

Review

Sensitivity and specificity in affective and social learning in adolescence

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Adolescence is a period of heightened affective and social sensitivity. In this review we address how this increased sensitivity influences associative learning. Based on recent evidence from human and rodent studies, as well as advances in computational biology, we suggest that, compared to other age groups, adolescents show features of heightened Pavlovian learning but tend to perform worse than adults at instrumental learning. Because Pavlovian learning does not involve decision-making, whereas instrumental learning does, we propose that these developmental differences might be due to heightened sensitivity to rewards and threats in adolescence, coupled with a lower specificity of responding. We discuss the implications of these findings for adolescent mental health and education.

Adolescence as a sensitive period of development

Adolescents have long been described as being emotional and particularly interested in peer relationships. Over 2000 years ago Aristotle described youth as 'passionate, irascible and apt to be carried away by their impulses ... the age when people are most devoted to their friends'. Adolescence, defined as the period of life between 10 and 24 years [1], is still considered to be an age of heightened affective and social sensitivity paralleled by protracted neuroplasticity [2]. Learning can also be heightened in adolescence. For example, autobiographical memories acquired in adolescence and early adulthood are more likely to be recalled than memories formed at other ages across the lifespan [3]. Adolescence is associated with an increase in learning following cognitive training in abstract reasoning: older adolescents (age 16–18 years) learn more efficiently than younger ages (11–16 years) [4]. It is also an important age for second language acquisition [5] and language innovation [6], the development of musical tastes [7], and sociocultural learning more broadly, compared to other stages of life [8]. Furthermore, early adolescence provides a window of opportunity to remediate the harmful effects of early-life stress [9]. However, heightened learning in adolescence could also contribute to some of the vulnerabilities associated with this period, where 14.5 years is the peak age of onset across all mental health conditions [10]. Although adolescence has been established as a period of altered affective and social processing, it remains less clear how affective and social factors influence learning in adolescence. How do adolescents learn from affective and social information, and is this learning different from that in adults? How do adolescents learn from positive and negative experiences? How do social stimuli influence adolescent learning, and how do adolescents learn from others? We first review the evidence that adolescence is a period of heightened affective and social sensitivity. We then explore how this sensitivity influences learning. We focus on associative learning (Figure 1) because of its experimental and computational tractability. Finally, we discuss the potential implications of these differences in learning for adolescent mental health and education.

Highlights

Adolescents display heightened affective and social sensitivity, as well as differences in associative learning of both appetitive and aversive stimuli, compared to children and adults.

Heightened sensitivity and decreased specificity in response to rewards and threats might explain differences in Pavlovian and instrumental learning in adolescence.

During learning, adolescent affective and social sensitivity contributes to strong acquisition, heightened generalisation, reduced extinction, and increased exploration.

Understanding social-affective learning in adolescence has implications for mental health and education.

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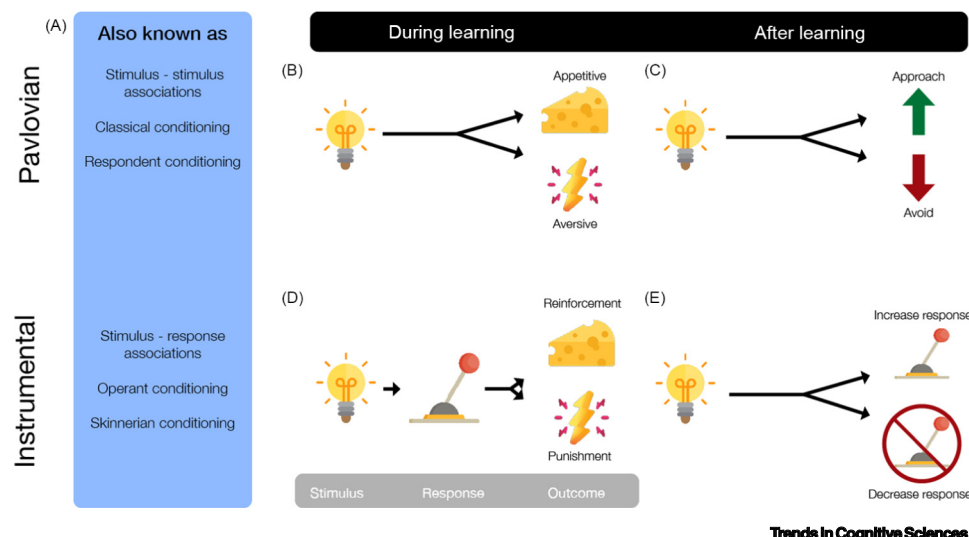


Figure 1. Associative learning. Associative learning occurs when two otherwise unrelated elements become explicitly or implicitly paired in memory (includes Pavlovian and instrumental learning). (A) Other terms commonly used in the literature. (B) During Pavlovian learning, a neutral stimulus (light) is repeatedly paired with an appetitive or aversive stimulus (food or shock). (C) After learning, the neutral stimulus (light) on its own produces an approach or avoidance response. (D) During instrumental learning, a neutral stimulus (light) signals for a response. A response (lever press) leads to an outcome that is either reinforcing (food) or punishing (shock). (E) After learning, the neutral stimulus (light) on its own produces increased or decreased responding (lever pressing).

Affective and social sensitivity in adolescence

There are marked changes in **affect** (see [Glossary](#)) in adolescence. Compared to adults, adolescents report emotions that are more frequent, intense, and volatile [11]. Historical studies demonstrated that adolescents (aged 14–18 years) reported feeling both more euphoric and more depressed in response to events over the course of a typical week, and their positive emotions did not last as long as those of adults [11,12]. Adolescent emotions tend to be more complex and nuanced than those of children [13] and self-conscious social emotions such as embarrassment, shame, and pride peak in adolescence [14]. Compared to adults, adolescents are particularly reactive to both positive and negative affective **valence**, and display, for example, both increased reward pursuit [15] and threat avoidance in some contexts [16,17]. Adolescents also show greater behavioural and neural sensitivity to both appetitive and aversive stimuli [18]. It has been proposed that neurodevelopmental changes in reward-related neural circuitry, coupled with the protracted development of the prefrontal cortex [19], contribute to heightened affective sensitivity in this period [20].

Heightened emotionality in adolescence is most often and most strongly experienced in social settings [11]. As adolescents progressively become independent from their caregivers and find their place amongst peers, the social world becomes increasingly salient. For example, adolescents found pleasant social photographs more rewarding to look at than pleasant non-social (nature) photographs, and the reverse was true for adults [21]. When viewing social-emotionally salient stimuli, such as photos of emotional faces, activity in the amygdala and hippocampus (structures involved in emotion processing and learning) decreased into emerging adulthood (between 10 and 24 years of age) for both positive and negative social cues [22,23], suggestive of heightened neural sensitivity to social-emotional information in adolescence. Studies have shown that self-reported 'desire to be liked' peaks in late adolescence (age ~21 years) [24] and that social rewards are subjectively more attractive than monetary rewards for children and adolescents, compared to

Glossary

Acquisition: the first stage of learning, when an association is established.

Affect: an underlying experience of feeling, emotion, or mood. Often characterised along three main dimensions – valence, arousal, and motivational intensity.

Confirmatory learning: also called choice confirmation bias. Refers to the observation that, when learning to navigate novel environments through trial and error, people and other organisms frequently learn more from outcomes that confirm their expectations than from outcomes that disconfirm them.

Epistemic/informational influence: social influence driven by the pursuit of accuracy.

Extinction: a gradual decrease in response to a conditioned stimulus that occurs when the stimulus is presented without reinforcement.

Extinction retention: the ability to retain an extinction memory over time.

Normative influence: social influence driven by the pursuit of acceptance by others.

Prediction error: in associative learning, prediction errors have been defined as the mismatch between what is expected and what actually happens. This is thought to be a core mechanism underlying learning. Rescorla and Wagner [33] posited that 'organisms only learn when events violate their expectations'. Prediction errors can be signed – positive (i.e., better than expected) or negative (i.e., worse than expected).

Simulated annealing: a type of stochastic optimisation algorithm that is initialised at high temperature such that it is initially flexible and tolerant to large errors. Like metals, which become harder to shape as they cool down, the solution of the algorithm becomes more difficult to change as the algorithm learns.

Stochastic optimisation algorithm: a method common in machine learning that generates and uses random (i.e., probabilistic) variables to individuate approximately optimal solutions in a given learning environment.

Valence: a dimension of affect that refers to the subjective spectrum of positive-to-negative evaluation. Can refer to the appetitiveness ('goodness') or aversiveness ('badness') of an event, object, or situation.

adults [25]. In participants aged 13–22 years, reward-related responses in the nucleus accumbens to having one's own content 'liked' on Instagram were highest at around age 16–17 years [26]. Social threats also become more salient in adolescence. For example, compared to children (aged 10–12 years), adolescents (aged 14–17 years) showed greater neural activity [midfrontal theta power as measured by electroencephalography (EEG)] to both social exclusion and threats of exclusion [27]. Neuroimaging studies have revealed that being rejected based on one's online profile picture results in increased activity in the medial prefrontal cortex in children aged 7–10 years [28] and in late adolescents/emerging adults aged 18–27 years [29] (although it should be noted there were no comparison age groups in these studies). Being rejected by peers in an online chatroom paradigm resulted in enhanced pupil dilation (a response elicited by emotional intensity) in adolescents aged 9–17 years, and this effect was stronger in older adolescents than in those in the younger age range [30].

Emotions affect multiple cognitive processes including learning and memory [31]. Therefore, the heightened affective and social sensitivity observed in adolescence suggests that learning might also be altered in this period of life. We review evidence that demonstrates an intricate and complex picture, suggesting that adolescence might be a period of heightened learning sensitivity, coupled with reduced learning specificity. This can lead to increased learning when it does not involve decision-making, as in Pavlovian conditioning, and – perhaps counterintuitively – decreased learning when it does involve decision-making, as in instrumental conditioning.

Learning from exposure to rewards and threats: Pavlovian conditioning

During Pavlovian conditioning, organisms learn that previously neutral stimuli (e.g., a bell sound, a light, a location) are predictive of a reward or threat [32,33]. This form of learning is relatively basic because the associations are learned by simple exposure to repeated pairings between neutral stimuli and rewards or threats; that is, the organism does not need to engage in any overt choice. Humans, as well as animals, single-celled organisms [34], and even plants [35] have demonstrated the ability to establish Pavlovian associations. These learned associations can have robust influences on behaviour in both adaptive and maladaptive ways. **Acquisition** (Figure 2) in Pavlovian learning can allow organisms to establish new reward/threat associations and engage in appropriate approach/avoidance behaviours. However, exaggerated Pavlovian learning can also play a role in the maintenance of unhealthy addictions and maladaptive anxiety responses [36,37]. Pavlovian learning changes in development in several ways.

Pavlovian reward learning in adolescence

Rodent studies show heightened Pavlovian learning of food and drug rewards in adolescent compared to adult rats [38,39]. Adolescent rats also show increased activity in dopamine neurons in the substantia nigra – a component of the striatal reward pathway – compared to adult rats during Pavlovian reward learning [40,41]. In human adolescents, Pavlovian reward learning has been studied using monetary rewards or positive written, verbal, or visual feedback. Older adolescents showed faster response times when learning to respond to stimuli that predicted rewards, compared to children and adults [42]. In a separate study, items paired with rewarding feedback were better recalled by adolescents on a later memory test, compared to adults [43], and this difference was associated with stronger functional connectivity between the hippocampus and the striatum during reward receipt. Elements of 'unlearning', called **extinction**, have also been found to differ between adults and adolescents. For example, one study showed that, once adolescent rats learned to associate a cue with a reward, it was more difficult for them than for adults to suppress their learned reward response, even if the cue was no longer predictive of a reward [44].

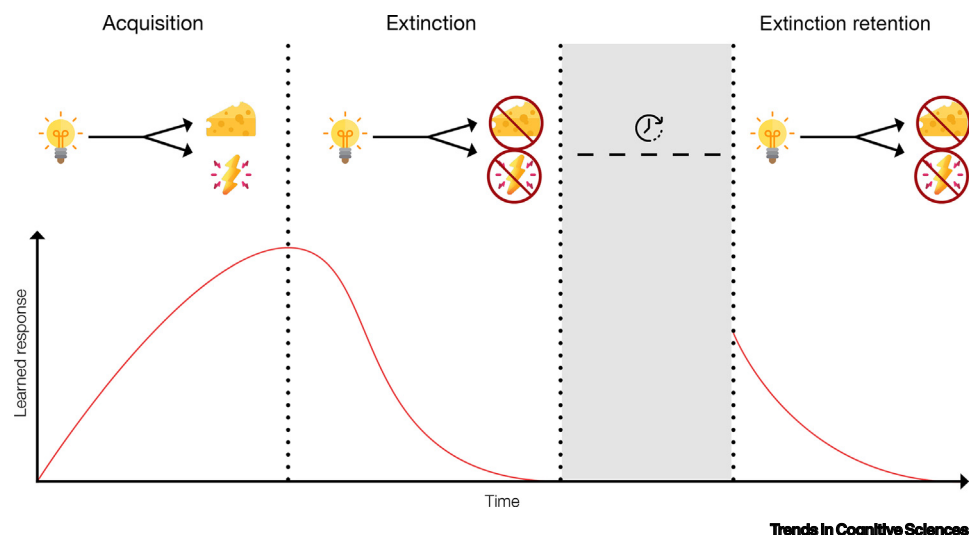


Figure 2. Associative learning stages. Associative learning consists of several stages. Learning is most often measured during acquisition, extinction, and extinction retention. Acquisition (the learning phase) is where associations are established and learned responding increases over time. Extinction is where repeated exposure to a stimulus without a previously learned outcome leads to diminished learned responding over time. Extinction retention measures responding after a delay, where previously learned and extinguished responding might re-emerge.

Social rewards can powerfully guide Pavlovian learning, and this type of social reward learning also seems to vary with age. For example, rodents learn to prefer locations that had previously been paired with a conspecific, and this socially conditioned place preference peaks in mice in mid-adolescence [45], before declining into adulthood [46]. One experimental study found that changes in sensitivity to social reward learning corresponded to developmental downregulation of synaptic plasticity in the nucleus accumbens, and that increasing plasticity (through drug-induced upregulation of oxytocin) reinstated adolescent levels of sensitivity to social reward learning in adult rats [46]. Social contact might also influence Pavlovian reward learning in adolescence. Adolescent rats exposed to social isolation required more sessions to reverse probabilistically learned rewards, and were slower to adjust their task strategy when reward contingencies were switched, compared to socially housed rats [47]. In another study, socially isolated adolescent rats demonstrated stronger Pavlovian learning to social versus amphetamine-paired contexts, whereas isolated adult rats showed the opposite pattern [48]. That adolescent rats learned from social rewards more than from drug rewards when deprived of social contact suggests that social contact acts as a powerful reward signal in adolescence. Indeed, one study found synergistic effects of social and drug rewards, where social reward enhanced the rewarding effects of drugs in adolescent rats [49]. In humans, objective isolation and subjective loneliness are related, but not identical, constructs in that feelings of loneliness can be high in humans even when they are surrounded by others and, conversely, time spent alone does not always lead to loneliness [50]. However, a recent experimental study in human adolescents found that a brief period of social isolation was associated with increased loneliness and reward responsiveness, particularly to social cues [51]. Increased reward responsiveness was positively associated with self-reported loneliness following isolation, with lonelier participants demonstrating higher levels of reward responsiveness [51].

Evidence suggests that, although Pavlovian responding by adolescents might be more sensitive than that of adults, it might not be as specific; that is, it might discriminate less well between

different reward probabilities or magnitudes. In one study, adolescent rats displayed a Pavlovian reward learning advantage relative to adult rats when cues were reinforced probabilistically (i.e., intermittently with some probability) but not deterministically (continuously) [44]. In addition, whereas adult rats learned proportionally about the probability of reward, adolescent rats did not display this fine-tuning [44]. In line with this, another study found that adolescent rats responded equally to both weakly and strongly predictive reward cues, whereas adult rats flexibly adjusted their pattern of responding based on the expected likelihood of reward [15]. Reduced specificity in social reward learning has also been found in human adolescents, who discriminated less between different amounts of positive social feedback than children and adults [52]. In the same study, adolescents showed greater neural activity than children or adults during social rewards in regions associated with motivation and action (putamen, insula, and supplementary motor cortex). Further research will be necessary to clarify the effects of the social environment on Pavlovian reward learning, particularly with regard to how social cues and social contact might influence the sensitivity versus specificity of reward learning.

Pavlovian threat learning in adolescence

Several studies have shown comparable learning of Pavlovian threat responses (also called 'fear learning') in children, adolescents, and adults (in both humans and animals) [53–56]. In line with Pavlovian reward learning, however, some studies have shown that adolescents display diminished extinction of learned threat responses, compared to both adults and pre-adolescents, in human and rodent models [53,57–59]. Although there has been contradictory evidence regarding this finding [54,55,60,61], it has been proposed that it is not the ability to extinguish threat responding *per se*, but rather the ability to retain threat response extinction, or **extinction retention**, that is attenuated in adolescence [62]. For example, in humans and rodents, adolescents have shown a heightened relapse of threat responding (less threat extinction retention) relative to both juveniles and adults [57,63,64], and reductions of extinction retention have been associated with age-related changes in fronto-amygdala circuitry in adolescence [65].

Research on human adolescent threat learning often employs social stimuli such as a face combined with an aversive scream [53,54,58,66,67]. Studies using social stimuli have frequently reported similar age-related reductions in extinction and/or extinction retention (in adolescents) as those using non-social stimuli [55,57,59]. However, there has so far been no systematic comparison of the effects of different stimulus types (social vs. non-social) on adolescent threat learning to determine whether social threats (like social rewards) hold particular significance for adolescents. In the absence of direct threat experiences, threat associations can also be acquired by observing a learned threat response in another individual (observational learning). This type of social learning is known as vicarious threat learning (sometimes called 'vicarious fear learning'). In rodent models, male adolescent mice show higher vicarious threat learning than male adult mice, although this age effect might not be uniquely social because direct threat learning was also higher in adolescent mice [68]. Rodents that were socially isolated in adolescence displayed both reduced vicarious threat learning and greater direct threat learning compared to socially housed mice [69,70]. In humans, loneliness has been associated with impaired threat extinction in young adults amid coronavirus disease 2019 (COVID-19)-induced social disconnection [71]. Further, social support can act as a safety signal to reduce fear learning and enhance fear extinction [72].

Evidence from Pavlovian threat learning further supports the proposal that this period is associated with increased sensitivity and decreased specificity. Adolescent mice overgeneralise learned threat associations compared to adult mice [73], with lasting consequences. In one study, threat associations learned in adolescence delayed the normative development of adult threat discrimination [74]. Human adolescents show reduced discrimination between learned threat and safety

cues, and tend to overgeneralise their threat response and respond to all cues (even neutral cues) as if they are more threatening [16,67]. Threat generalisation in humans has been shown to decrease linearly between 8 and 17 years of age [75], suggesting changes in discriminative threat learning processes in adolescence. Relatedly, adolescent humans overgeneralised their threat response compared to adults during vicarious threat learning, and rated a threat cue as significantly more aversive even before faux electrodes were attached [76,77]. Another study found that participants aged 6–17 years vicariously learned from threats experienced by a parent over threats experienced by an unfamiliar adult [78]. However, no study has looked at developmental changes in this effect or at how adolescents learn about threats from peers in addition to parents and adults.

Learning from decisions: instrumental conditioning

The evidence reviewed above suggests that, in Pavlovian learning, adolescents frequently show heightened learning relative to adults, possibly owing to heightened affective and social sensitivity. The evidence suggests that the same might not be true for instrumental learning. Like Pavlovian learning, instrumental learning requires participants to learn the association between a novel cue and a valenced outcome such as a reward or a punishment. However, instrumental learning additionally involves decision-making because different choices are linked to different outcomes. For example, in a simple instrumental learning task, people might need to choose between two novel symbols, each leading to monetary gains or losses with a given probability. By repeatedly sampling the outcomes associated with each option, participants learn which option tends to be best. Although these learning environments might not be highly ecological, they allow researchers to computationally characterise learning and thus to investigate more precisely how the parameters that define learning change with age [79–81]. As articulated below, these studies suggest that lower specificity might lead adolescents to frequently (but not always) learn less efficiently than adults during instrumental learning.

Over the past decade an increasing number of studies have addressed how instrumental learning changes with age. Many of these studies have found that adults typically outperform adolescents in instrumental learning [80,82–84]. For example, adults tend to require fewer trials than adolescents to learn which options are best, make fewer errors, and thus learn more efficiently. Using social stimuli does not substantially offset this adult advantage. For example, learning from positive social feedback [52] or by observing others [85,86], as well as learning from others [87], about their cooperative behaviour [88] or preferences [89], are all learning abilities that improve between adolescence and adulthood. One possible exception to this developmental trend is social influence or social contagion, which has typically been found to be heightened in adolescence relative to adulthood [90]. We speculate that this could be an exception because, as in Pavlovian learning, choices do not affect outcomes in typical social influence paradigms (Box 1).

A metaphor to describe these age-related improvements in instrumental learning has been borrowed from a **stochastic optimisation algorithm**, called **simulated annealing** [91]. When learning about reward contingencies in novel environments, this algorithm initially tests random guesses and makes large adjustments based on feedback. Like metals, which are more difficult to shape as they cool down, these adjustments become smaller and less likely to occur as the 'guesses' of the algorithm become more accurate. In a computational comparison of human learning with this form of artificial learning, one study showed striking similarities in the way learning improves across human development and across different stages of simulated annealing [83].

Box 1. Social influence

Experimental and observational studies find that people of all ages are susceptible to social influence – participants often adjust their beliefs and preferences to be aligned with the beliefs and preferences of others. Because social influence involves behavioural adjustments in response to learned norms, there is an ongoing debate as to whether this type of learning involves similar neurocognitive mechanisms as reinforcement learning [127]. Over the past decade many studies have investigated developmental changes in social influence. Across multiple domains, including risk perception [128,129], risky behaviour [101,130–132], prosocial behaviour [133–135], and preferences for delayed rewards [90], studies have consistently shown that, similarly to Pavlovian learning, social influence is heightened in adolescents relative to adults. Notably, although heightened social influence in adolescence has frequently been investigated as a source of vulnerability to, for example, dangerous risk-taking behaviours, it could also be adaptive [17]. Indeed, two studies found that adolescents who were more susceptible to social influence benefited from greater levels of social integration [90,101]. At least two explanations compete to explain the developmental trend of social influence. One is that, because of their heightened social sensitivity, adolescents feel more normative pressure to align with their peers to fit in with them (sometimes called **normative influence**). The other is that, because adolescents have less experience with their preferences than adults, they might be less certain about their preferences, and thus might more easily be influenced (**epistemic/informational influence**). In line with the second explanation, a well-powered longitudinal study [90] found that age differences in social influence were no longer observed after controlling for preference uncertainty. Further studies employing more ecological forms of peer influence could shed light on whether normative influence also plays a role in this heightened form of learning in adolescence. This literature has implications for education and public health. For example, student-led interventions to reduce bullying in schools were more effective than control schools that did not carry out peer-led interventions, and this effect was strongest for highly connected students [136]. Thus, adolescents have the capacity to be highly influential among their peer group.

At the computational level, cooling down can be captured by a temperature parameter. Temperature specifies how precisely one's choices discriminate between positive and negative values and their magnitudes or probabilities. In other words, temperature regulates the extent to which option values direct choices. For low-temperature learning, a small difference in the outcomes associated with each option will direct choices towards the better option, while a larger difference might be necessary for higher temperature learning. Temperature can thus be interpreted as a measure of specificity in that it regulates how closely choices track reward and punishment contingencies. For example, learning with high temperature leads to more frequent deviations from an optimal choice, such as a known and liked restaurant or who to sit next to in a school cafeteria. This could occur because the learner does not fully know what they like and dislike, or it could more purposefully aim to explore novel alternatives. Conversely, learning with low temperature could lead to a more exploitative learning style, characterised by repeatedly choosing options that proved optimal in the past. Notably, across different experimental paradigms and different modelling approaches, many studies have shown that temperature decreases with age in adolescence [80,84,92].

Several non-mutually exclusive proposals have been developed to account for age-related improvements in instrumental learning and changes in specificity. One broad approach has focused on facets of cognitive control that also improve in adolescence, such as working memory and non-verbal reasoning abilities. Abilities such as these facilitate instrumental learning by favouring the sustained attention necessary to monitor reward-related contingencies in stochastic environments [93], or by favouring the use of computationally more sophisticated forms of learning [94,95]. For example, one study found that, between adolescence and early adulthood, age correlated both with non-verbal reasoning and inverse temperature in a reinforcement learning paradigm [84]. However, this study, as well as others [96,97], suggest that, although facets of cognitive control might explain part of the age differences in instrumental learning, they are unlikely to explain them entirely.

In addition to facets of cognitive control, many of which tend to develop steadily in adolescence before reaching an asymptote in early adulthood [98], other processes related to reward sensitivity develop non-linearly in adolescence. For instance, across cultures,

sensation-seeking behaviours increase during the teenage years, are at their highest in the late teens, and then decrease throughout the twenties [99]. Similarly, behavioural economics studies have found that adolescents display a uniquely high tolerance to ambiguity and uncertainty in risky decision-making [100], and, especially in situations involving peers, adolescents tend to accept riskier gambles than adults [101]. These considerations are consistent with the hypothesis that adolescents might learn more from positive than negative outcomes in instrumental learning, potentially leading to a behavioural form of optimism bias or a riskier learning style [102]. However, over the past decade several studies have addressed this hypothesis and a consistent picture remains elusive [102–105]. For example, some studies have found that adults (as opposed to adolescents) tend to learn more from positive than negative feedback [105] (Box 2).

Indeed, a growing body of research suggests that people of all ages (as well as non-human primates and rodents) tend to learn more from positive than negative outcomes, and thus display a **confirmatory learning** style [106]. Notably, simulations and experiments have shown that this asymmetry in learning frequently improves performance in instrumental learning, possibly because it buffers the impact of environmental noise, thus protecting people from excessive doubt when optimal options occasionally deliver suboptimal outcomes [107]. One study suggested that, although the magnitude of the positive versus negative learning discrepancy does not systematically vary with age, confirmatory learning increases with age between adolescence and early adulthood, while specificity increases (i.e., temperature decreases) [84].

Moreover, although several of the studies described above suggest that performance in instrumental learning improves with age in adolescence, this might not always be the case. More specifically, both increasing specificity and confirmatory learning (as seen across adolescence) can optimise learning when evidence history is not misleading, but the same features can be problematic when it is. This can occur in at least two situations. First, even if one option has proved optimal in the past, this could change. In this case, continuing to exploit outdated evidence can be detrimental. This raises the hypothesis that adult advantages in instrumental learning might be reduced in more volatile environments. In line with this, several studies have shown that, especially in more volatile environments in which reward/punishment contingencies gradually or suddenly change (e.g., a previously optimal option becomes suboptimal), the adult advantage in instrumental learning is no longer observed [84] or can even reverse,

Box 2. Disentangling prediction errors and valence

During reinforcement learning using trial and error, outcomes can be 'better' than expected (a positive prediction error) or 'worse' (a negative prediction error) based on past experience. Either outcome can occur in both appetitive and aversive contexts (in the gain vs. loss domain, respectively), and this has potential implications for learning. For example, in an appetitive context, in which a participant can gain different amounts of money or gain nothing, but losses cannot occur, the participant can gain more money than expected (a positive prediction error), which could lead them to re-select the option that led to that outcome, or they can gain less than expected (a negative prediction error), which might lead them to switch away from that option. In an aversive context, where the participant can lose different amounts, but gains are not possible, the participant could also experience positive and negative prediction errors. However, possibly because gains and losses are known to have a different impact on neural processing and behaviour [137,138], prediction errors occurring in the appetitive/gain versus aversive/loss context might not have the same impact on learning. Most reinforcement learning paradigms mentioned above involved choices that either led to a gain or a loss. In such cases, we suggested that people of all ages tend to learn more from positive than from negative outcomes, and that this tendency might increase in adolescence [84,105]. However, those paradigms conflate positive and negative outcomes with appetitive and aversive contexts. Reinforcement learning paradigms have also begun to orthogonalise positive and negative outcomes with appetitive and aversive contexts, and studies using these paradigms have found that, although adults learn equally well across these contexts, adolescents are less likely to learn from punishments (aversive context) than from rewards (appetitive context) [95,139].

thus favouring adolescents [92,108]. Second, in many cases the available evidence might not objectively favour any option. In such cases there is no way to improve performance, but continued attempts to interpret outcomes as evidence can consume cognitive resources. In line with this, one study showed that when reward and punishment history did not favour one option over the other (when participants were asked to repeatedly choose between two novel symbols that had the same chance of being rewarded/punished), adults took longer than adolescents to reach decisions, thus incurring greater cognitive costs in terms of time spent to reach the decision [84].

These findings are consistent with the notion that adult learning might be generally optimised for narrower tasks such as instrumental learning in stable environments, but that adolescent learning styles might be adapted for detecting novel solutions in more volatile environments for the purpose of exploration and innovation [91]. Adolescents might have some learning advantages over adults in novel environments because they encounter such environments more frequently. Indeed, adolescence can be considered to be a stage of environmental volatility because of the gradual detachment from one's caregivers and exploration of new activities and new social and romantic relationships [109]. Under this lens, lower specificity in learning (or higher temperature) in adolescence could also be due to adolescents having less knowledge about themselves and the world than adults (in Bayesian terms, they have broader priors). In other words, many of the environments adolescents face are novel to them. As adolescents explore, their uncertainty about themselves and the world gradually decreases [90,110], and thus specificity increases (temperature decreases) with learning [111]. As outlined above, by providing a computational understanding of the developmental trajectories in learning, studies such as these can provide insights into what type of learning environments might be optimal for people of different ages.

Implications for mental health and education

Pavlovian learning and mental health

Differences in Pavlovian learning have been associated with mental health outcomes across development. Evidence of increased Pavlovian reward learning in adolescence has led researchers to propose that adolescence is a critical period of addiction vulnerability [37], and addictive disorders commonly begin in adolescence [112]. Further, the synergy between social and drug rewards during this period might increase the potential for socially motivated substance abuse. Indeed, adolescents are more likely to use drugs and alcohol if those in their social group do [113]. Beyond addiction, reduced Pavlovian reward learning has also been associated with depression in adults and adolescents, and depressed individuals show blunted neural and behavioural responses to reward [114,115]. In line with this, novel depression treatments, such as positive affect treatment, propose targeting reward learning by emphasising and encouraging learned associations between rewarding behaviours and positive mood (although this remains to be investigated in adolescents under age 18 years) [116].

Pavlovian threat learning is a key component in the development and maintenance of threat-related mental health conditions such as anxiety and phobias. The ability to extinguish and retain the extinction of a threat response is a crucial component of anxiety treatments such as exposure therapy [117] in which individuals are helped to overcome anxiety through repeated exposure to feared scenarios. Although traditional methods of exposure therapy might be less effective for adolescents (particularly younger adolescents) than for adults [118,119], harnessing the salience of social cues might have positive ramifications. For example, researchers have proposed using safety cues to increase tolerability and reduce attrition in the treatment of adolescent anxiety [120]. Although parents and caregivers might successfully serve as safety cues for children

[121], a supportive friend might better help adolescents to effectively buffer stress [122,123]. Considering experimental evidence regarding Pavlovian learning in adolescence might help clinicians to create a developmentally tailored treatment approach.

Instrumental learning and mental health

Computational psychiatry studies have shown that a variety of mental health problems, which often emerge in adolescence, are characterised by aberrant instrumental learning computations [124]. For example, in 18–25-year-olds, heightened punishment learning was associated with tighter coupling between neural signals and some computational measures (negative **prediction errors**) in individuals with higher levels of anxiety [125]. A recent meta-analysis also demonstrated that adults with depression or anxiety exhibit higher punishment and lower reward learning rates relative to adults without anxiety or depression [126]. Impaired learning from prediction errors has also been observed in other psychiatric disorders, including psychosis, alcohol abuse, and obsessive-compulsive disorder [124]. Although the majority of this research has been conducted with adults [124], researchers have proposed that combining computational psychiatry and developmental neuroscience could inform our understanding of the cognitive processes and neural mechanisms that lead to mental health disorders in adolescence.

Education

Applying this sensitivity versus specificity framework to associative learning also provides insights into adolescent education. In the classroom, students might benefit from increased novelty and changing environments – for example, a variety of lesson formats and rotating period schedules. Educators could encourage the exploration of different problem-solving approaches, which might strengthen the internal motivation of students by encouraging their natural tendency to explore. Finally, peers are highly salient for adolescents and could be leveraged to achieve behavioural change, for example by emphasising peer-led learning or and co-production in educational settings.

Concluding remarks

Across the lifespan, adolescence is characterised by heightened affective and social sensitivity, but does this enhance or impair learning? Based on evidence from human, rodent, and computational studies, we have suggested that the answer to this question might depend on the extent to which learning demands sensitivity versus specificity. In Pavlovian conditioning, increased sensitivity might make it possible for adolescents to learn associations quickly and robustly, and even incur difficulties in extinguishing (or suppressing) learned associations. However, even in this simple form of learning, adolescents show elements of reduced specificity. For example, with regard to Pavlovian learning of both reward and threat, adolescents are less able than adults to discriminate between various magnitudes and probabilities, and are more likely to generalise learning to novel situations. This reduced specificity might have a larger impact on instrumental learning which more centrally involves decision-making. Indeed, adolescents frequently show disadvantages relative to adults in instrumental learning, although these might reverse in more volatile environments. Overall, we propose that a developmental shift from sensitivity to specificity might account for disparate findings across the Pavlovian and instrumental learning literature where adolescents show strong acquisition, generalisation, and exploration relative to adults who show stronger discrimination, exploitation, and extinction (Figure 3). These findings raise several unresolved issues (see Outstanding questions) and provide an increasingly nuanced picture of how affective and social learning develops in adolescence. In future research it will be important to investigate not only how affective and social factors influence learning performance but also how these factors might affect shifts in sensitivity versus specificity distinctions in learning during adolescence.

Outstanding questions

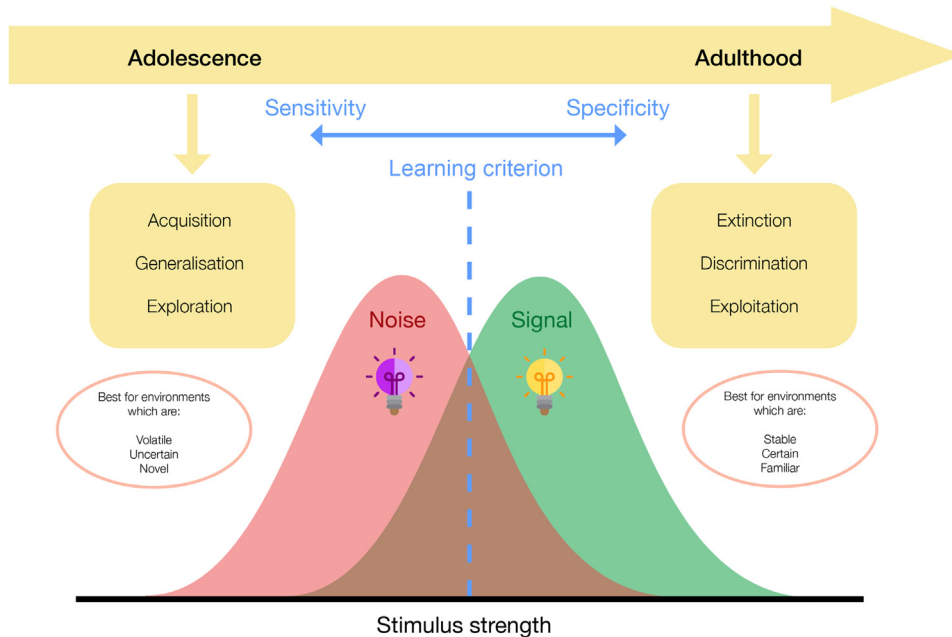
How does Pavlovian versus instrumental learning differ as a function of age in adolescence? Do they involve overlapping or discrepant neural substrates?

Do non-social and social rewards and threats affect learning differently in adolescence relative to other age groups?

How do adolescents learn under conditions of social isolation, social exclusion, social evaluation, or social threat?

How can knowledge of adolescent sensitivity versus specificity be extended beyond associative learning to more ecological learning environments?

How do the computational underpinnings of learning change across development, and how do these trajectories relate to mental health disorders?



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Figure 3. Sensitivity versus specificity. Adapted from signal detection theory, the figure shows a theoretical model of how this framework might be applied to understand differences in associative learning across adolescent development. The learning criterion (broken blue line) represents the strength a signal must reach to be detected – or, in this case, learned (information to the right of the learning criterion is learned). Shifting the learning criterion to the right affords the learner greater specificity but lower sensitivity (fewer hits and fewer false alarms). Shifting the learning criterion to the left affords the learner greater sensitivity but lower specificity (more hits and more false alarms). For example, as shown in Figure 1, an individual might learn to associate a yellow light with a food reward. Yellow lights represent a meaningful 'signal' in this learning environment because they are frequently paired with a food reward. However, this environment also contains other stimuli, such as purple lights. Therefore, purple lights represent 'noise' in this learning environment. Whether an individual responds to the signal or noise depends on the stimulus strength and the learning criterion. The learning criterion (broken blue line) represents the optimal signal-to-noise ratio for the given distribution (maximising hits while minimising false alarms).

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Declaration of interests

No interests are declared.

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