

Reward processing and reinforcement learning: from adolescence to aging

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Abstract

The neurocognitive systems that underlie the ability to process rewards and learn from reinforcement undergo substantial changes across the adult lifespan. Adolescence is often characterized as a developmental period with a heightened sensitivity to reward and healthy aging is typically associated with a decline in learning from reinforcement. In this Chapter we review how the psychological and neural mechanisms that underpin reward processing and reinforcement learning change from adolescence to older adulthood. We consider behavioral and neuroimaging studies, as well as how different reward and learning contexts, such as gain vs. loss and social vs. non-social information, may alter reward processing and reinforcement learning abilities. We end by considering the challenges and opportunities of conducting developmental and aging studies in computational neuroscience and suggest future directions for the field.

Keywords

Adolescence, adulthood, aging, ambiguity, behavior, decision making, discounting, effort, learning, punishment, reinforcement, reward, risk, social, uncertainty.

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Key Points

- We review studies examining reward processing and reinforcement learning across the adult life course
- Reward processing is affected by several factors including time, effort, uncertainty and anticipation that may each display different age-related trajectories
- Reinforcement learning includes different types of learning such as habitual, goal-directed, instrumental and Pavlovian learning, which may each display different age-related trajectories
- The neural architecture supporting reward and reinforcement undergoes change from adolescence to older age
- Reward processing and reinforcement learning in different contexts such as social vs. non-social can show different age-related trajectories
- These findings suggest important targets to scaffold healthy reward processing and learning across the lifespan

Introduction

Processing rewards and learning from reinforcement is essential in everyday life. When we make a choice, we must compare the rewards – such as money – with the costs – how long we need to wait, how much effort is required, or how uncertain the outcome is. After the choice, we need to learn whether to repeat it or try a different course of action. But how do we decide whether rewards are worth the costs and then learn from reinforcement? Despite the centrality of reward processing and learning throughout our lives, research suggests that these abilities change profoundly from adolescence to old age. Adolescence is often considered a developmental period with heightened sensitivity to reward, resulting in risky and impulsive behaviors (Galván, 2013; Van Leijenhorst et al., 2010). In parallel, aging is associated with declines in cognitive processes that are crucial for learning, such as working memory (Samanez-Larkin and Knutson, 2015). There are also co-occurring neural changes throughout the lifespan, particularly in basal ganglia and prefrontal cortex, which underpin reward processing and reinforcement learning (Hartley and Somerville, 2015; Samanez-Larkin and Knutson, 2015). Understanding why, when, and how behavioral and neural changes happen is essential if we want to optimize reward processing or learning strategies and intervene when these go wrong.

We start the Chapter by discussing studies of reward processing where learning is not required and putative similarities and differences across the adult lifespan. We then discuss different types of reinforcement learning and end by considering the influence of different contexts, as well as challenges and opportunities for adult lifespan research.

Reward Processing

First, we focus on studies that have examined reward processing outside the context of learning. We review studies of delay discounting, effort-based decision making, decisions under uncertainty, and reward anticipation.

Intertemporal Decision Making

Temporal discounting, also known as delay discounting, refers to the phenomena that the same reward is valued less if you have to wait for it, than if you were to receive it immediately (Frederick et al., 2002). Typical paradigms involve choices between a smaller but sooner (often immediate) reward and a larger reward with a longer delay (Figure 1A). For example, would you prefer \$10 today or \$20 next month? People of all ages generally behave economically ‘irrationally’, discounting delayed rewards to choose sooner rewards, even when they are smaller. Sensitivity to delay can be

measured in individuals using computational models of discounting (Green et al., 1996, 1994). An early neuroimaging study in young adults found activity in frontal and striatal regions including ventromedial prefrontal cortex (vmPFC), posterior cingulate cortex (PCC) and ventral striatum tracked the value of delayed rewards, based on individuals' tendencies to be patient or impatient (Kable and Glimcher, 2007).

Adolescence

Robust evidence shows willingness to wait for rewards increases between childhood and adulthood (de Water et al., 2014; Olson et al., 2007; Ripke et al., 2012; Scheres et al., 2014, 2006; Steinberg et al., 2009; van den Bos et al., 2015; Yu et al., 2021). Willingness to wait increases sharply around age 15-16 (de Water et al., 2014), reaches adult levels by late adolescence (Steinberg et al., 2009), or peaks at age 14 and then declines into adulthood (Scheres et al., 2014). Higher patience from childhood to adolescence is apparent even when delays are short (Scheres et al., 2006) or how much participants value money is taken into account (de Water et al., 2014). Neurally, decreasing discounting during adolescence has been linked to frontostriatal (Christakou et al., 2011) and parietal regions (Ripke et al., 2012). One study showed that delay length was linked to parietal regions whereas striatal areas were associated with the amount of money on offer (de Water et al., 2017). Finally, studies using electroencephalogram (EEG) recordings and delay discounting tasks have also suggested that electrical activity linked to immediate rewards develops early, whereas signals reflecting waiting for delayed rewards develop later in adolescence (Yu et al., 2021).

Aging

Initial studies of delay discounting comparing young and older adults showed increased willingness to wait for rewards in older age (Eppinger et al., 2012; Green et al., 1994; Löckenhoff et al., 2011). However, results were inconsistent with some showing no effect (Löckenhoff and Samanez-Larkin, 2020; Rieger and Mata, 2015; Samanez-Larkin et al., 2011) or decreased patience with age (Read and Read, 2004). A recent meta-analysis combining all of this work (n=104,737) found evidence for no difference in how money is discounted across the adult lifespan (Seaman et al., 2022). Despite no differences in levels of discounting between older and younger adults, it is possible that intertemporal decisions rely on distinct processes, motivations, and neural systems at different ages. Evidence for more nuanced differences was suggested by opposing effects of decision conflict on discounting between older and younger adults (Eppinger et al., 2018). High decision conflict – two options close to the participant's indifference point rather than one that was strongly preferred – made older adults more impatient but younger adults more patient, and this was linked to their working memory ability. Another factor perhaps explaining inconsistency is that

individual income strongly predicts temporal discounting, with older adults on low incomes less willing to wait for rewards than those on higher incomes (Green et al., 1996).

Although the meta-analysis suggested financial discounting is stable across adulthood, discounting rewards that are not economic shows differing age trajectories. When rewards are social or health-related, older adults have stronger preferences for the sooner rewards than young adults (Seaman et al., 2016). Age differences in discounting were also found for choices involving charitable donations. Only older participants chose timing options that maximized their overall donations, whereas preferences were similar between young and older adults when money was for themselves (Sparrow and Spaniol, 2018).

Effort-based Decision Making

Just as people discount or value rewards less if they have to wait for them, rewards are valued less if we have to work for them (Apps et al., 2015; Hull, 1943; Kool and Botvinick, 2018; Westbrook and Braver, 2015). If all else is equal, people choose options that require less effort as effort is aversive. Various experimental paradigms have been used to manipulate effort. For example, participants might choose between a small reward that does not require effort and a high-reward high-effort option that requires them to solve cognitive problems (Figure 1B), remember lots of numbers (cognitive effort), squeeze a grip force device (Figure 1C) or click a button many times (physical effort) to obtain it. Like temporal discounting, the impact that the effort required has on devaluing the reward available can be captured by a discounting parameter (Białaszek et al., 2017; Hartmann et al., 2013; Klein-Flugge et al., 2015). The discounting parameter can vary in shape (linear, hyperbolic and parabolic functions are commonly-used discount functions). Different types of effort, for example cognitive vs. physical have been associated with different discounting preferences. For example, computational models of cognitive and physical effort discounting have shown that individuals have preferences to specifically avoid either cognitive or physical effort or both, despite no overall differences in discounting (Chong et al., 2017). Studies in young adults have linked dorsal anterior cingulate cortex (ACC) and anterior insula with effort and motivation (Chong et al., 2017; Le Heron et al., 2018; Lockwood et al., 2022; Pessiglione et al., 2018) and frontal and striatal regions with reward (Klein-Flugge et al., 2015; Lopez-Gamundi et al., 2021; Müller et al., 2021). All these regions also track subjective value, which combines the effort required and reward available (Croxson et al., 2009; Holroyd and McClure, 2015; Soutschek et al., 2018; Vassena et al., 2014; Verguts et al., 2015).

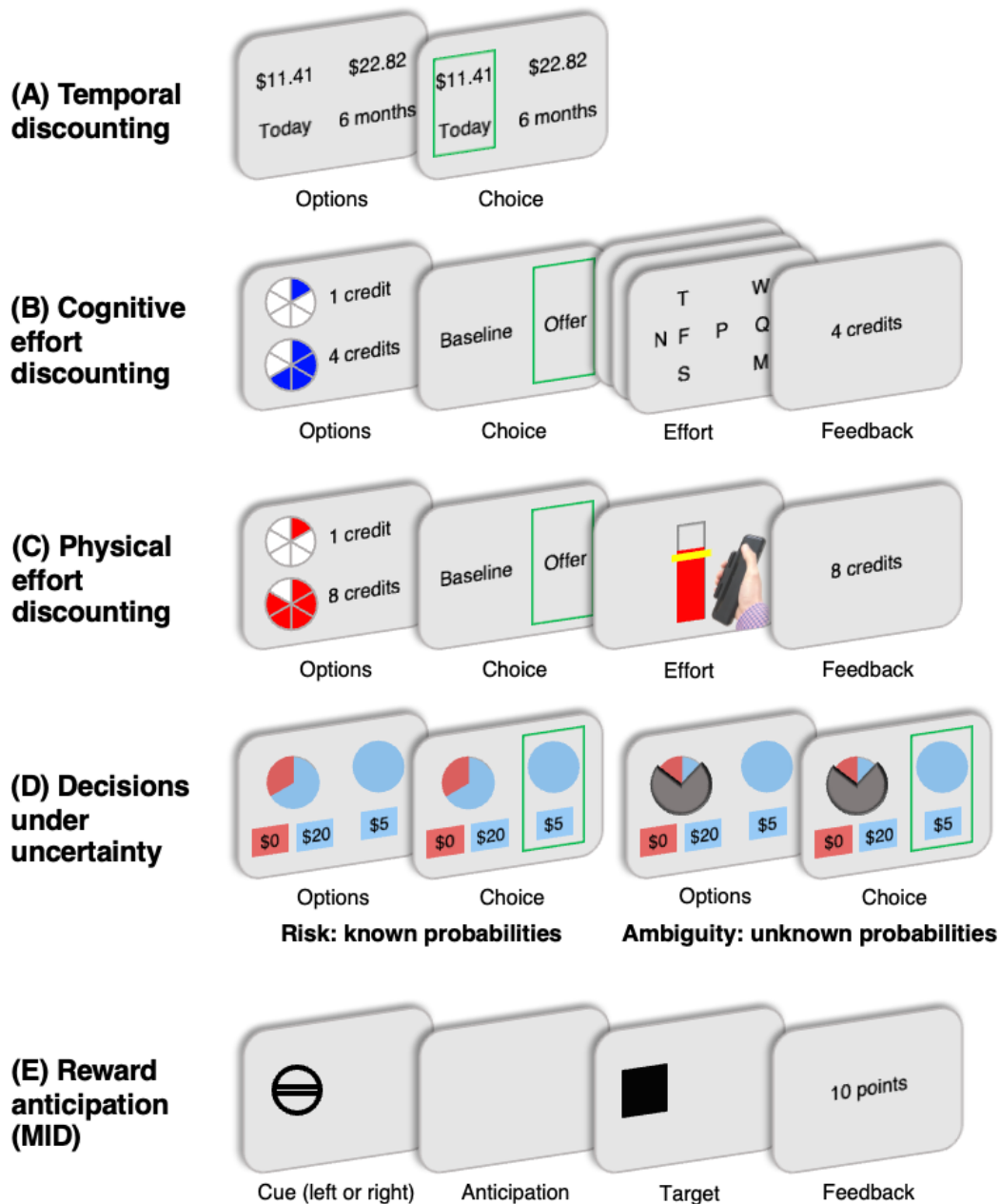


Figure 1. Experimental tasks to measure reward processing during decision-making and reward anticipation. (A) Example of a canonical temporal discounting task with a choice between an immediate smaller reward and a delayed larger reward (e.g. Seaman et al., 2016). (B) Example of tasks measuring decisions under uncertainty involving risk (left) or ambiguity (right). In risk tasks the uncertain option has known probabilities whereas in ambiguous tasks they have unknown probabilities. Blue full circles represent a certain smaller reward whereas the red and blue “spinner” gives a chance of no reward and a chance of a larger reward (e.g. Blankenstein et al., 2016). (C) Example of a cognitive discounting task using a visual search of differing difficulties to manipulate levels of cognitive effort. Participants choose between a low-reward, low-effort baseline option and a high-reward, high-effort offer. (D) Physical effort task with the same structure as (C), both from (Chong et al., 2017). (E) Example of the Monetary Incentive Delay task to separately measure brain activity during reward anticipation and feedback showing a reward outcome (e.g. Knutson et al., 2000).

One factor that seems to moderate age differences is whether uncertain outcomes are gains or losses. Multiple studies have shown lower risk seeking in older age is limited to the gain domain with either no age differences for losses (Best and Charness, 2015; Rutledge et al., 2016) or increased risk seeking in the loss domain (Best and Freund, 2018; Mather et al., 2012; Tymula et al., 2013) but also see (Kurnianingsih et al., 2015). This pattern of risk preferences was distinct from ambiguity where older adults' preferences were identical to adults of other ages for gains (ambiguity aversion) but only older adults were also averse to ambiguity for losses (Tymula et al., 2013).

Adolescence

There is evidence that pre-adolescent children (aged 5-11) are sensitive to different levels of cognitive effort (Ganesan and Steinbeis, 2021). For example, adolescents aged 13-17 are less willing to invest cognitive effort for rewards when the level of cognitive effort required increases (Kramer et al., 2021) and discount monetary rewards by physical effort like adults do (Rodman et al., 2021). Similar brain areas have been shown to be involved in adolescents and adults during cognitive effort discounting, particularly dorsal ACC and anterior insula (Mies et al., 2018).

Other studies suggest the type of reward and effort is an important factor for any age related differences. Adolescents are more willing than adults to exert physical effort when rewards are success in a computer game (Sullivan-Toole et al., 2019) and to obtain feedback from a peer (Rodman et al., 2020). Another factor is ability. Adolescents' willingness to invest cognitive effort has been associated with their accuracy at performing the cognitive task (Kramer et al., 2021), which increases with age (Pelegrina et al., 2015). Moreover, adolescents might waste energy by exerting more force than required and exerting effort for small rewards, rather than saving energy for large rewards (Rodman et al., 2021). These studies highlight the importance of accounting for age-related differences in reward value (for example money, computer games or social information) and physical or cognitive ability to assess the development of effort discounting (Contreras-Huerta et al., 2020; Davidow et al., 2018).

Aging

Declines in cognitive abilities in older adulthood may lead to cognitive tasks being experienced as subjectively more effortful, making it difficult to isolate age-related changes in willingness to exert cognitive effort (Hess and Ennis, 2012). Indeed, one study showed older adults experienced cognitive effort as more costly than younger adults (Westbrook et al., 2013). Physical abilities also decline with age (Faulkner and Brooks, 1995). However, physical effort can be individually tailored to participants' ability in experimental tasks by using percentages of their maximum grip strength,

always under 100%, as different levels of effort. Using this approach one study showed older adults were more willing to invest effort when gaining money for themselves and another person compared young adults (Lockwood et al., 2021). Interestingly the difference in motivation between young and older adults was larger when rewards were for another person, compared to the participant themselves. Age effects may also differ between gain and loss domains, with older adults more likely to choose physically easy options than young adults in gain contexts, but no difference between age groups in loss contexts (Byrne and Ghaiomy Anaraky, 2020). Finally, other research has considered levels of apathy, a symptom of reduced motivation that characterizes many psychiatric and neurological disorders but is also present to varying degrees in the general population (Husain and Roiser, 2018). A review on apathy in older adulthood found age-related increases in samples with diseases or disorders but concluded healthy aging is not associated with increased apathy (van Reekum et al., 2005). Future work could build on these behavioral studies to assess how the neural mechanisms of motivation and effort-based decision making interact with age-related changes in the biology underlying cognitive and physical capabilities.

Decision Making Under Uncertainty

Another type of decision that may show age-related differences is when outcomes are uncertain. Interestingly, neuroimaging evidence in healthy young adults has suggested overlap between decisions involving time, effort and uncertainty in regions such as vmPFC, striatum, and lateral prefrontal cortex, as well as activations unique to each cost (Soutschek and Tobler, 2018). There is also evidence that distinct subregions in medial and orbitofrontal cortex are involved in each context (Floresco et al., 2008). An important distinction within uncertainty is between risk and ambiguity (Figure 1D). Risky outcomes have a known probability, like a lottery with 100 tickets creating a 1% chance of winning. Ambiguity refers to unknown probabilities, for example if you don't know how many lottery tickets have been bought. A functional magnetic resonance imaging (fMRI) meta-analysis in young adults separating risky decisions and ambiguous decisions, with perceptual decisions as a control, found common regions across risk and ambiguity but also differences (Poudel et al., 2020). Choices involving risk were associated with activity in striatum and ACC whereas decisions under ambiguity were linked with lateral prefrontal cortex and insula.

Adolescence

Adolescence is often characterized as a time of risk-taking or risk-seeking behaviors (van Duijvenvoorde et al., 2016) and there is evidence adolescents are more likely to choose uncertain gambles than adults in reward-based decision-making tasks (Defoe et al., 2015; van den Bos and Hertwig, 2017). Increased neural sensitivity to reward

has been suggested as a potential mechanism and adolescents have shown increased ventral striatum activity when accepting risky gambles, even when risk-taking behavior is matched with adults (Barkley-Levenson and Galván, 2014). However, other work has found adolescents do not differ in choices involving risk, with known probabilities. This was despite declining impatience in the same samples, suggesting a dissociation between the development of decisions involving risk compared to time (de Water et al., 2014; Olson et al., 2007; Scheres et al., 2006). In contrast, many studies have found lower aversion to, or increased tolerance of, ambiguity in adolescence compared to adulthood. Adolescents have been shown to have lower ambiguity aversion both when choosing between a risky and an ambiguous reward (Li, Brannon and Huettel, 2015) and between a certain and an ambiguous reward (Blankenstein et al., 2016; Tymula et al., 2012).

These differing findings highlight the possibility of distinct developmental trajectories for processing risk and ambiguity (Blankenstein et al., 2021) and individual differences in neural activity within adolescents (aged 11-24) support this distinction. Increased risk-taking has been associated with higher ventral striatum activity, whereas ambiguity was linked to lower insula and dorsomedial PFC activity during decisions, but higher dorsolateral PFC activity during outcomes (Blankenstein et al., 2018). Real-life “risk-taking” behaviors might be more accurately characterized by ambiguity, as the chance of negative outcomes like injury or death is unknown. Tolerance to ambiguity but not risk has been associated with real-life risk-taking, such as taking drugs or drinking and driving (Blankenstein et al., 2016; van den Bos and Hertwig, 2017), although risk-taking and associated nucleus accumbens activity predicted future binge drinking (Morales et al., 2018). While these studies highlight negative outcomes of risk-taking, behaviors involving uncertainty can be positive, for example attending an audition or helping others (Crone and van Duijvenvoorde, 2021; Duell and Steinberg, 2019).

Aging

Older adulthood has been associated with declines in self-reported impulsivity, suggesting that processing uncertainty may also differ across the adult lifespan (König, 2021). Initial work suggested age differences in risk-taking were only apparent when choices relied on learning, due to reduced learning ability not different risk preferences (Mata et al., 2011), or when one option was certain but not when deciding between two uncertain options (Mather et al., 2012). Older and younger adults were similar in probability (and effort and time) discounting behavior and neural activity, with subjective value across tasks and ages associated with medial prefrontal cortex response (Seaman et al., 2018). However, a systematic review found evidence that older adults were less willing to take risks than younger adults, across experimental tasks (Best and Charness, 2015). Longitudinal and cross-sectional analysis of self-

report and experimental measures in a large sample concluded risk-taking was a trait (reasonably stable over time) but still decreased with age. This decrease translated into substantially different preferences in choices between a 50:50 chance to win €300 (expected value €150) and a safe option of varying amounts. Participants aged 18-30 required the safe option to be €93.60 on average to be preferable to the risky lottery, whereas older participants (70-85) preferred the safe option when it guaranteed them just €44.70 (Josef et al., 2016). Data on self-report and similar lottery questions from over 80,000 people in 76 countries also showed robust evidence for decreasing risk tolerance with age (Falk et al., 2018). Declining tolerance for risky rewards in old age has been linked to decreasing grey matter in the right posterior parietal cortex, with individual differences in this measure accounting for risk preferences better than age (Grubb et al., 2016).

Reward Anticipation

In the sections above, we have considered differences in how adolescents and older adults integrate rewards and costs, including time, effort and uncertainty, to make decisions. In the next section we review findings on age-related differences in reward anticipation before covering reward learning. Some of the first developmental studies on changes in reward processing invoked a now infamous paradigm, the monetary incentive delay task (MID; Knutson et al., 2000; Figure 1E). The adoption of the MID was inspired by concurrent work by Wolfram Schultz and colleagues that had shown firing of dopamine neurons in monkeys in the ventral tegmental area (VTA) to cues that indicated the high probability of receiving a reward during anticipation of rewards (Schultz et al., 1997). These same neurons did not fire in anticipation of a low probability of reward. The MID was designed to examine similar patterns of activity using human fMRI. In the MID, participants see a colored square and then respond to a white target with a speeded button press (Knutson et al., 2000). They then receive feedback showing whether they have won the reward or not. The task outcomes are calibrated to participants' own reaction times such that participants succeed on roughly two thirds of trials. This separation of cue anticipation and reward or punishment delivery allowed researchers to measure neural responses at different stages of reward and punishment processing, with a focus on anticipation, paralleling the work by Schultz and colleagues (Schultz et al., 1997). Meta-analyses of fMRI studies in healthy adults showed the striatum, which receives strong input from the VTA, was involved when anticipating rewards (Figure 2A), receiving rewards (Figure 2B) and anticipating losses (Figure 2C), as well as other regions linked to anticipation such as anterior cingulate cortex and insula (Oldham et al., 2018; Wilson et al., 2018).

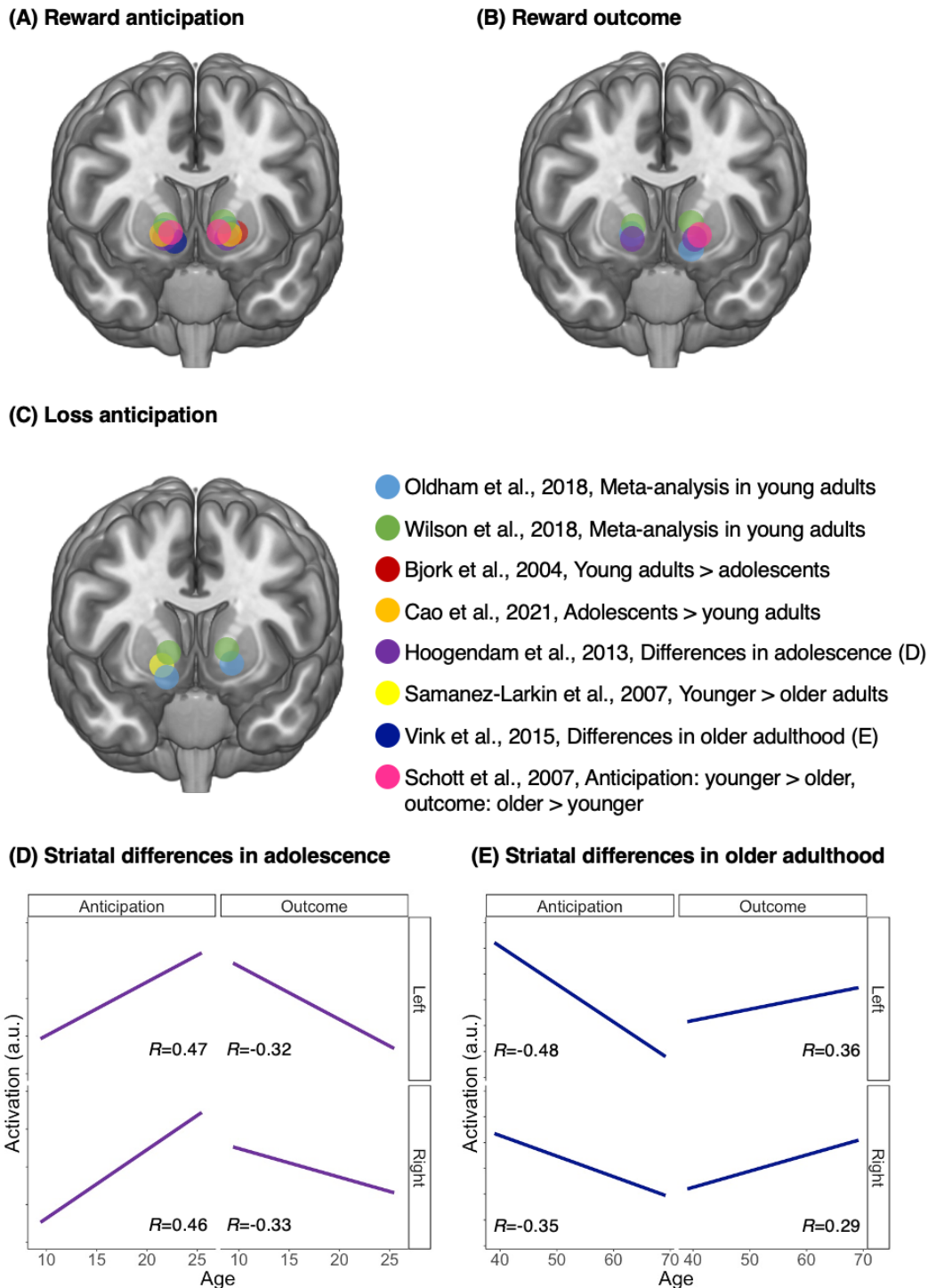


Figure 2. Striatum activity during reward processing and differences across the lifespan. Results from the monetary incentive delay task (Figure 1E) show activity in the striatum during **(A)** reward anticipation **(B)** reward outcome and **(C)** loss anticipation. Findings are from meta-analyses in healthy adults (Oldham et al., 2018; Wilson et al., 2018) and developmental work on adolescence (Bjork et al., 2004; Cao et al., 2021; Hoogendam et al., 2013) and aging (Samanez-Larkin et al., 2007; Schott et al., 2007; Vink et al., 2015). **(D)** Across adolescence, age is associated with increasing activity during reward anticipation (left) but decreasing activity during reward outcomes (right) in both left and right ventral striatum (Hoogendam et al., 2013) **(E)** The opposite pattern is found across older adulthood suggesting older adults also show reduced activity during anticipation but increased activity for reward outcomes like younger adolescents (Vink et al., 2015).

Adolescence

Differences between adolescents and adults in neural responses during reward anticipation were predicted based on the idea that adolescence is a developmental period with increased risky behavior and impulsivity, as well as heightened sensitivity to reward. Generally, work using the MID and other similar tasks has supported the idea that reward anticipation is processed in similar brain structures in adolescents compared to adults (Figure 2). These regions include the basal ganglia (striatum, caudate and nucleus accumbens) as well as medial prefrontal and orbitofrontal areas (Bjork et al., 2007, 2004; Cao et al., 2021, 2019; Lorenz et al., 2014). An early study found that adolescents showed less ventral striatal activity than adults when anticipating rewards, but no age differences when rewards were consumed (Bjork et al., 2004). Lower activity in adolescents was interpreted within a hypoactivation framework, where diminished ventral striatal activity could lead to seeking more extreme incentives (Spear, 2000). However other work, including a recent longitudinal study (age 14 to 19) with a large sample of adolescents (n=1,241), showed adolescents have increased activity or hyperactivation in ventral striatum during reward anticipation (Cao et al., 2021; Lorenz et al., 2014). Striatal hyperactivation in adolescence compared to adulthood has been found when consuming, as well as anticipating, reward in multiple studies (Braams et al., 2015; Ernst et al., 2005; Galvan et al., 2006; Schreuders et al., 2018; Silverman et al., 2015) and linked to other factors such as increased dopamine signaling and risk-taking (for reviews see Somerville et al., 2010; Telzer, 2016; van Duijvenvoorde et al., 2016). Finally, one study found an age-related increase across adolescence (age 10-25) for activity in ventral striatum during reward anticipation (as well as other striatal regions, insula and ACC) but age-related decline in reward outcome activity in ventral striatum (Hoogendam et al., 2013; Figure 2D). These opposing effects of age on striatal activity for reward anticipation and consumption were interpreted as the development of ability to predict rewards, which shifts activation away from the reward itself, to the anticipatory cue. This distinction may also explain inconsistencies in other findings as the nature of the task, cues and instructions may affect how easily or quickly the cue is associated with the reward outcome.

Aging

It is well known that levels of dopamine can decline even in healthy aging (Peters, 2006). Therefore, studies of the MID in healthy aging can be informative for understanding if responses in dopamine-rich basal ganglia areas such as caudate and striatum also display age-related differences. Intriguingly, despite age-related dopaminergic declines, there is some evidence of intact striatal activation to anticipated rewards in older adults (Samanez-Larkin et al., 2007; Spaniol et al., 2015). However, there was an age-related reduction in neural responses and negative

feelings for loss cues (Samanez-Larkin et al., 2007). In contrast, other studies have found lower activity in the striatum during reward anticipation in older, compared to younger, adults (Dreher et al., 2008; Schott et al., 2007; Vink et al., 2015). These studies also found evidence that older adults had increased activity during reward receipt relative to younger adults (Schott et al., 2007; Vink et al., 2015). As with the findings in adolescence, age differences in opposing directions for reward anticipation and receipt were interpreted as due to age differences in predicting the cue, which shifts activation from the outcome to the anticipatory cue (Figure 2E). This shift occurs in younger adults and is critical for reinforcement learning. Finally, findings from comparing reward anticipation in adolescents, young adults, and older adults have shown increased insula and ACC activity for both adolescents and older adults, relative to younger adults, and increased activity in dorsolateral PFC and inferior parietal lobule activity for the older group only (Lorenz et al., 2014). These results suggest that while ventral striatum is a key region for reward anticipation and reward receipt, and activity here changes across the adult lifespan, a wide network of regions is involved.

Reinforcement Learning

From our first days in the world, we learn from reinforcement by reward. Ten-week-old infants increase the rate at which they kick their feet towards a brightly colored wooden mobile (Rovee and Rovee, 1969). Six-month-old infants are able to learn to look more often at a colored shape if it leads to a video cartoon (reward) than leads to nothing (Tummeltshammer et al., 2014). Given this early aptitude for learning, it is perhaps surprising that learning abilities could change so dramatically across development. However, several studies suggest that reinforcement learning does change substantially in adolescence and older adulthood. In the next section we introduce reinforcement learning theory and the biological basis of learning from rewards, then examine age differences in different types of learning.

Findings from the monetary incentive delay task suggest similar basal ganglia and prefrontal regions are involved across adolescence and older age during the first steps of learning: anticipating reward and processing reward receipt. But what about when that information needs to be integrated for learning? Reinforcement learning theory (RLT) provides a theoretical, mathematical, and biologically plausible framework to understand how these learning and reward processing effects occur. RLT states that we learn based on expectations of reward and punishment. When our expectations are different from what happens we learn a lot, but when what we expect to happen does happen, we learn much less. RLT is arguably one of the most important influences on psychology, neuroscience and economics (Dayan and Balleine, 2002; Sutton and Barto, 1998).

Associative Learning

Common tasks to assess reinforcement learning require participants to learn associations by performing an action, such as selecting one of two symbols, and observing the outcome (e.g. Pessiglione et al., 2006; Figure 3A). Outcomes can be rewards or punishments and learning about these different outcomes might show different developmental trajectories. Many tasks are probabilistic, meaning that actions are not always associated with a given outcome and participants must learn the more frequent associations. In reversal learning tasks, the pairing between actions and outcomes switches during the task to measure participants' ability to flexibly learn new associations.

Adolescence

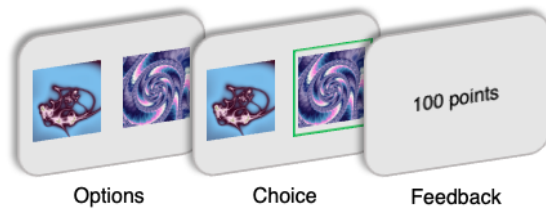
Developmental studies of reinforcement learning suggest that adolescents are more optimal in their learning than children, and young adults more optimal than adolescents (Nussenbaum and Hartley, 2019). Similarly, results from a deterministic learning task found increasing learning rates across adolescence (Master et al., 2020). While adults have been shown to be able to learn from both reward and punishment, there is evidence that adolescents learn better than adults from reward (Xia et al., 2021), but are less likely to learn from punishment (Palminteri et al., 2016). This imbalance in learning or heightened reward sensitivity may help explain the negative real-life outcomes common during adolescence such as increased alcohol intake, substance use and risky sexual behaviors. However, other studies have found heightened reward sensitivity resulted in more optimal learning and memory for rewards in adolescents compared to adults (Davidow et al., 2016). Here, prediction error signals were found in the hippocampus and stronger connectivity between hippocampus and striatum during reinforcement was linked with better learning. There is also inconsistency in whether reward, punishment or both differ across this developmental period. One issue in the literature is whether studies evaluate the optimal learning rate or the association between learning rate and accuracy for a given task (Zhang et al., 2020). The nature of the task also determines whether focusing on positive or negative prediction errors is beneficial. For example, one study showed that when ignoring irrelevant negative feedback was beneficial, learning ability increased from childhood to adulthood and was associated with connectivity between ventral striatum and medial prefrontal cortex (van den Bos et al., 2012).

Reversal learning tasks (with changeable outcome probabilities) require more flexible learning and there is evidence that overall accuracy and ability to use appropriate strategies increases from childhood to adulthood (Crawley et al., 2020). Using these tasks, adolescents have shown poorer punishment learning in compared to adults (Javadi et al., 2014), increase in reward learning rates in early adulthood (Eckstein et al., 2022) or increased punishment learning in adolescents compared to adults (Hauser et al., 2015; van der Schaaf et al., 2011). These differences have been associated with activation in anterior insula (Hauser et al., 2015) or no differences in neural response (Javadi et al., 2014). Recent work highlights the importance of experimental paradigms that can distinguish reward and punishment learning ability from impulsivity, characterized by a bias to initiate action versus withholding responses. Data from such a paradigm with a large sample (n=742) from several countries across Europe demonstrated that punishment learning improves across adolescence (from 9-18) whilst reward learning remains stable. In parallel, action initiation biases decrease with age (Pauli et al., 2022).

Aging

Aging is associated with alterations in several cognitive abilities. In contrast to some studies of basic reward processing and monetary incentive, that suggest relative stability across adulthood, it is generally agreed that learning declines in old age (Eppinger et al., 2011; Samanez-Larkin et al., 2014). This is also the case when non-learning tasks (MID) and learning tasks are compared within the same participants (Eppinger et al., 2011; Samanez-Larkin et al., 2014). Studies have found that how the brain represents learning signals about reward is reduced in healthy aging. When older adults complete experimental tasks where they need to learn associations between their choices and outcomes, they appear to be worse at learning, particularly when the associations are probabilistic (Eppinger et al., 2011) or change (Mell et al., 2005). Studies suggest that dopamine receptors in the ventral striatum that are crucial for learning decline with age (van Dyck et al., 2002), which might help to explain learning changes. Intriguingly, one study found that learning could be improved in older adults if they were given a drug called L-DOPA, which increases the level of dopamine in the brain (Chowdhury et al., 2013). Therefore, learning abilities seems to improve from childhood to adolescence before somewhat declining in older age.

(A) Reinforcement learning



(B) “Model-based” vs. “model-free” learning (2-step task)



(C) Pavlovian vs. instrumental learning task

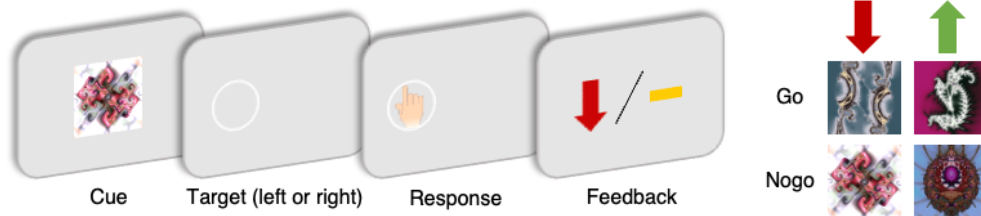


Figure 3. Learning tasks used in research on lifespan development. **(A)** Basic reinforcement learning tasks require participants to choose one of two images or symbols. One is associated with a higher chance of reward and the other with a lower chance of reward. Participants see whether they received a reward and learn by trial and error to choose the option which maximizes rewards (e.g. Pessiglione et al., 2006). This task therefore measures “model-free”, instrumental learning. Other versions use punishments instead of rewards. **(B)** Two-step task used to separate habitual from goal-directed or “model-free” from “model-based” learning (Daw et al., 2011). Participants first choose between one of two images (green) and their choice probabilistically leads to one of two states depicted by different colors (blue or grey; common transition 70%, uncommon transition 30%; see right panel). In the second choice, participants choose between these options, which are probabilistically associated with reward (or punishment versions). **(C)** Task to measure Pavlovian biases during learning (e.g. Guitart-Masip et al., 2012). Participants see a single cue and either respond with a button press (“go” response, same side as the target is shown) or do not respond (“nogo”). Feedback is either punishment (red arrow), reward (green arrow) or no outcome (yellow line). Four cues each have a unique combination of outcome valence (reward / punishment) and the correct action (go / nogo). Pavlovian bias would promote learning or performance about go-reward and nogo-punishment cues but impair learning about nogo-reward and go-punishment cues.

Habitual vs. Goal-directed Learning

An important distinction is between the habitual learning outline above, which is 'model-free' – focused only on action-outcome associations, and learning that is goal-directed and 'model-based' – reliant on forming internal models to maximize reward (Gläscher et al., 2010). Understanding this distinction is particularly acute for characterizing development. Model-free learning is thought to be simple and easy, with such basic learning mechanisms even being shown in plants (Gagliano et al., 2016). In contrast, model-based learning is characterized as more effortful and require greater cognitive control from the learner to successfully execute (Kool et al., 2016). Data from tasks that separate model-free from model-based learning (Figure 3B) in young adults, showed model-free and model-based prediction errors are encoded in ventral striatum, during both reward and punishment (Daw et al., 2011; Lockwood et al., 2020b).

Adolescence

Research separating model-free and model-based learning has shown young adults (aged 18+) rely on a hybrid of model-free and model-based strategies whereas adolescents rely more on model-free learning, with model-based learning abilities increasing with age (Decker et al., 2016; Vaghi et al., 2020; Figure 4A). The increasing reliance on model-based learning is thought to reflect the protracted development of cognitive control from childhood to adolescence and adulthood (Davidow et al., 2018). In line with this idea, age-related improvements in working memory have been associated with co-occurring differences in prefrontal cortex (Satterthwaite et al., 2013). Other work has suggested development of fluid reasoning, or solving problems by integrative diverse concepts, is a key component in the emergence of model-based control during adolescence (Potter et al., 2017). There is debate as to whether children engage in model-based learning at all. While there is evidence that some model-based abilities are present in childhood, children either do not arbitrate effectively between strategies (Smid et al., 2022) or cannot integrate model-based strategies in decision-making processes (Hartley and Somerville, 2015). Fewer studies have focused on the neural mechanisms, particularly using a computational modelling approach, to track reinforcement learning processes over time. Resting-state functional connectivity in a large sample of adolescents suggested that the ventral striatal and broader basal ganglia structures that track model-free and model-based prediction errors exhibit substantial reorganization during development (Váša et al., 2020). However, there may be differential recruitment of frontal areas between the two strategies, with model-based learning additional recruiting lateral prefrontal cortex and posterior parietal cortex (Daw et al., 2011; Drummond and Niv, 2020; Lee et al., 2014; Lockwood et al., 2020b).

Aging

As in adolescence, working memory ability and sensitivity to incentivization might be an important component of understanding aging-related changes in model-based compared to model-free learning. For example, one study showed that while in older adults their use of a model-based strategy was lower than in young adults, ability to be model-based was associated with memory performance (Worthy et al., 2014). Evidence that older adults display reduced model-based control compared to younger adults has been found on both tasks that incentivized model-based learning (Bolenz et al., 2019; Figure 4B) and without incentives (Eppinger et al., 2013). This is important to establish whether older adults are simply unwilling to engage the effort required for model-based learning when it is not incentivized, rather than displaying reduced learning. Another study also found reduced model-based learning in older adults, driven by a focus on the outcomes themselves, rather than updating the model (Hämmerer et al., 2019). Behavioral evidence of impaired model-based learning in older age are consistent with imaging work suggesting lower engagement of prefrontal regions when learning task contingencies (Eppinger et al., 2015).. Future work should directly relate age-related differences in model-based control to underlying neural systems.

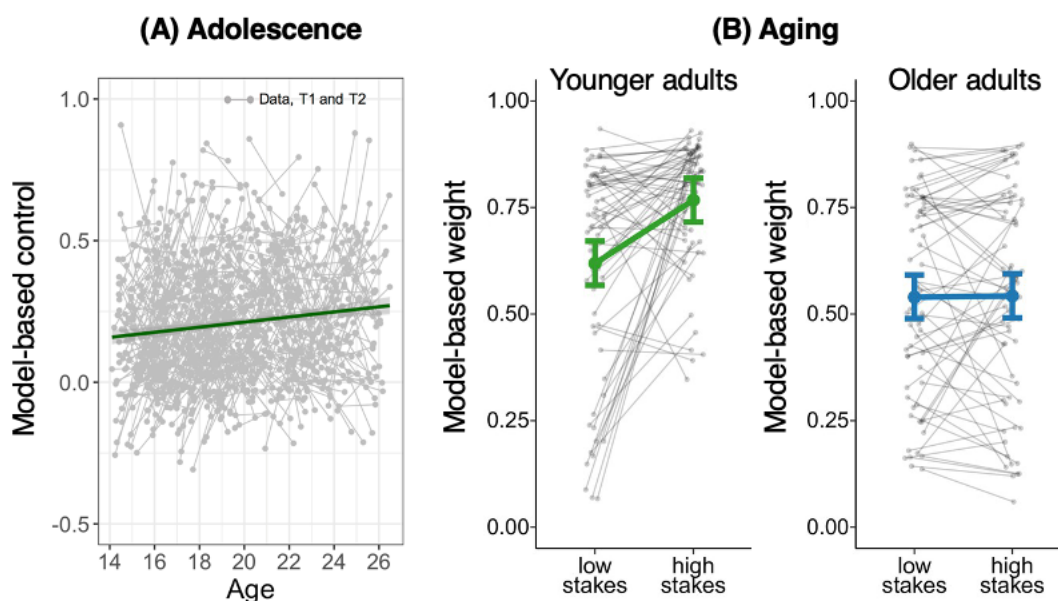


Figure 4. Development of model-based learning during adolescence and decrease in older age. (A) Longitudinal data from adolescents shows development of model-based control with age (Vaghi et al., 2020). (B) Older adults show less model-based influence than younger adults. Younger adults also increase the contribution of model-based processing when it is incentivized (high stakes) compared to not incentivized (low stakes), whereas this is not the case for older adults (Bolenz et al., 2019).

Pavlovian vs. Instrumental Learning

Another key distinction in learning is whether learning is Pavlovian or instrumental. Pavlovian learning is thought to reflect evolutionarily ancient learning processes that bias humans and other animals to automatically approach rewards in the environment and to withdraw from losses or punishments. This Pavlovian system is thought to interfere with instrumental learning systems, which can be model-free or model-based, that flexibly learn associations between actions and outcomes without being unduly influenced by pre-wired responses. Dissociating these different processes has often been done during experiments that directly pit action (make a response or withhold a response) and valence (reward or punishment outcomes; Figure 3C). In healthy adults this work has shown that people display a strong Pavlovian bias, that is they have tendency to approach rewards and avoid losses (Algermissen et al., 2020; Guitart-Masip et al., 2012, 2011). Additionally, the ventral tegmental area and striatum have been associated with go compared to no-go responses (Algermissen et al., 2020; Guitart-Masip et al., 2011).

Adolescence

Raab & Hartley (2020) compared reward and punishment learning as well as the tendency to 'go' (initiate an action) vs. 'no-go' (withhold an action) in children (8-12), adolescents (13-17), and adults (18-25 years). Relative to both children and adults, adolescents exhibited attenuated 'go' and Pavlovian (action-consistent-with-valence) biases, which the authors hypothesized might promote unbiased exploration in novel contexts. Another more recent study had learning conditions where participants had to respond to reward to win but not respond to punishments to avoid losing. In a large sample across childhood to adolescence (age 9-18, n=742) it was found that go biases decreased with age (Pauli et al., 2022). So far, to our knowledge, the development of associated neural systems has not been addressed.

Aging

In older adult samples, research is still in its infancy on age-related changes in Pavlovian biases. However, one study used a motor-based Pavlovian learning task and found a decrease in Pavlovian attraction towards rewards across age (n = 26,532, aged 18-70) (Chen et al., 2018). Because of the nature of the task this decrease in Pavlovian attraction meant that older adults were less optimal at the task. The authors discussed the possible influence of neurobiology on these effects since Pavlovian biases have been shown to involve opponency between dopaminergic and serotonergic systems. Given that both systems show age-dependent differences (van

Dyck et al., 2002, 2000) future pharmacological studies could manipulate these systems and measure resulting age differences in Pavlovian behaviors.

Impact of Outcome Type

Much of the research on reward-based decision making and reinforcement learning generally, and the work reviewed on adolescence and aging, uses financial gains as the outcome. However, for some categories of decision making, the nature of age-related differences can vary depending on the type of outcome. In particular, social rewards like smiling faces, peer feedback and helping others may differ from purely self-benefitting financial outcomes.

Social vs. Non-social Outcomes

Increased sensitivity to social rewards has been shown for both adolescents and older adults relative to younger adults in theoretical accounts, behavioral and neural data, and in animals as well as humans (Almeling et al., 2016; Carstensen et al., 1999; Foulkes and Blakemore, 2016; Somerville, 2013). Comparing data from adults of different ages has shown greater nucleus accumbens activity during social reward delivery (smiling faces) than money in older adults but the reverse pattern in young adults (Rademacher et al., 2014). Similarly adolescents and children may prefer social rewards to money whereas young adults have more equal preferences (Wang et al., 2017). Social interactions can also introduce risks or costs in a similar way to effort, time and uncertainty (Soutschek and Tobler, 2018). In the trust game, money transferred by the “investor” is at risk as it may not be returned by the trustee. Interestingly studies that showed age-related declines in financial risk-taking found willingness to transfer money in the trust game was either stable (Josef et al., 2016) or increased in later life (Falk et al., 2018). Adolescents may place particularly high value on what others think. When the risk of peer rejection must be weighed up against other risks, adolescents’ sensitivity to social outcomes could result in dangerous behaviors like drug use (Blakemore, 2018). The literature on how peer observation impacts learning and decision making in adolescence is outside the scope of this Chapter but can promote positive behaviors such as prosociality as well as more negative choices (Andrews et al., 2021). Robust evidence is now emerging that older adults are relatively more prosocial than younger adults on measures of choices, as well as temporal and effort-based discounting (Cutler et al., 2021a; Lockwood et al., 2021; Mayr and Freund, 2020; Sparrow and Spaniol, 2018).

Differences across the lifespan in how (pro)social rewards are valued and the impact this has on effort-based or intertemporal choices links to the question of whether social information is processed by different areas or computations in the brain (Lockwood et

al., 2020a). For example, learning when rewards are for another person can be captured by the same reinforcement learning models as learning for oneself but depends, in part, on distinct brain areas and neurotransmitter systems (Lockwood et al., 2016; Martins et al., 2022). Consistent with the findings above, when learning for themselves, older adults (age 60-80) were slower and were not as influenced by previous rewards that they received compared to younger adults (age 18-36). Intriguingly however, young and older adults were just as good at learning what would help the anonymous other person. Therefore, older adults' ability to learn what helped others was 'preserved' (Cutler et al., 2021b). Future work can investigate whether these preserved learning abilities could be used to support healthy aging. Differences in the development of learning for oneself compared to another person were also found in adolescence (aged 9-21). Learning for other showed more protracted development than learning for self, in both analysis of learning rates and relative brain activity (Westhoff et al., 2021).

Challenges and Opportunities

Advances in neuroimaging, computational modelling and behavioral tasks have enabled a wealth of research on reward processing and learning across the lifespan. Future developments in these areas bring further exciting opportunities, both for progress in research and a variety of applications. Adolescence is a period of high risk for the onset of mental disorders (Kessler et al., 2007) and the development of disorders involving antisocial or disruptive behavior (Maughan et al., 2004). Difficulties or differences in reinforcement learning have been linked to mood and anxiety disorders (Pike and Robinson, 2022), antisocial behavior (Blair, 2013; Pauli and Lockwood, 2022) and autism (Crawley et al., 2020). Older adulthood is associated with changes in cognitive functions, including learning and decision making, as part of healthy aging or age-related disorders (Lighthall, 2020; Sparrow and Spaniol, 2016). Research on reward processing and learning across the lifespan is therefore vital to support development from early childhood to later life. However, there are also challenges associated with any developmental research and particularly when assessing age-related changes in neural data or parameters from computational models.

Cross-sectional vs. Longitudinal Designs

For practical reasons, much of the work on adolescence and aging has adopted cross-sectional designs. Particularly for samples to compare young adulthood to old age, the timespan could be as high as 82 years (age 18-100). Given that interest in reinforcement learning with formal mathematic models has possibly only been around for the last 30 years, it is unsurprising that longitudinal datasets simply do not yet exist,

and there are many challenges in establishing these. However, cross-sectional work is not necessarily a problem if the design and interpretation are appropriate. For example, with cross-sectional data it is highly debated whether it is correct to use mediation analysis, due to the assumptions of causality and how predictors relate to each other in time (O’Laughlin et al., 2018; Pek and Hoyle, 2016; Raz and Lindenberger, 2011; Rohrer et al., 2022).

Another issue is whether age differences are due to aging itself or cohort effects (Fosse and Winship, 2019), particularly if the process might be more susceptible to historical or cultural influences such as social behaviors. There are several ways this question can be addressed. First, examining behaviors with clear neurobiological underpinnings like reinforcement learning allows testable hypotheses about the expected changes with age in the associated brain structures or function. For biological mechanisms such as dopamine function, with established age-related changes, one possibility for future work is to relate direct measures of that function to choices or behaviors, instead of numerical age (Berry et al., 2019). Another approach that is gaining attention for benefits such as generalizability and inclusivity is data collection in multiple different cultures and countries. This also has benefits for lifespan research, as any age differences thought to be due to universal and biological processes should be found regardless of culture or nationality. One important consideration in this work is to account for differences in life expectancy between countries, particularly when examining financial behaviors. Adjusting age for life expectancy is one way of resolving this and has the additional benefit of mixing cohorts (Cutler et al., 2021a). Large datasets additionally allow age to be modelled as a continuous predictor, rather than between-group comparisons, with enough power to detect non-linear effects (for example quadratic and cubic trends). Finally, accelerated longitudinal designs combine benefits of longitudinal research with the practical constraints of generating results more quickly (Galbraith et al., 2014). Studies using this approach of following multiple cohorts each at a different age for a shorter time than fully longitudinal designs are already common in adolescent research and could be applied more to development in later life.

Measuring and comparing neural signals at different ages

The most common neuroimaging technique discussed in this Chapter is fMRI, which measures blood oxygenation in the brain as a proxy of neural activity. This presents challenges with comparing signals between participants of different ages as vasculature changes with age and this affects blood flow. One approach to minimize the risk of misinterpreting age differences is to use breath holding paradigms as an index of vasculature reactivity that can be incorporated in analysis (Moses et al., 2014; Tsvetanov et al., 2021). The very loud noise and requirement to stay still for long periods also raise issues with using fMRI to study development in the youngest and

oldest participants. Developments in other brain imaging methods such as magnetoencephalography (MEG) or functional near infrared spectroscopy (fNIRS) may offer exciting opportunities for future research, particularly with young children or older participants who cannot travel.

Comparing cognitive computational models across ages

A final challenge and opportunity is applying computational models of behavior to different age groups. There are different model-fitting procedures available and researchers must select the best approach (Lockwood and Klein-Flügge, 2020). One choice is whether to fit the model across all participants, meaning a single model will be selected for further analysis, or run model comparison on each age group separately, allowing different models to “win”. If fitting models separately reveals a different model is best for each age group, it is impossible to compare any parameters that are not present in all models. One study using a reversal learning task found the best model of adolescents’ learning had static learning rates for reward and punishment, whereas adults’ learning was best captured with a learning rate that varied over time (Crawley et al., 2020). Other findings showed adults integrated more information, such as whether it was a gain or a loss, than adolescents during learning (Palminteri et al., 2016). While this makes some parameters incomparable, it provides insight into broader differences in how adolescents and adults complete the task. Differences in model fit between age groups may also support the results of comparing parameter values. For example, while young adults’ learning to benefit themselves and someone else was best captured with separate recipient-specific learning rates, there was stronger evidence in favor of a model with a single combined learning rate for older adults (Cutler et al., 2021b).

Future Directions

While the paradigms outlined can provide unique insights into how human decision-making changes across the lifespan, recently it has been highlighted that most of the tasks take on a narrow form that may not reflect all real-world decision problems (Mobbs et al., 2018). Specifically, participants are presented with binary choices between two options. However, in the real world, decisions are often about whether to move on from a current location to another (Le Heron et al., 2020), or whether to engage with one action for rewards or keep searching for another (Khalighinejad et al., 2021), for example whether to leave one job or search for a better alternative. Such continuous, sequential decisions may involve a range of the individual decision variables outlined above (effort, delay, risk), such that making an optimal choice involves integrating several of them to understand how time can be best allocated

within an environment. Such an approach may offer a more ecological representation of how humans learn to make good decisions over the lifespan.

Paradigms based on these principles have already proven fruitful. They have revealed important insights into the role of the ACC in guiding decisions in young adults (Kolling et al., 2012), been used to probe decision-making in older adults (Le Heron et al., 2020), and revealed how higher levels of exploration in adolescence may actually be optimal for navigating new, unknown environments (Lloyd et al., 2021). Future research using these tasks and approaches may be able to disentangle some of the contradictory findings outlined above, by examining how people make sequential choices in different environments.

Conclusions

The behavioral and neural systems supporting reward and reinforcement learning show similarities and differences across the adult lifespan from adolescence to older age. There are many challenges and opportunities for the future of adult lifespan research and important directions for the field to take.

Glossary

Adolescence: phase of the lifespan beginning with the onset of physical puberty and ending with the assumption of adult roles.

Aging: the sequential or progressive change in an organism that leads to an increased risk of debility, disease, and death. Senescence consists of these manifestations of the aging process.

Temporal discounting: The rate at which time delay devalues reward.

Effort discounting: The rate at which cognitive or physical efforts devalue reward.

Subjective Value: predicted or experienced benefits of an outcome, given the individual's internal and external state. Often a quantity in a computational model of decision-making or learning.

Risk: the degree to which all situational outcomes and their mathematical probabilities are known.

Uncertainty: The degree to which past, present or future states and events are known.

Computational model: a mathematical formalization of the interactions among assumed underlying cognitive processes required to perform a task, which allows for estimating contributions of component processes in complex cognition.

Reinforcement learning: incremental learning from feedback such as rewards or punishments, or other valenced outcomes, which depends on the detection of value signals and their integration over repetitions.

Model-based learning: acquiring a contingent or transitional structure of the environment to represent sequences of choices or actions to maximize valuable outcomes through incremental reinforcement.

Model-free learning: acquiring the structure of associations between choices or actions and valuable outcomes through incremental reinforcement.

Pavlovian learning: the tendency to seek reward and avoid punishment regardless of feedback.

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Conflict of interest

The authors declare no competing interests.

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