.m. Screen shot used with permission from Cambridge Cognition.

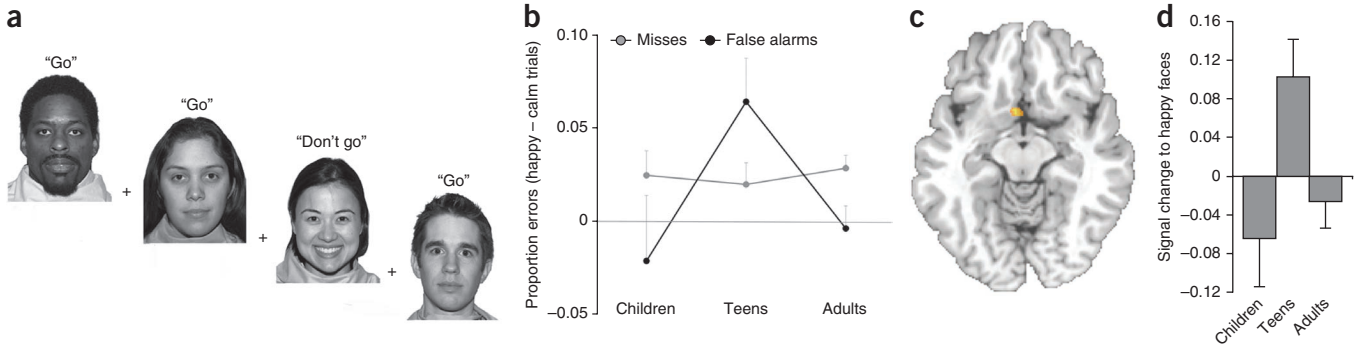

Figure 5 The emotional go/no-go task. (**a**) Four trials from the task[68]. In this example, calm faces are the target stimuli and happy faces are the nontarget (no-go) stimulus. (**b**) Behavioral performance: proportion of incorrect misses out of total go trials and proportion of false alarms out of total no-go trials. The *y* axis represents the proportion of responses for happy trials adjusted for proportion of responses for calm trials. The teenage group made significantly more false alarms than did children or adults. (**c**) Region of the ventral striatum that showed different activity as a function of age. (**d**) Ventral striatum response to happy faces (no-go and go conditions collapsed) relative to rest as a function of age. Adolescents showed a significantly larger magnitude of activation relative to both children and adults. Error bars, s.e.m.; $n = 62$. Redrawn from ref. 68 with permission from L. Sommerville.

Several developmental fMRI studies have demonstrated that, compared with adults and children, adolescents exhibit different responses to reward in reward-processing regions such as the ventral striatum[58,59]. Several recent studies of reward processing and prediction errors have reported nonlinear changes across adolescence, with a peak in activity in reward-processing regions in response to reward during mid-adolescence. In one study measuring neural responses to low- and high-risk gambles across development, regions associated with cognitive control, including the dorsal ACC, exhibited a linear decrease in activity with age, whereas reward-related regions (ventral striatum and vmPFC) exhibited a peak in activity in adolescence[60]. In contrast, early studies indicated that the ventral striatum showed less activity in adolescents than in adults during the anticipation of rewards[61]. However, this effect was not replicated in a recent study. It was found that in an anti-saccade task in which accurate performance on some trials was financially rewarded, performance on such reward trials was higher and that this effect was largest in adolescents[62]. In addition, knowing that the next trial would potentially result in reward was associated with increased activation in the ventral striatum in adolescents, suggesting an exaggerated response in this region to the anticipation of rewards[62]. The inconsistencies in the literature might be attributable to the type of reward paradigm used; but what seems to emerge from these studies is that the ventral striatum is differently activated in adolescents and adults at different stages of reward processing. Heightened risk-taking and novelty-seeking in adolescence is not specific to humans; it is also present in adolescent rats[63,64]. There is evidence that anticipation of reward and delivery of reward are processed differently in the striatum and other parts of the reward system in adolescent versus adult rats[65].

When decision value and prediction error were dissociated in a learning paradigm in participants aged 8 to 30 years, the peak in reward sensitivity in adolescents was specifically associated with a peak in the dopaminergic prediction error signal (associated with unpredictable rewards) in the ventral striatum[66]. With training, all participants became faster and more accurate at responding to predictable stimuli, but only the adolescent group (aged 14–19) responded more quickly to stimuli associated with a higher reward value compared with small rewards. In addition, compared with children and adults, the adolescent group exhibited higher ventral striatum responses to higher, unpredicted reward. This suggests that responsiveness to dopaminergic prediction error is higher in adolescents, which might contribute to elevated reward seeking in this age group.

Impact of emotion on decisions

Hypersensitivity of reward-processing regions in response to reward delivery, in tandem with the relatively slow development of impulse control–related regions, has been proposed to account for heightened risk-taking in adolescence, and this might especially be the case when decisions are made in an emotional context[67]. A nonlinear pattern of ventral striatum activity was reported in a recent study that used an emotional variant of the go/no-go task. In this fMRI study, 6–29-year-olds carried out a go/no-go paradigm with emotional cues (happy faces) and neutral cues (calm faces)[68]. The ability to resist neutral no-go stimuli improved linearly with age in parallel with a linear increase in PFC activity. In contrast, adolescents exhibited a reduction (relative to children and adults) in the ability to resist emotional no-go stimuli. In other words, the ability to inhibit the prepotent response followed a nonlinear developmental trajectory, with a dip in adolescence. In parallel, there was an inverted U-shaped trajectory of activity in the ventral striatum, which peaked in adolescence[68] (**Fig. 5**).

Counterfactual emotions such as relief and regret have a role in decision-making. Regret arises from experience of an outcome that one could have chosen but did not. This emotion is important because decision-makers presumably anticipate the aversive emotion of regret based on past experience when making their choices. Regret differs from disappointment in that its experience depends on active (that is, instrumental) choices rather than passive (Pavlovian) contingencies. This is reflected in the neural network activated by regret in adult humans, which includes the putamen and the OFC[69,70]. The ability to think counterfactually about the outcomes of decisions may continue to develop during adolescence[71]. We investigated whether this was reflected in a developmental change in the use of counterfactually mediated emotions when making decisions[72]. In each trial, males aged 9–35 chose between two gambles differing in expected value and risk as well as the potential to generate relief and regret[69,70,72]. The ability to maximize expected value increased linearly with age, whereas risk-seeking followed a quadratic relationship with age, and the proportion of risky choices peaked in mid-adolescence. The strength of counterfactually mediated emotions increased between childhood and adolescence: on learning the outcome of each gambling decision, 12–15-year-olds responded with stronger evaluations of relief (and, to a lesser extent, regret) than did 9–11-year-olds[72]. Thus, adolescents are more likely than children and adults to make risky decisions in emotionally 'hot' contexts, for example, when they have to evaluate how a gambling outcome makes them feel. In contrast, in 'cold' tasks, with no

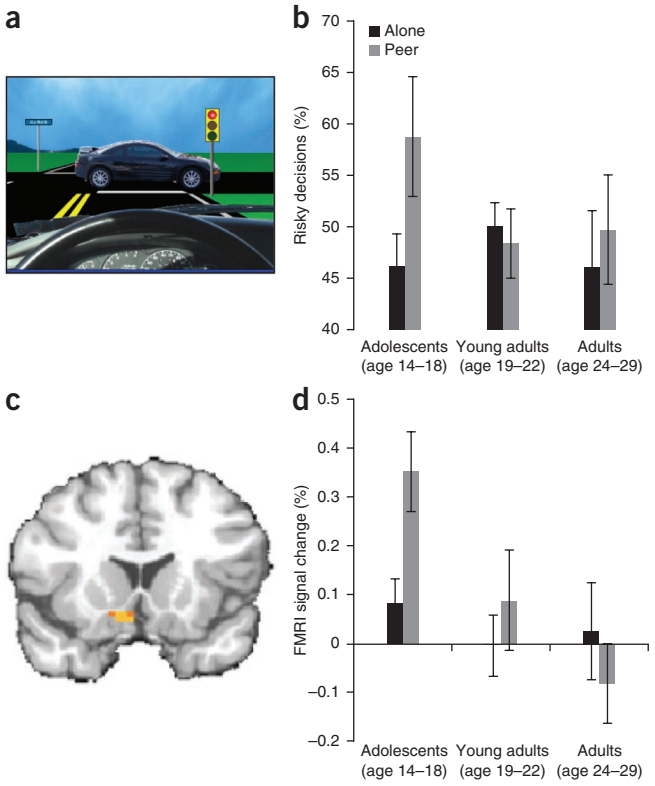

Figure 6 The stoplight driving game study. (**a**) Image from the Stoplight driving game in which participants are instructed to reach the end of a track as quickly as possible. In this study participants played alone or while being observed by peers[81]. (**b**) Percentage of decisions that were classified as risky, for adolescent, young adult and adult participants when playing the Stoplight task alone and with a peer audience. (**c**) Region of the ventral striatum that exhibited an age × social condition interaction. (**d**) Plot of activity in the ventral striatum in the three age groups in the 'alone' and 'peers present' conditions. Reprinted from ref. 81 with permisson.

emotional evaluation or affective context, risk-taking is either similar in adolescents and adults or there is a reduction with age[73,74].

Social influence on decision-making

Other challenges for rational economic theory come from analysis of social decision-making, typically assessed via behavior in economic games[75]. In the ultimatum game, for example, adults may refuse offers they consider unfair, even though they are disadvantaged financially as a consequence[76]. It appears that apes (for example, chimpanzees) behave 'rationally' and are insensitive to 'fairness', accepting all offers[77]. An early fMRI study of the ultimatum game showed that when responders were faced with unfair offers (from humans, as distinct from computers), there was activation bilaterally in the anterior insula, the ACC and the dorsolateral PFC[78]. Parallel difficulties for decision-making theories are posed by 'moral dilemmas', where again there is conflict between 'utilitarian' principles (for example, maximizing what is good for the majority) and emotional factors[79].

Social context is a particularly salient influence on adolescent decision-making. Anecdotally, adolescents are especially prone to taking risks with peers, an obviously 'hot' context in which the potential reward is peer approval. Studies have used driving simulation games, which arguably have higher ecological validity than behavioral economics tasks, to evaluate driving risks taken when alone or with two peers. Adolescents (age 13–16), youths (age 18–22) and adults (age 24 and over) took around the same number of driving risks when alone, whereas the adolescents took almost three times that number in the presence of their friends. In contrast, peers had no impact on risk-taking in adults and had an intermediate effect on risk-taking in youths[80]. In an fMRI version of this task, in the condition with peers present, two friends communicated with the participant in the scanner over the intercom[81] (**Fig. 6**). Adults aged 24–29 exhibited higher activity in lateral PFC than adolescents aged 14–18 or younger adults aged 19–22 when they had to make critical decisions in the driving game, both when alone and when peers were present. Relative to both groups of adults, adolescents exhibited higher BOLD signal in the ventral striatum and OFC during the driving decisions with peers present compared to when they were alone.

One factor that has thus far been overlooked in explanations of adolescent risk-taking in the presence of peers is the possibility that a developing 'mentalizing' system differently modulates adolescent and adult decisions made in social contexts. Mentalizing is defined as the ability to attribute mental states to predict others' behavior, and recent studies have shown that this cognitive process undergoes development throughout adolescence. Until recently, it was generally assumed that mentalizing was fully developed by middle childhood and as a result there were few paradigms suitable for older children or adolescents. However, paradigms have since been developed to test some aspect of mentalizing in the absence of ceiling effects, even in adults. Using one such paradigm, female participants aged 7–28 years were instructed to move objects in a set of shelves as instructed by a 'director' character[82]. The director could see objects in only some of the shelves, and therefore correct interpretation of the director's instructions required participants to take into account the director's visual perspective to interpret which object the director intended them to move. The ability to account for someone else's perspective in order to guide decision-making continued to improve in late adolescence[82].

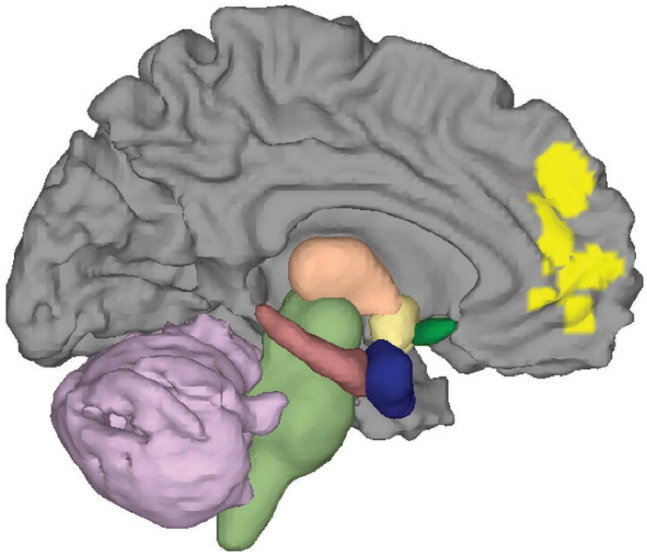

Figure 7 A qualitative meta-analysis of the region of dmPFC that consistently shows decreased activity during mentalizing tasks between late childhood and adulthood. This meta-analysis shows voxels in mPFC (yellow) that are within 10 mm of the peak voxel found to have a significant negative relationship with age in three or more of eight published developmental fMRI studies of social cognition[86–88,90,97–100]. Meta-analysis was performed using Neurosynth software (http://www.neurosynth.org/).

Several developmental fMRI studies have pointed to an anterior-to-posterior shift of activity within the mentalizing network, which includes dorsomedial PFC (dmPFC), posterior superior temporal sulcus (pSTS), temporoparietal junction and anterior temporal cortex[83], during adolescence. The dmPFC BOLD signal observed during social cognition tasks generally decreases between early adolescence and adulthood, whereas activity in posterior mentalizing regions increases[84] (**Fig. 7**). For example, when adolescents and adults were inferring the communicative intent of a speaker, the dmPFC was more active in adolescents than in adults, whereas adults relied more than adolescents on the fusiform gyrus[85]. When adolescents or adults were thinking about intentions, the dmPFC was more active in adolescents than in adults, whereas the right pSTS exhibited the opposite developmental pattern[86]. In a social emotion paradigm, adolescents exhibited higher activity in dmPFC compared with adults, who exhibited higher activity in pSTS at the temporoparietal junction, when thinking about guilt and embarrassment[87].

Behavioral studies have shown that the tendency to use mental state information strategically to win money in economic games continues to develop during adolescence. The tendency to make a generous offer in a modified ultimatum game was increasingly modulated during adolescence by the perceived power of one's co-player to punish a selfish offer[88]. A developmental fMRI study used the trust game to investigate the development of reciprocity. Participants were given a sum of money by another player that they could either divide fairly between themselves and the other player (reciprocate) or keep mostly for themselves (defect)[89]. There was an age-related decrease in dmPFC activity during reciprocal choices during adolescence. Thus, the mentalizing system continues to develop during adolescence, and this appears to influence the decisions adolescents make during economics games.

Considerations for future research

This is a relatively young field, and many questions remain to be answered. The distinction between hot and cold decision-making is admittedly rather simplistic, and the definition of when a context is hot versus cold is not entirely clear. There are likely to be individual-to-individual and developmental-stage differences in the level of emotion or arousal evoked by different contexts, which may in turn differentially affect decision-making. In addition, inconsistencies are emerging in developmental fMRI of impulse control and decision-making[90]. For example, different studies investigating similar cognitive processes report different directions of BOLD signal change with age. Possible explanations, requiring further investigation, include the following. (i) The age range considered to be 'adolescence' is not always consistent between studies. For example, in some studies the adult group is aged around 18–22 years, whereas in other studies this group is considered late adolescence[91]. (ii) There is currently little understanding of how gender, differences among individuals, hormonal changes at puberty, culture and the environment influence brain development. (iii) The cellular basis of the BOLD signal and the possibility that neurovascular coupling might change with age are critical issues[92]. Neurovascular coupling might develop differently in different brain regions, and this will influence the direction of BOLD signal change observed across age. How developmental changes in BOLD signal are related to underlying changes in neurophysiology, including synaptic and vascular development, and in cognitive strategy or motivation, is currently unclear. (iv) How well decision-making paradigms designed for adults (such as the IGT) and their associated monetary rewards generalize to adolescents needs to be considered, as money has different inherent value at different ages.

Conclusion

Although many components of human decision-making have been identified, it is still a challenging prospect to weld them into a single theory of decision-making that convincingly combines economic and psychological, including social and emotional, factors. That being the case, it is even more difficult to ensure that the neural computations and system interactions governing such complexity can be rigorously defined and disentangled. Studying the development of such neural networks in the context of decision-making cognition is a promising strategy for this purpose, as it appears likely that the different components of decision-making 'mature' at different rates and hence may be uncoupled in the adolescent brain.

We have reviewed evidence from empirical studies that adolescents are more likely than children and adults to make risky decisions in 'hot' contexts, where emotions are at stake or peers are present and social cognition is involved. The peak in risk-taking during adolescence might, at least in part, be due to asymmetrical functional development of the dopaminergic reward system (including the ventral striatum), which is hyper-responsive to reward in adolescence, and the prefrontal systems implicated in impulse and inhibitory control, which develop more gradually over childhood and adolescence[67]. We suggest that the developing social brain also needs to be taken into account because mentalizing additionally modulates decision-making, especially when adolescents are in social contexts.

Many adult psychiatric disorders have developmental origins[93], possibly in neural systems governing decision-making. Vulnerability to addiction, depression, anxiety and psychosis in adulthood could potentially be detected via the behavioral and neural changes occurring during adolescence. Longitudinal studies of adolescents that use structural and functional neuroimaging, as well as neuropsychological assessment, to predict psychopathology, may eventually prospectively provide markers for risk of psychiatric disturbance[94], which could lead to interventions that prevent such disorders, with considerable benefit to society.

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The authors declare competing financial interests: details accompany the online version of the paper.

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