

Review

Understanding patch foraging strategies
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Patch foraging is a near-ubiquitous behaviour across the animal kingdom and characterises many decision-making domains encountered by humans. We review how a disposition to explore in adolescence may reflect the evolutionary conditions under which hunter-gatherers foraged for resources. We propose that neurocomputational mechanisms responsible for reward processing, learning, and cognitive control facilitate the transition from exploratory strategies in adolescence to exploitative strategies in adulthood – where individuals capitalise on known resources. This developmental transition may be disrupted by psychopathology, as there is emerging evidence of biases in explore/exploit choices in mental health problems. Explore/exploit choices may be an informative marker for mental health across development and future research should consider this feature of decision-making as a target for clinical intervention.

Should youth explore?

Across the lifespan, individuals often face choices to either stay with familiar options or explore new alternatives. Does a teenager stay at home during the holidays or attend a summer camp where they may only know a few people? Looking further back in evolutionary history, should a hunter-gatherer searching for fruits look in an area where they have previously encountered these resources, or search a new clearing further away? Such decisions can be understood in the context of patch foraging, a near-ubiquitous behaviour across the animal kingdom [1]. Although recent work has examined how foraging strategies change across development [1–6] and, separately, the neural correlates of foraging in adults [7–9], these lines of research have not yet been integrated to consider how neural developments might influence foraging strategies from childhood to adulthood. This is surprising, given that evolutionary pressures have likely shaped neurocognitive development to prepare the organism for developmentally relevant experiences, optimising their functioning across the lifespan [10].

Identifying the neurocognitive developments that give rise to age-related changes in foraging strategies can inform our understanding of how exploration and exploitation behaviours support the individual to achieve important developmental goals, such as independence from caregivers [10]. This topic also has the potential to advance our understanding of behavioural phenomena associated with adolescence, such as heightened novelty-seeking and reduced uncertainty aversion [11,12], which are both implicated in explore/exploit choices [13]. We propose that neurocognitive changes between childhood and adulthood shape explore/exploit strategies, leading to a reduction in exploration across development. Given our focus on how typical trajectories of explore/exploit choices have emerged to support developmentally relevant goals, we pay particular attention to patch foraging paradigms, as these tasks resemble conditions under which cognitive abilities that support explore/exploit choices evolved [14].

Highlights

From adolescence to adulthood, there is a decrease in exploration choices in foraging decision-making problems.

In youth, a disposition to explore when faced with explore/exploit choices can support the individual to learn the structure of their environment, enabling them to effectively exploit rewards in maturity.

Such age-related differences are likely driven by neurocognitive changes to reward processing, learning, and cognitive control across development.

Individual differences in foraging strategies can be indicative of cognitive biases implicated in mental health outcomes.

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Understanding how exploration changes from childhood to adulthood can help us identify when individuals deviate from developmentally appropriate explore/exploit strategies. Biases in foraging strategies are associated with mental health problems [15], which may be particularly impactful for adolescents, who have a heightened risk of developing psychopathology relative to other age groups [16]. As such, we highlight directions for future research to examine how biases in explore/exploit choices may be informative in studying the development of mental health problems.

Defining patch foraging problems and their solutions

Patch foraging is a sequential decision-making problem that requires the organism to optimise an **explore/exploit trade-off** [2] (see [Glossary](#)). For example, animals foraging for food can allocate their finite energetic resources to collecting items from the patch they are located at (e.g., a bush containing berries). Alternatively, animals can expend energy exploring to find a new patch, during which time no new food can be collected (Figure 1) [17]. The amount of food available depletes the longer the organism remains at the patch, meaning that as the forager's time within a patch increases, they accrue progressively fewer rewards per exploit decision [18]. There is a point at which the overall reward intake from exploring to find a new patch with a fresh distribution of resources surpasses the potential rewards acquired from further depleting the current patch and, therefore, exploration becomes the rational choice [2].

A prominent theory of optimal foraging is the **marginal value theorem (MVT)** [19]. MVT states that the forager should explore when the rewards expected from exploiting the current patch fall

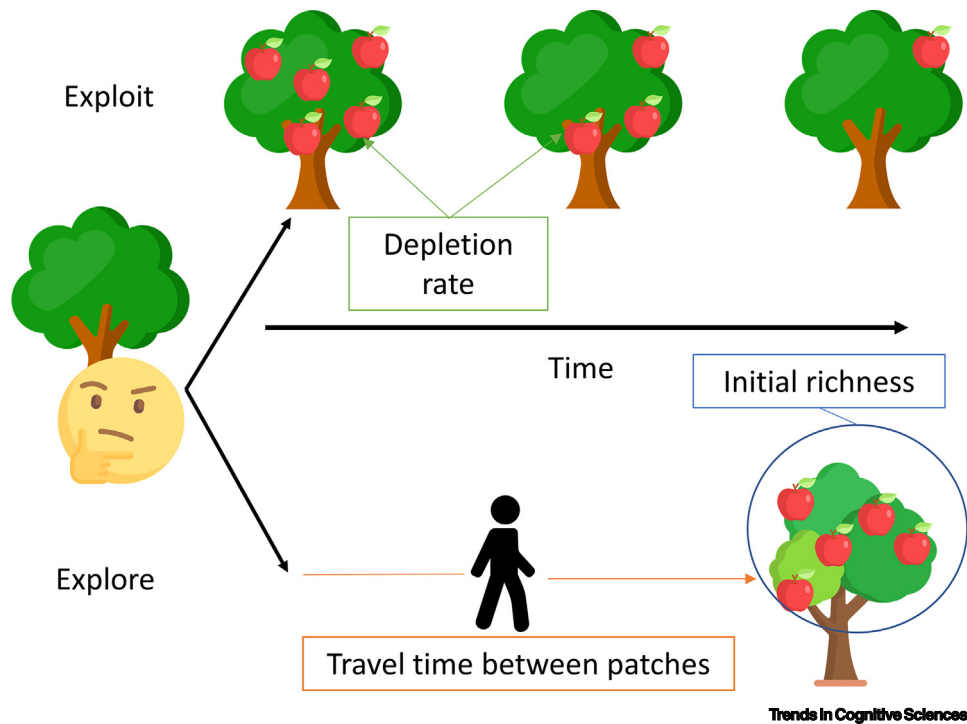


Figure 1. Patch foraging task. The individual at a patch (in this example, a tree) can choose between exploiting the patch they are currently at (top panels) and collecting rewards (in this example, apples). The longer the forager remains within the patch, the fewer rewards are available to collect. The rate at which rewards deplete within patches is known as the depletion rate. Alternatively, the forager can choose to leave their current patch and explore to find a new patch (bottom panels). The travel time between patches is a period during which no rewards can be collected. The number of rewards on the first harvest of a new patch is the initial richness of the patch.

Glossary

Background reward rate: average reward rate available in the foraging environment. The individual must estimate this quantity from previous encounters with patches in that environment.

Cooling off: a theory of development that proposes exploration becomes less stochastic from childhood to adulthood, such that in maturity, adults exploit high-reward options.

Depletion rate: the rate at which rewards deplete within a single patch, which can be steep (i.e., quickly depleting) or shallow (i.e., slowly depleting; see Figure 2 in the main text).

Expected value: the reward value expected from selecting a particular option available to the decision-maker. Reinforcement learning models provide an explanation of how the decision-maker estimates the expected value of options available to select.

Explore/exploit trade-off: a decision-making problem in which the individual must choose between exploiting an option with a known history of rewards and exploring a novel option with an unknown reward value.

Marginal value theorem (MVT): a formal model of optimal patch foraging. The model prescribes that the forager should leave their current patch when the rewards expected from the next exploit decision fall below the background reward rate for the environment.

n-Armed bandit: explore/exploit decision-making tasks where the participant decides between n (usually two or more) bandits or slot machines that probabilistically yield a reward. The participant must learn which of the bandits has the highest likelihood of yielding a reward by sampling the options available to them.

Prediction error: discrepancy between the reward predicted from sampling an action or stimulus, and the reward received.

Reinforcement learning (RL): a formal computational model of how humans and non-human animals learn from reward and punishment. RL models quantify how the individual integrates feedback from their actions to estimate the outcomes associated with available stimuli.

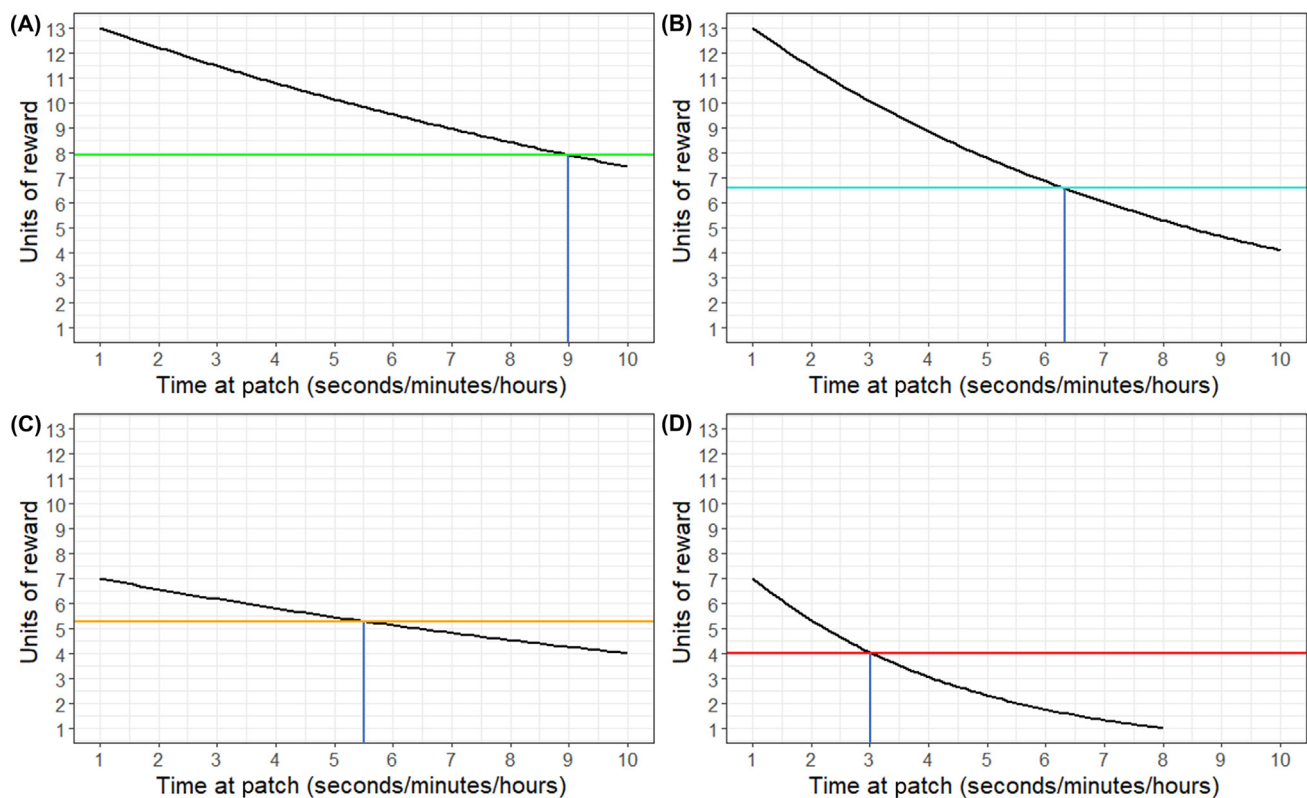
Reproductive fitness: describes the organism's ability to pass their genetic material to their offspring.

below the **background reward rate** of the environment [7]. The forager estimates this quantity from the average rewards encountered on patches in that environment, which inform whether the environment is richer or poorer in quality (Figure 2). In richer environments where the background reward rate is higher, organisms should exploit individual patches less extensively, whereas in poorer environments where the background reward rate is lower, organisms should exploit patches until fewer rewards remain [20]. Adjusting explore/exploit choices to changes in the background reward rate is an important skill for foragers to maximise reward intake [21].

MVT has provided a powerful explanation of patch foraging behaviour. Humans and non-human animals exhibit behaviour that approximates the predictions made by MVT [2,3,7,20,22,23], including when making decisions about romantic partnerships [24], online information seeking [25], and retail purchasing [26]. These findings suggest patch foraging problems and their underlying computations are prevalent across human decision-making. Building on MVT, recent work has utilised **reinforcement learning (RL)** models to explain how organisms learn the background reward rate [27,28]. Drift diffusion models have been used to explain how evidence about the reward availability within patches is accumulated [18,29] (Box 1).

Stochasticity: the degree to which an individual deviates from selecting the option that, to their knowledge, has the highest expected value. An individual who is highly stochastic will more often divert from the option they expect to yield the highest reward, whereas individuals that are not stochastic will more reliably select the option expected to yield the highest reward.

Temperature: the reference to temperature in cooling off accounts is based on annealing in metallurgy. At high temperatures, large adjustments can be made to the parameters. As the material cools off, the range of possible adjustments becomes smaller, as some parameters have already been set at a higher temperature.



Trends in Cognitive Sciences

Figure 2. Marginal value theorem in different quality environments. Simulated data demonstrating how manipulating the initial richness and depletion rate change the quality of the environment. The blue vertical lines highlight the time, denoted on the x axis, that the forager should stay within patches in each environment type. Panel A denotes a single patch in a rich environment, with a high initial richness, and a shallow depletion rate. In such an environment, the forager should leave when the number of rewards expected from staying within the patch is still high, as the true background reward rate (denoted by the horizontal green line) is also high. Panel B denotes a patch in a medium quality environment, where the initial richness of patches is high, but the depletion rate is steep. In such an environment, the forager should exploit patches until fewer rewards remain on the patch, as the true background reward rate of the environment (denoted by the horizontal teal line) is lower in such an environment. Panel C indicates another medium quality patch where the initial richness is low, but the depletion rate is shallow. The true background reward rate for this environment is denoted by the horizontal orange line. Panel D denotes a patch in a poor environment, where the initial richness is low, and the depletion rate is steep. In a poor environment, the forager should exploit patches until there are fewer rewards remaining on the patch, as the background reward rate (denoted by the horizontal red line) is low.

Box 1. Formal models of patch foraging decisions

MVT

MVT prescribes that the forager should explore when the rewards expected from the next exploit decision on their current patch fall below the background reward rate of the environment. Formally, this can be expressed as [2,28]:

$$ks_i < \rho h \quad [I]$$

ks_i refers to rewards (s) on trial (i) multiplied by the **depletion rate** (k) to estimate the rewards expected from the next exploit decision. ρ refers to the background reward rate multiplied by the time taken to harvest rewards from the patch (h).

RL models of patch foraging

RL models explain how individuals learn reward contingencies by sampling available options and updating expectations associated with those options based on reward feedback. Unlike Equation I, RL-informed models specify how individuals estimate key quantities involved in MVT, including the background reward rate (ρh in Equation I). Here, we summarise one example of how RL models can be applied to foraging tasks [28] (however, see [13,20,27,119]).

RL models propose that foragers learn the background reward rate by integrating reward feedback from explore/exploit decisions [28]:

$$\rho_i = (1 - \alpha)^{T_i} \frac{S_i}{T_i} + (1 - (1 - \alpha)^{T_i}) \rho_{i-1} \quad [II]$$

ρ denotes the background reward rate and α refers to the learning rate, which is the degree to which foragers use recent versus historic feedback to update the background reward rate estimate. s refers to the rewards received on a trial (i), subject to the time associated with explore/exploit decisions (T). The background reward rate is then entered into Equation III:

$$P(a_i = \text{stay}) = 1 / (1 + \exp(- (c + \beta[k_{i-1}s_{i-1} - \rho_{i-1}h]))) \quad [III]$$

Equation III gives the probability that foragers will exploit on trial (i). This decision relies on comparing the value expected from the next exploit decision (ks_i) with the forager's estimate of the background reward rate of the environment (ρh). β measures stochasticity.

Evidence accumulation models

Evidence accumulation models suggest that foragers determine whether to stay with their current patch using a decision threshold rule [18,29]. The rate at which foragers reach this threshold is subject to the availability of rewards on patches, the estimate of the reward distribution on patches, and decision stochasticity [120]:

$$dx = (\rho e^{-t} - \alpha) dt + \sqrt{2B} dW(t) \quad [IV]$$

d refers to a decision threshold that, once reached, means the forager will leave their current patch. x refers to the forager's motivation to stay within a patch. ρe^{-t} refers to the forager's intake of food and α refers to the energy loss associated with foraging [120]. B represents the stochasticity in how the forager encounters food on the patch and t refers to the length of time the forager remains with the patch. Evidence accumulation models have not yet been applied to study developmental differences in patch foraging but could provide insight into the threshold adolescents require before exploring.

Human and non-human animals also estimate the background reward rate in other explore/exploit tasks, such as the ***n*-armed bandit** task [6,30]. In *n*-armed bandit tasks, options are presented simultaneously, and the reward value is estimated from sampling available options [31]. The computational solution to such tasks relies on estimating the maximal **expected value** for individual bandits, though the likelihood of selecting the bandit with the highest expected value can be influenced by the background reward rate, estimated from the average rewards acquired from bandits. Specifically, organisms are more likely to persist with higher value bandits in environments with a higher background reward rate. This observation is consistent with MVT, as it suggests organisms have a higher threshold for exploring novel bandits in richer environments (Figure 2) [6,30]. Estimating the background reward rate is an important cognitive skill present across real-world decision-making. For example, the decision to accept a job offer relies on the individual's estimate of the

average quality of other positions available on the market [28]. However, unlike n -armed bandits, the rewards collected while foraging typically deplete the longer the organism remains with a patch and therefore the forager must also estimate the rewards expected from continuing to exploit the current patch [28]. Further, there is a time cost to exploration in foraging tasks, whereas bandit tasks do not incur such costs [7]. The additional features of patch foraging tasks, such as their depleting rewards and cost for exploring, make these tasks more reminiscent of the conditions under which explore/exploit strategies evolved to maximise **reproductive fitness** [22].

Cognitive development supports optimal exploration strategies across the lifespan

Optimising explore/exploit choices requires the integration of multiple sources of information, including rewards expected from continuing to exploit the current option and the background reward rate [7]. Due to their complexity, explore/exploit problems rely on a combination of cognitive processes, including reward-based decision-making and cognitive control [6,8,32]. Notably, these processes undergo significant development during adolescence (i.e., ages 10–24) [33], a period of profound neurocognitive change [12,34,35]. Here, we review how explore/exploit strategies vary between childhood and adulthood, and how age-related differences in explore/exploit strategies may be driven by neurocognitive development.

Exploration ‘cools-off’ across development

Exploration declines from childhood to adulthood in foraging [2,5,23,36–40] (however, see [1,41]) and other explore/exploit paradigms [31,42,43]. This trajectory is also seen in non-human animals, as adolescent primates explore their surroundings more than adults, who exploit known foraging options [4]. Humans are adept at adjusting their foraging behaviour to the richness of the environment. Consistent with MVT, adolescents and adults explore more in richer foraging environments but exploit patches more extensively in poorer foraging environments [2,3,7,20,28,44]. Notably, the heightened exploration exhibited by adolescents produces more optimal patch foraging behaviour according to MVT [2,5], whereas adults overexploit patches [3,7,20,28]. Compared with adults, adolescents also exhibit improved decision-making in n -armed bandit tasks, which is driven by adolescents’ exploratory tendencies [43,45]. Cross-species evidence from humans and other primates indicates that exploration declines from childhood to adulthood [2,4,23].

Age-related changes in explore/exploit strategies can be illuminated by theories that propose a shift from highly exploratory strategies in youth to more exploitative strategies in maturity – referred to as a **cooling off** process [46]. Derived from formal models of simulated annealing [47], cooling off accounts propose that a naive learner placed in a new environment should initially explore the available options in a **stochastic** manner, randomly sampling stimuli without expecting to maximise reward intake (Figure 3, Key figure). Through this process, the learner develops knowledge of options expected to yield greater or fewer rewards [48]. Over time, the learner explores less, instead utilising the knowledge they have gained about the environment to exploit options expected to yield more rewards [46]. While this account places emphasis on the single parameter responsible for choice stochasticity, an alternative account has suggested that cooling off refers to an optimisation process whereby multiple parameters responsible for learning are adjusted across development, with the **temperature** of the optimisation algorithm cooling off into maturity [38]. On this account, children and adolescents make greater adjustments to the parameters, trialling a wider range of configurations, whereas adults make smaller, more precise adjustments, having converged on more optimal configurations over the course of their development [38].

Applied to human development, it has been suggested that children and adolescents engage in more exploration either due to the single parameter responsible for stochastic exploration [49] or

Key figure

Cooling off across development

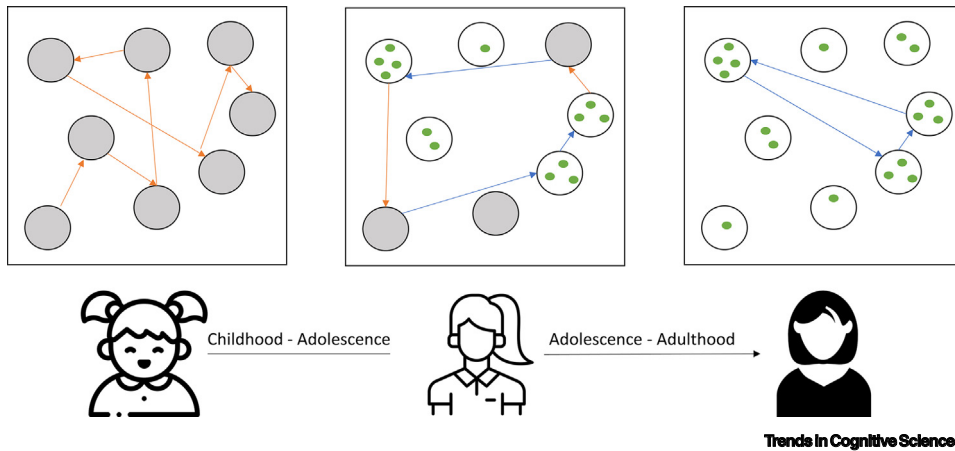


Figure 3. Image depicting the cooling off account of reward learning across development that attributes reduced exploration to the single parameter measuring stochasticity. In childhood (leftmost panel), the individual is naive about the reward structure of their environment and explores options, or patches, with a higher degree of randomness (orange arrows). This process provides information about options that yield greater or fewer rewards (green circles). As the individual matures into adolescence (middle panel), they have developed some experiential knowledge of their surroundings, allowing them to sometimes exploit high value patches (blue lines), though they still exhibit some randomness, or stochasticity, in their choices. In adulthood (rightmost panel), the organism has acquired the experiential knowledge to exploit only high reward options, or patches, avoiding those with fewer rewards. In this example, we assume that the individual can choose between patches to move between (as in some paradigms [119] and real-world patch foraging contexts [22]), whereas in other tasks the individual can only choose when to explore to find a new patch (e.g. [2]).

through making large adjustments to several parameters responsible for learning [38], with both accounts suggesting this produces noisier goal-directed behaviour. As the individual matures into adulthood, they accumulate experience-based knowledge, allowing them to identify actions that lead to more rewarding outcomes [50]. However, studies have found that adolescents collect more rewards than adults on foraging and n -armed bandit tasks [2,43,45], which may appear inconsistent with cooling off accounts that propose adults should be more effective at acquiring rewards than adolescents [46]. Adults' suboptimal performance on explore/exploit tasks is due to their overexploitation bias [2,31], indicating exploitation strategies can be disadvantageous in artificial, experimental environments. Indeed, adolescents adapt faster than adults when faced with new environments, supported by exploratory strategies [43,51]. The developmental transition from exploratory to exploitative strategies is thought to provide the organism with the opportunity to learn about their real-world environment so that in maturity, they can effectively exploit their environment to maximise reward acquisition [38].

Cooling off accounts are supported by evidence that children and adolescents are more exploratory than adults across other cognitive domains. Compared with adults, children and adolescents sample unknown stimuli more noisily to learn whether they produce rewarding or aversive outcomes [48,52] and explore more diverse hypotheses about the causal relationships between cues and outcomes [36]. Behavioural changes from adolescence to adulthood, such as the reduction of novelty-seeking [53], are consistent with a shift from exploratory to exploitative strategies described by cooling off theories.

Formal models, such as RL models [27,54], can be used to test different conceptualisations of cooling off theories. These models have provided evidence that age-related changes in exploration are associated with a decline in stochasticity from childhood to adulthood. In RL models, deterministic decision-makers always select the option that, to their current knowledge, will yield the highest reward [43]. Yet, occasionally diverting from the option expected to yield the highest reward (i.e., exhibiting more stochasticity) can be an effective strategy to learn the structure of environments [5,55]. Indeed, some versions of cooling off accounts propose that stochastic responding is a crucial mechanism whereby the individual learns the reward structure of their environment. Stochastic responding can be advantageous, as in environments where the associations between stimuli and rewards are changeable, exploring options with a lower expected value can uncover changes to the reward structure faster than exploiting options expected to yield the highest return [42,43,55]. The association between stochasticity and exploration has been confirmed in a free-moving patch foraging task, where rodents' increased exploration was attributed to the model parameter measuring stochasticity [56].

Developmentally, stochastic exploration declines from childhood to adulthood in foraging [38], n -armed bandit [49,57,58], and other explore/exploit tasks [42]. Stochastic decision-making can lead younger participants to forfeit rewards, as they do not always select the option expected to yield the highest reward [42]. This finding is consistent with evidence that adolescents evaluate risk similarly to adults [59] but are still more likely to sample risky options compared with adults [60]. Adolescents' more stochastic choices, relative to adults, can also confer benefits in environments with changeable or volatile reward contingencies [43]. These findings suggest adults exploit high-reward options, whereas adolescents are more likely to stochastically explore their environment [36]. However, it will be important to consider how additional forms of exploration, such as uncertainty- or novelty-directed exploration [61,62], are used across development to solve explore/exploit foraging problems. For example, adults' bias to overexploit can be explained by their representation of the environment structure, and their degree of uncertainty in this representation [13]. Adolescents' reduced uncertainty aversion compared with adults may therefore explain their heightened exploration while foraging [2]. Methodological developments in the design of explore/exploit and foraging paradigms will be necessary to advance our understanding of the processes involved in these behaviours (e.g., meta-learning about the environment structure) and of how the 'cooling off' account is best conceptualised [38].

Developmental experiences influence foraging strategies in maturity

Heightened exploration in adolescence, relative to adulthood, can support reward maximisation in maturity by providing the organism with information about the background reward rate of their environment. Cooling off accounts propose exploration is used in development to learn the reward structure of the environment. However, options considered to be high reward are dictated by the richness of the environment. A bush with ten berries is a highly rewarding patch in a desert, but less valuable in a rainforest, as the latter environment has a higher background reward rate [19]. Studies have demonstrated that adult organisms use foraging strategies that are well adapted to their rearing environments. Juvenile *Caenorhabditis elegans* deprived of food exhibit reduced exploration in maturity relative to controls [63], an effect also found in *Drosophila* [64]. As the absence of food indicates a low background reward rate, this information should direct the forager to exploit patches more extensively, indicating the reduced exploration of starved juvenile organisms is consistent with MVT [19]. This adaptation persists even when adult *C. elegans* are placed in a new, plentiful environment, and the juvenile strategy is no longer adaptive [63]. Similar effects are also present in humans: adults exposed to childhood trauma (including neglect) explore less while foraging relative to those without these experiences [3].

Reduced exploration in humans with experience of childhood trauma [3] may be informed by evidence that has examined how perceived (in)stability in the association between cues and outcomes during development can affect outcomes in maturity. Early instability leads to a poorer ability to estimate the temporal association (i.e., when to expect an outcome following a stimulus) between cues and outcomes in maturity. The impoverished ability to estimate the temporal association following early instability has been implicated in reduced anticipation of reward following these experiences [65], which may extend to the organism's anticipation of rewards in the environment (i.e., the background reward rate).

Evidence from hunter-gatherer communities has suggested that the ability to effectively forage in maturity is supported by exploration in youth, perhaps indicating that the transition from exploration in adolescence to exploitation in adulthood has arisen from evolutionary pressures. A recent analysis of 28 hunter-gatherer societies found that the number of resources individual foragers return increases during development, with foragers reaching adult-like proficiency by age 20 years [66]. Childhood and adolescence provide juvenile foragers with the opportunity to learn the distribution of patches containing foods [66–69] and skills for more complex foraging behaviours (e.g., hunting, which, like laboratory-based patch foraging tasks, is also informed by the background reward rate) [70,71]. The increased exploration observed in adolescence may, therefore, reflect a period of skill acquisition whereby organisms learn to exploit their foraging niche [66]. For example, adolescents from a Tanzanian hunter-gatherer group known as the Hadza roam over a wider geographical distance during foraging excursions compared with pre-adolescent children (although no data were reported for adults) [72]. Similar age-related changes in roaming have been evidenced in humans in industrialised societies, primates, and rodents [4,73,74]. These studies indicate that heightened exploration in adolescence is a cross-species and crosscultural phenomenon, allowing juvenile organisms to develop skills required to collect resources in their foraging niche.

Neurocognitive development facilitates age-related changes to explore/exploit strategies

As resources collected through foraging relate to the organism's likelihood of survival, and therefore their reproductive fitness, it has been proposed that aspects of human cognition have evolved to solve patch foraging problems [75]. Specifically, it has been proposed that reward processing and cognitive control have partly evolved to optimise patch foraging decisions [14,76]. Compared with other primates, humans have a protracted period of childhood and adolescence [77], which supports the development of complex cognitive abilities that allow humans to exploit their foraging environment [66]. The developmental reduction in exploration coincides with significant changes to neural regions implicated in explore/exploit decision-making, which undergo their most rapid development during adolescence [33]. Several explanations have been offered for these changes, including dual systems models [12], developmental mismatch [78], and circuit-based accounts [79]. These accounts propose there is heterogeneity in the rate at which different regions of the brain develop during adolescence, with several of these regions implicated in explore/exploit choices [80,81]. We suggest that the developmental trajectories of the anterior cingulate cortex (ACC) and ventral striatum facilitate age-related changes to explore/exploit strategies, supporting adolescents to learn about their environment through exploration.

The transition from exploration in youth to exploitative strategies in maturity may be supported by developments in cognitive control, which includes processes such as goal selection. Cognitive control improves from childhood to adulthood, reaching maturity around age 24 [82], and has been associated with protracted synaptic pruning across the prefrontal cortex and ACC [83,84]. Regions involved in cognitive control have been implicated in solving foraging problems. Seminal work in adults has identified the role of the ACC in estimating the background reward rate

[80], findings that have been replicated in subsequent studies [8,9,85]. Activity in the ACC positively correlates with estimates of the background reward rate and negatively correlates with the value of the current patch [80] (however, see [86]). The ability to estimate the value of unknown options in patch foraging tasks recruits different neural regions to those implicated in exploration in n -armed bandit tasks (e.g., the dorsolateral prefrontal cortex [87]).

The development of cognitive control abilities from childhood to adulthood may improve proficiency in explore/exploit tasks, as cognitive control is responsible for utilising reward feedback to inform future decision-making. Children collect fewer rewards than adults on n -armed bandit tasks [88] due to their inability to generalise previous experience to inform future decisions (a manifestation of cognitive control abilities) [48]. In computational models of patch foraging choices (Box 1), estimating the background reward rate relies on utilising experiences of encountered options (i.e., generalising encounters to estimate the quality of other options) [6,89]. Therefore, the maturation of regions responsible for cognitive control from childhood to adulthood may facilitate improved accuracy when estimating the background reward rate in real-world settings, where information gained during development is used to maximise reward acquisition in maturity.

Consistent with dual process models [12], the protracted increase in cognitive control abilities during adolescence coincides with rapid developments in the dopaminergic reward system. At the onset of puberty, gonadal hormones are released causing significant synaptic pruning in neural regions responsible for processing reward, which reach adult-like maturity around age 16–17 years [90,91]. Development within the dopaminergic reward system produces higher activity in the ventral striatum and nucleus accumbens in adolescence relative to adulthood and childhood [90,92,93]. Increased striatal activity also supports improved learning in adolescence, relative to childhood [81,94,95], which can aid adolescents to learn the reward structure of their environment [43,95,96] (Box 2).

While no work to date has examined the neural correlates of patch foraging choices across development, the ventral striatum is responsible for estimating the value of explore/exploit choices [97]. Pharmacological work in adults has further demonstrated that dopamine agonists increase participants' estimate of the background reward rate [7]. According to MVT, a higher perceived

Box 2. Learning and the dopaminergic reward system

The dopaminergic system is vital for learning reward contingencies associated with environmental cues. The method by which individuals learn reward contingencies can be explained by theories of RL [121]. In RL models, the decision-maker learns that a stimulus can be used to predict reward outcomes. To learn the reward values associated with available stimuli, the decision-maker compares the experienced reward with the reward that was expected. When an individual's behaviour results in a different reward than expected, the individual should update their estimate of the association between stimulus and reward-outcome associated with that behaviour. The degree to which individuals update their knowledge of the association between behaviours and reward outcomes is controlled by a learning rate, which measures how much emphasis the individual places on recent versus more historic reward feedback [57]. The discrepancy between expected and actual reward is known as a **prediction error**, which can be positive if the rewards received are higher than expected, or negative if the rewards received are lower than expected [43,122]. Prediction errors elicit neural activation in the bilateral ventral striatum, part of the dopaminergic reward system [123].

The dopaminergic reward system comprises several neural regions implicated in foraging choices, including the striatum, nucleus accumbens, and prefrontal cortex [107,124,125]. These networks have been shown to control effort and vigour in the pursuit of rewards in human and non-human animals [126,127]. Functional magnetic resonance imaging (fMRI) studies have reliably found activity in the dopaminergic reward system in the pursuit of rewards across the human lifespan, including within the ventral striatum and nucleus accumbens [128]. Notably, there is greater activity in these areas during reward-based decision-making in adolescence compared with other age groups [92]. Several studies have demonstrated that the dopaminergic reward system contributes to explore/exploit decisions during patch foraging [7,129], specifically through estimating the background rate of rewards [7].

background reward rate signals a greater availability of rewards and therefore that the forager should exploit patches less extensively [3]. Evidence for the role of dopamine in estimating the background reward rate could indicate that adolescents have an increased estimate of the background reward rate due to hyperactivity in the dopaminergic reward system relative to adults [90,92,94], motivating them to explore regardless of the true background reward rate of their environment and reflecting the stochastic exploration proposed by some cooling off accounts. However, activity of neural regions responsible for reward processing exhibits a quadratic developmental trajectory [93], unlike exploration choices which decline from childhood to adulthood [38]. This discrepancy may be due to exploration strategies being influenced by factors beyond dopaminergic activity, such as improved goal selection throughout adolescence [82,90].

Adolescents' unique combination of improved reward learning compared with children [81,94] and heightened exploration compared with adults [4,43] can support the individual to learn the reward structure of their environment [2]. Indeed, such abilities may be facilitated by the onset of puberty, which is associated with increased neuroplasticity that can support experience-dependent learning [98]. The reduction of activity within the dopaminergic reward system from adolescence to adulthood can support the transition from exploratory foraging in youth to strategies that exploit high reward options, which the adolescent has learned through exploration, in adulthood [2,5,99].

In contrast to evidence that has identified the role of the dopaminergic reward system in estimating the background reward rate [7], studies leveraging computational modelling suggest that differences in adolescents' and adults' use of exploratory strategies are linked to reduced stochasticity in adults [38]. Indeed, adolescents' greater stochasticity relative to adults may be driven by the hyperactivity of their dopaminergic reward system, as pharmacological and chemogenetic manipulation that increases dopaminergic activity causes more stochastic exploration in *n*-armed bandit and foraging tasks [56,100]. A question for future research is whether dopaminergic activity increases adolescents' exploration through their estimate of the background reward rate and/or through increasing stochasticity. Further, not all learning occurs in an asocial context, and adolescents can effectively use information from peers to learn about their environment [50,59,101]. Future research should examine how social learning affects the ability to learn appropriate explore/exploit choices, and whether there are developmental differences in the degree to which social influence affects this behaviour.

Explore/exploit strategies and developmental psychopathology

Explore/exploit strategies may serve as an informative marker of psychopathology. For example, research in adults has revealed that symptoms of depression and substance use disorders are associated with overexploitation on patch foraging tasks [15,102–107], which has been attributed to reduced motivation in depression [108] and behavioural inflexibility in substance use disorders [109]. By contrast, anxiety disorders are associated with under-exploitation of patches [110,111], which has been attributed to the intolerance of uncertainty associated with these disorders [112].

Yet, only a handful of studies have examined the association between explore/exploit strategies and psychopathology in developmental samples [1,5,104]. This dearth of evidence is notable, as adolescence is a period during which we see the onset of the majority of psychopathology [16]. Exploration serves a developmental purpose by providing adolescents with experiential knowledge about their environment that is utilised in maturity [38]. Biases in exploration associated with psychopathology may have profound consequences for adolescents, as they can deprive

them of developmentally important opportunities to learn from their surroundings in ways that prepare them for later life. For example, overexploitation biases associated with psychopathology [15,105] may prevent adolescents from engaging in novel, formative experiences that support mental health, such as going to a summer camp and forming new friendships.

Early adversity, a known risk factor for mental health problems [113,114], is associated with biased foraging strategies [3]. Early adversity can confer a latent vulnerability for psychopathology by impacting cognitive abilities, such as RL [115]. As foraging relies on learning the reward structure of one's environment [27,28], childhood adversity may disrupt computational mechanisms used to learn from reward feedback, thus increasing the risk for psychopathology. Future research should consider the genetic basis for individual differences in explore/exploit strategies, as genetic differences substantially contribute to individual differences in mental health [116]. One study has identified a candidate gene (*PRKG1*) associated with reduced foraging exploration in humans [117]. Variations in *PRKG1* have also been implicated in the association between childhood trauma and alcoholism [118], suggesting there are genetic vulnerabilities that may interact with childhood adversity to bias foraging strategies and increase the risk of substance use disorders. Longitudinal research into foraging that incorporates assessments of genetic and environmental risk is needed to advance our understanding of how explore/exploit strategies may increase the risk of mental health problems across development.

Concluding remarks

Patch foraging is a pervasive context of decision-making across species and has been formative in the evolution of human cognition [1]. Recent evidence suggests there are developmental changes in explore/exploit choices, with younger organisms exploring more whereas older organisms utilise more exploitative strategies, consistent with cooling off accounts [36,46]. Such effects may be driven by developmental changes, including neural pruning within the dopaminergic reward system and ACC during adolescence, as well as the decline in stochastic exploration across development [57,82,92]. Recent research has yielded insight into how exploration and exploitation behaviours can support human development, although it will be important for future research to examine foraging strategies, and their neurocomputational correlates, longitudinally (see [Outstanding questions](#)). We have suggested that exploration in youth can assist the individual in learning the structure of their environment, allowing them later, during maturity, to better navigate their surroundings independently of caregivers. Understanding the typical developmental trajectory of exploration strategies may also be informative for studying how mental health problems develop, though more research is required to understand how individual differences in explore/exploit strategies are associated with different outcomes across the lifespan.

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Declaration of interests

No interests are declared.

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Outstanding questions

Does the hyperactivity of neural regions responsible for reward processing (i.e., the ventral and nucleus accumbens) motivate greater exploration in adolescence, relative to other age groups? If so, is this through inflating adolescents' estimate of the background reward rate or by motivating more stochastic choices compared with other age groups?

Does the development of the ACC from childhood to adulthood coincide with an improved ability to estimate the background reward rate of the environment?

What are the longitudinal trajectories of foraging choices across the lifespan and are these associated with structural and functional changes to the dopaminergic reward system?

To what extent do non-human animals demonstrate cooling off across development and can comparative studies be leveraged to inform our understanding of the evolution of age-related changes to foraging strategies?

Are there developmental differences in how explore/exploit choices are affected by social influence and can estimates of the background reward rate be influenced through social learning?

Are biases in foraging explore/exploit choices a transdiagnostic predictor of mental health problems in adolescence and adulthood?

Do experiences of childhood adversity impact foraging strategies in adolescence, and are these associated with later mental health outcomes?

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