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Perspective

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Connecting extinction learning in the laboratory and the wild

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Abstract

In extinction learning, a behaviour that was previously learned is extinguished when it no longer occurs in response to a target stimulus. However, laboratory research with non-human animals has revealed 'paradoxes' that consist of relapses or amplifications of the extinguished behaviour. In this Perspective, we examine extinction learning as a psychological mechanism and as an evolutionary adaptation. Relapse effects (including spontaneous recovery, renewal and reinstatement) and amplification effects (including extinction burst, increased behavioural variability and the partial reinforcement effect) reflect evolutionarily developed strategies to optimize survival in unpredictable environments. In the wild, reward loss motivates exploration and enables organisms to re-engage when success is possible. This functional interpretation combines psychological and ecological interpretations to redefine extinction as an adaptive search process and provides new insights for psychology and neuroscience.

Sections

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Introduction

Memories enable humans and other animals to predict the future. However, memories can only serve as useful predictions if they are updated every time the predictions prove to be wrong. Because new encounters are rarely radically different from those of the past, most updates only need to slightly alter the memory traces[1]. But in extinction learning, a prediction from the past is completely wrong when an expected reward does not occur. How the animal adapts to this scenario is informative to recognize the evolutionary embedding of extinction learning and to understand why so many of its features are difficult to explain by learning theory.

In laboratory studies of extinction in non-human animals, a reinforcer is presented with a stimulus, which leads to learning of this association. The reinforcer can be positive, such as food, which induces appetite and approach behaviour during acquisition, or negative, such as an electric shock, which produces fear or avoidance reactions. A typical example is seen when observing the behaviour of a rat in a conditioning device called a Skinner box that is used to study animals in operant or classical conditioning paradigms. In classical conditioning, a ringing tone serves as the conditioned stimulus, which reliably predicts the occurrence of a shock (unconditioned stimulus). The rat then starts to freeze as a fear response when the ringing tone is presented. When extinction learning begins, the conditioned stimulus (ringing tone) is no longer followed by the unconditioned stimulus (shock). Thus, the rat's prediction regarding this association fails. When the conditioned stimulus is presented several times without the unconditioned stimulus, the rat gradually decreases their response to the stimulus – a behaviour known as extinction. Reinforcer suppression extinguishes the reinforced behaviour irrespective of whether the stimulus is predictive of the reinforcer (conditioned, as in this example) or sets the occasion for action to obtain or avoid the reinforcer (discriminative, as in instrumental conditioning).

Psychological studies have described many core processes of behavioural change related to extinction. In certain scenarios, the animal demonstrates transient relapse or amplification of the extinguished behaviour (during and after classical or instrumental extinction[2]), called 'paradoxes'[3]. These paradoxes form two categories: relapses of behaviours (in which an initial behaviour re-emerges after a time or in another place) and behavioural amplifications (in which an initial behaviour is invigorated, lengthened or varied). In the example above, the rat might initially stop freezing after the ringing tone, then later freeze again when the conditioned stimulus is heard again. So, relapses occur when time passes after extinction (spontaneous recovery), when the context changes after extinction (renewal) or when the unconditioned stimulus is presented again shortly after extinction (reinstatement). Relapse effects depend on the change in context between acquisition and extinction and/or extinction and reacquisition. By contrast, amplification effects are persistence of the behaviour. These include a sudden increase in response rates to the previously rewarded stimulus (extinction burst), a flood of new behaviours (greater behavioural variability) and greater resistance to extinction after a sparse reinforcement schedule (partial reinforcement effect).

Extinction learning is widespread and involves fundamental evolutionary components for survival. Extinction has been shown in highly similar ways in mammals (including humans[4–6]), birds[7], fish[8], amphibia[9], insects such as honeybees[10] and *Drosophila*[11], and molluscs[12]. Due to the existence of various animal models, the neuronal mechanisms of extinction learning have also become a highly successful field of neuroscientific inquiry[13,14]. Indeed, many animal studies attempt to explain the 'how' of extinction and describe various psychological and neuroscientific conditions that lead to paradoxical relapses into extinguished behaviour. However, many key questions remain, including why similar phenomena have evolved throughout the animal kingdom and why context is so important for extinction learning and relapses in particular. Surprisingly, this evolutionary 'why' of extinction learning is almost ignored in the biopsychological literature, even though these behavioural and cognitive mechanisms have certainly arisen through natural selection due to an associated survival advantage[15].

However, behavioural ecologists and ethologists study situations in the wild that are identical or quite similar to each of the phenomena of non-human animal extinction and routinely ask these 'why' questions. But these ecological studies remain completely separate from psychological and neural studies of extinction. Integrating these two parallel and perfectly complementary scientific traditions could enable a deeper understanding of the evolutionary, behavioural and neural principles of extinction learning. It would explain the various behavioural paradoxes of extinction learning through evolutionary principles and could provide ecological studies with a mechanistic understanding that ranges from learning theory to the synapse.

These mechanisms have important translational implications, because conditioning obeys the same principles in animals and humans. Anxiety disorders are thought to mostly originate from aversive conditioning events. In Europe, 10–14% of adults suffer from an anxiety disorder each year[16], with specific phobias being the most common. Exposure therapy is the gold standard for treating phobias and other forms of anxiety[17]. In exposure therapy, the patient is confronted with an object that causes the anxiety response without the option to leave the situation. Because the feared negative consequence does not occur, the anxiety response lessens over time and subsequently reports a reduction of anxiety to the objects used in the therapy. However, approximately 19–62% of patients who initially benefit from exposure therapy later experience a relapse of fear when encountering the aversive condition again[18–21]. Many relapses occur because patients are confronted with contextual stimuli that differ from those they were exposed to during psychotherapy[17], where extinction learning took place. These relapses represent some of the 'paradoxes' of learning[3]: extinction does not erase the learned behaviour, even if it is not exhibited at the behavioural level until relapse.

In this Perspective, we argue that the mechanisms and the functions of extinction learning are complementary and must be considered together to understand the paradoxical effects of extinction. In doing so, we show that extinction in laboratory animals has functional equivalents for animals in the wild and that the paradoxes identified by psychologists vanish when the 'why' of those behaviours is investigated. We first discuss relapse and the key role of context in these effects, followed by amplification effects. Finally, we present our framework, which posits that extinction-related effects in the wild mostly evoke motivations to 'try harder', 'try later' or 'try differently' – behaviours that look paradoxical in laboratory settings but reflect adaptive attempts for animals to reach their survival and reproductive requirements.

We mostly focus on foraging behaviour in instrumental situations. Although there are important differences in the neurobiological and psychological mechanisms of classical and instrumental conditioning, as well as between appetitive and aversive preparations, there are strong parallels in the behavioural effects obtained in these different conditioning types[3]. The observed unity in these effects suggest that extinction is controlled by similar evolutionary pressures, irrespective

Table 1 | Mechanistic and functional interpretations of extinction-related effects

Category	Extinction-related effect	Psychological description	Analogous ecological scenario
Relapses of behaviour	Spontaneous recovery	Reappearance of an extinguished response with the passage of time	Travelling back to an exploited food patch after gradual repletion
	Renewal	Reappearance of an extinguished response when the spatial context is altered after extinction learning	Leaving a moderately profitable feeding location for another in which the success rate is expected to be higher
	Reinstatement	Reappearance of an extinguished response due to re-exposure to the learned unconditioned stimulus after extinction	Increasing vigilance (if the unconditioned stimulus is a threat) or promoting seeking behaviour (if the unconditioned stimulus is a reward)
Amplifications of behaviour	Extinction burst	Sudden absence of reward after continuous reinforcement creates conditioned stimulus ambiguity, which boosts responding	Investing more effort in the task to quickly determine its reward-related value (and go away in case of failure)
	Behavioural variability (in early extinction, including resurgence)	The interruption of reward delivery in response to a cue induces a response to alternative cues	Trying alternative behaviours when the previously learned successful response does not work anymore
	Partial reinforcement extinction effect	Exposure to intermittent cue–outcome association during acquisition makes the animal more tolerant to the absence of reward in extinction	Lengthening reward-seeking behaviour to maximize success under harsh environmental conditions

of the appetitive or aversive conditions in which conditioning takes place. This similarity makes sense given that situations encountered in the wild are not as cleanly separated as those in the laboratory. For instance, behavioural responses can be instrumental while being influenced by specific cues and often consist of trade-offs between overlapping appetitive and aversive contingencies (for instance, looking for food under a predation risk). We therefore consider extinction-related effects without distinguishing between appetitive or aversive conditioning paradigms.

Relapses of behaviour

Relapses are characterized by a sudden reappearance of the conditioned response after successful extinction learning. As a rule, these relapses are accompanied by a change in context and their existence poses a major challenge for human psychotherapy. Here, we will briefly introduce three relapse phenomena in the laboratory (spontaneous recovery, renewal and reinstatement) and their counterparts in behavioural ecology (Table 1). In addition, we show how much these phenomena depend on contextual cues. We begin with spontaneous recovery — a phenomenon that marks the historical beginning of extinction learning research.

Spontaneous recovery

In a classic study, dogs were conditioned to salivate to the sound of a metronome that was followed by flesh powder[22]. After this response was extinguished, an experimental break of minutes to hours was sufficient for the conditioned stimulus to trigger relapse: a renewed occurrence of the conditioned response. The researcher concluded that extinction is a novel type of learning process that cannot be explained by forgetting, as the restoration of conditioned response proved that the memory trace had not disappeared. The more time that passes between extinction and the next session, the stronger the spontaneous recovery[23]. But this recovery is then negatively accelerated and decreases in strength with further repetitions of extinction sessions[17] (Fig. 1a).

However, the function of spontaneous recovery was unclear. The original study author posited that the conditioned response had been inhibited and that inhibition is less stable than excitation, which leads to a re-emergence of excitation over time[22]. Later views assume that the passage of time after extinction can be learned by the animal as a context stimulus similar to a visual cue that can serve as the context. As a change of a visual context can cause a relapse, so then does the passage of time. Changes in context not only provide a common explanatory concept for all relapse phenomena but also overlap with neurobiological findings[22].

Behavioural ecologists have described many phenomena in the wild that resemble spontaneous recovery. These are often referred to as ‘traplining’, which consists of ‘revisiting behaviour of feeding sites’ and has been documented for species across different ecosystems, including bumblebees[21], pumas[24], little egrets[25], elephants[26] and ungulates[27]. These and further species leave an area when its resources are depleted (similar to extinction learning), but later repeatedly revisit these sites when they offer replenishable resources such as fruit, nectar or prey (similar to spontaneous recovery)[27,28]. Compared with constantly searching for novel feeding grounds, traplining improves foraging efficiency when the foraged resources are slow to replenish and the revisit occurs when the resource is at its peak[29]. Above all, the efficiency of traplining depends on cognitive resources such as cumulative learning, memory and estimation of the passage of time[30,31]. In fact, hummingbirds and bumblebees can remember the time between flower visits and adjust their next return visit to feeding sites accordingly[32–35] (Fig. 1a).

The spontaneous recovery phenomena in the biopsychological literature are therefore similar to ecological observations, including in their details. For example, spontaneous recovery has been observed in the laboratory with rats even after more than a hundred extinction attempts[36]. According to the ecological literature, this pattern is sensible if there is a possibility that an exhausted feeding site contains a renewable resource[35]. Although rats show a large number of spontaneous recoveries, these recoveries are negatively accelerated, so their strength decreases with each repetition[23,37]. Similarly, predators spend negatively decreasing time in visiting areas if they record declining catch rates each time due to a lack of prey[38]. The similarity between psychological and ecological studies is also evident when considering the temporal context of extinction learning in the laboratory: these studies show that the strength of spontaneous recovery is proportional to the time that has elapsed since extinction learning[23,39]. Ecological studies also observe that the efficiency of revisiting an area is proportional to the time that has elapsed since the last visit[21,29]. Taken together, laboratory and ecological studies show that animals spontaneously

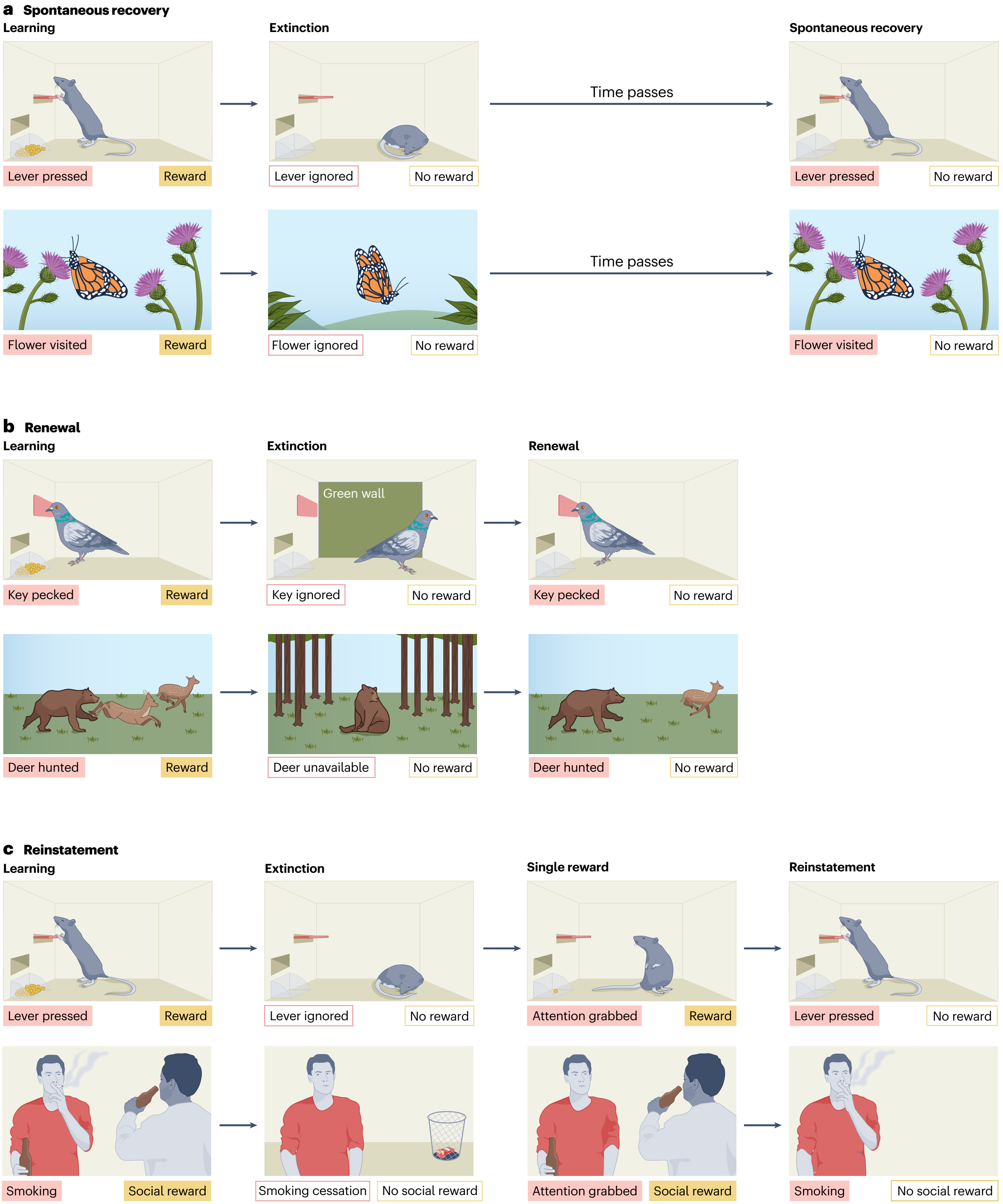
a Spontaneous recovery
Learning
Lever pressed
Reward
Extinction
Lever ignored
No reward
Time passes
Spontaneous recovery
Lever pressed
No reward
Flower visited
Reward
Flower ignored
No reward
Time passes
Flower visited
No reward
b Renewal
Learning
Key pecked
Reward
Extinction
Green wall
Key ignored
No reward
Renewal
Key pecked
No reward
Deer hunted
Reward
Deer unavailable
No reward
Deer hunted
No reward
c Reinstatement
Learning
Lever pressed
Reward
Extinction
Lever ignored
No reward
Single reward
Attention grabbed
Reward
Reinstatement
Lever pressed
No reward
Smoking
Social reward
Smoking cessation
No social reward
Attention grabbed
Social reward
Smoking
No social reward

Fig. 1 | Relapses in the laboratory and similar behaviours in the wild. **a**, Spontaneous recovery of a rat that presses a lever for food reward (upper left panel) and stops doing so after extinction (upper centre panel). When time passes, the rat is placed back into the conditioning chamber and immediately takes up its operant behaviour under extinction conditions (upper right panel). In the wild, similar behaviour is known as 'traplining'. Butterflies visit flowers for nectar (lower left panel) and visit other flowers (lower centre panel) once nectar resources are depleted. They then come back after some time has passed to exploit the replenished nectar (lower right panel). **b**, During an ABA renewal task, a pigeon pecks a key for food reward in context A (tan wall, upper left panel). When the wall colour changes to green (context B), extinction starts and the animal stops pecking (upper centre panel). As soon as the wall colour changes back to tan (context A), the pigeon starts the operant response again (upper right panel). Similar situations occur in prey–predator interactions when a bear hunts deer (lower left panel). Hunting results in deer leaving this patch, which causes the bear to leave too (lower centre panel). When the bear is gone, deer come back, which can result in reappearance of the bear (lower right panel). **c**, In a reinstatement study, a rat operates the lever for a food reward and stops doing so under extinction conditions. A single food delivery can reinstate the operant response (upper panels). Similar situations are typical for relapses of smoking, where quitting smoking can be followed by a reinstatement after experiencing a smoking situation (lower panels).

retry to obtain resources from once-rewarding settings. This learning theoretical paradox makes sense when minding the ecological conditions of animals that were positively selected for revisiting areas with replenishable resources.

Renewal

Environmental dynamics and an animal's actions can induce context changes that might lead to renewal of activities that were extinguished in a different context. Renewal can take three forms depending on the context in which a behaviour is acquired, extinguished and renewed. ABA renewal is the most common form, involving Context A and Context B. In a rat classical conditioning paradigm, white noise (Context A) is present during aversive learning. When extinction learning begins, the white noise is switched to blue noise (Context B) and the conditioned stimulus is unexpectedly no longer followed by the unconditioned stimulus. This process creates a second memory that predicts the absence of the unconditioned stimulus in Context B[40]. In this competition between memory traces, the context in which extinction took place has a key role[41]. During initial acquisition, contextual cues such as white noise are not completely ignored, but play a subordinate role overall[42]. During extinction, contextual cues such as the blue noise are strongly integrated[43]. As a consequence, the rat again expects the aversive stimulus when Context A is delivered again.

This experimental ABA renewal design demonstrates something important about the psychology of extinction learning: animals do not forget an extinguished behaviour[43] (Fig. 1b). The originally learned conditioned stimulus can activate two different memories – one in which the unconditioned stimulus is predicted and one in which it is not – depending on the context. If the extinction context (blue noise) is present, the corresponding memory (unconditioned stimulus not predicted) is activated, and the rat is relaxed. If this extinction context is removed, the originally learned acquisition memory (unconditioned stimulus predicted) is usually reactivated, and the rat expects a painful shock. Thus, the original memory is largely context-independent, whereas the extinction memory is not. Because renewal has also been observed in ABC designs, it is highly likely that it is the absence of the extinction context that reactivates the conditioned response[3]. Indeed, ABA relapses (in an operant design) depend on the expectation of a reward upon release from the extinction context, regardless of whether the extinction memory underwent cellular consolidation or not[44,45].

Evidence for ABA renewal in nature is not so clear, because the context elements that cause extinction are biologically significant rather than initially neutral. For instance, for a diurnal animal, night acts as an extinction context for the foraging activity performed the day before, which is renewed the next day. But the decrease in light intensity at dusk physiologically prepares the animal to reduce foraging and other behaviours. In other situations, ABA renewal-like behaviour involves the recognition that a place is safe or unsafe again, due to the identification of biologically meaningful components such as predators (Fig. 1b). For example, Trinidad guppies often swim near the water surface to feed on mosquito larvae. When an artificial bird of prey flew over the water, the guppies immediately retreated to deeper areas and remained there until the predator had disappeared and then they returned to the surface[46]. This ABA renewal-like behaviour also applies to predators looking for prey. Once they catch prey in a certain area, that area can remain profitable and the predator should stay there. However, prey responds to the predator's presence by fleeing or hiding, which makes the area less profitable[38], and alert prey is difficult to catch. Thus, predators should leave an area and only return when the prey's alertness has sufficiently decreased[47]. For example, little egrets dynamically adjust their return to different fish ponds based on previous reward probability and fish behaviour[48]. Prey therefore resembles a renewable resource that requires a strategic delay in visiting the same area[24,28]. If a predator returns too quickly, the prey is still hidden, but if they return too late they miss the opportunity to catch it. As a consequence, predator and prey play a complex and interactive waiting game[49]. Optimal foraging theory captures this dynamic by assuming that animals dynamically adjust their behaviour to these interactions while distinguishing between high-quality and low-quality areas[50]. In conclusion, the biological significance of context makes ABA renewal approximative in the wild, although it could represent the evolutionary foundation that enables animals to learn that any specific context can be associated with non-reward and cause extinction.

AAB renewal occurs when acquisition and extinction take place in the same context A and the acquired response reappears in context B. For example, in one study rats were conditioned in Context A to freeze, using an auditory cue to then extinguish this behaviour in the same environment (Context A)[51]. The conditioned freezing to the extinguished cue was renewed in a novel context (Context B). This AAB renewal is sometimes also referred to as 'disinhibition of extinction'. Thus, the violation of expectations about the nature, location or timing of a stimulus can make animals vigilant again – in case the unexpected event is significant. In the wild, a novel stimulus prepares an individual to encounter an opportunity for rewards or a risk of harmful events, even if the stimulus itself is neutral. Correspondences to AAB renewal in nature are often related to switching between different food sources. The marginal value theorem is a mathematical model used to predict the optimal time for a forager to leave an exhausted food source in favour of another[52,53]. The theorem's rationale is that it is more profitable to leave spot A and move to spot B when the marginal return in spot A falls below the average return that could be achieved by moving to spot B[54–56]. At this point, food is still available in area A, but the decision to leave it is made when the search time per item collected exceeds a certain threshold.

The renewal-like behaviour in foraging largely corresponds to the laboratory findings but also has two differences. First, the context change in the laboratory is controlled by the experimenter, whereas in the wild it is controlled by the animal itself. Second, the extinction context in the laboratory offers no reinforcement, whereas in nature it is characterized by a decline in reward below the threshold predicted by the marginal value theorem. However, ecological studies clearly show that non-human animals not only remember the contingencies of the previous context but also actively and strategically compare the promise of different locations and make decisions accordingly.

Reinstatement

The re-exposure to an unconditioned stimulus ‘reinstates’ the previously extinguished conditioned response[57] (Fig. 1c). Thus, reinstatement defines the return of a conditioned response when the unconditioned stimulus is presented once again after successful extinction. As is possibly true for all relapse phenomena of extinction learning, reinstatement is context-dependent and therefore strongest in the context in which acquisition took place and mostly absent outside this context[39]. For instance, rats that had acquired an operant response for an intravenous injection of cocaine and subsequently underwent extinction restarted their operant response after having received one injection of cocaine[58].

Reinstatement-like conditions are abundant in the wild. Unlike in the laboratory, food resources in the wild are rare but not randomly distributed; for instance, vegetation produces an abundance of seeds, fruits and nuts that can be found in irregularly distributed patches[59]. Thus, even when an animal has given up looking for food at one location, finding a single edible item somewhere else reinvigorates search behaviour for further food because this item could signal the presence of another patch[60]. The resulting movement pattern of searching for heterogeneously located food patches can sometimes resemble a Lévy walk, a scale-free movement pattern used by many animals, including humans[61].

Reinstatement-like behaviour also occurs in social contexts. For example, a brood of mallard ducks reared without a hen showed reduced alarm call responsivity (such as freezing) compared with isolated rearing conditions[62]. However, stimulating these ducklings with distress calls immediately reinstated high levels of freezing. In the ecology of modern human life, a classic example for reinstatement is the observation that smoking a single cigarette after having successfully quit smoking[63] can reinstate chain smoking (Fig. 1c). Thus, reinstatement is a key problem for psychotherapy because the object of fear or desire can appear unexpectedly in a similar context after successful therapy[64,65]. Taken together, ecological studies show that animals that had given up on a depleted food resource and left the area instantly started searching again when finding a food item. This phenomenon is possibly the evolutionary background of laboratory-based reinstatement studies in which the animal restarts to show its extinguished conditioned response once the unconditioned stimulus is delivered again.

Context as the driving force of relapse

Spontaneous recovery[66], renewal[67] and reinstatement[68] are sensitive to contextual changes or even dependent on them. Neurobiological studies suggest that the hippocampus has a key role in contextual integration during extinction learning[69]. A deep neural network with hippocampus-like experience replay was used to attempt to understand the mechanistic contribution of the hippocampus[70]. This neural network simulated an animal roaming a platform in an ABA extinction learning study and exhibited typical ABA renewal behaviour without being programmed to do so and without explicit information that some aspects of the context had changed. Without experience replay, the context-dependent renewal did not occur. In a subsequent study, the same neural network spontaneously exhibited spatial representations typical of the hippocampal regions CA1 and CA3 (such as place cells) after having learned the ABA renewal task[71]. This spatial representation was globally reassigned during the change from context A to context B and reversed when the agent returned to context A. This reversal was accompanied by a renewal of the conditioned behaviour.

Animal studies have shown similar evidence for hippocampal mechanisms. For instance, electrophysiological recordings in the hippocampus of rats in a similar ABA renewal paradigm revealed that spatial and task-relevant contextual variables were jointly represented as the neural mechanism underlying renewal[72]. Based on these findings, extinction learning in pigeons was tested using a paradigm with multiple stimuli; stimuli that showed the highest contiguity between context change and extinction onset led to the strongest renewal, and no renewal occurred when there was low contiguity[41]. Thus, it is likely that context can be understood mechanistically as a property that follows the dynamics of reinforcing learning and combines experience replay in the hippocampus along with the learned spatiotemporal coding properties. These findings provide a partial answer to how relapse occurs in extinction.

Neurobiologically, the concept of reward prediction error is important to understand how animals manage the transition to extinction. Dopamine neurons encode the difference (the ‘error’) between a predicted reward and the received reward[73]. If the reward is unpredicted, dopamine neurons transiently increase their activity (a positive reward prediction error signal). By contrast, if the reward is predicted but does not occur or is lower than predicted, dopamine neurons transiently decrease their activity (a negative reward prediction error signal). Finally, if the received reward fits the prediction, no noticeable change in dopamine release is observed compared with baseline activity. A prediction error signal seems necessary to adjust future expectations and guide associative learning, such as shown in Pavlovian conditioning and instrumental conditioning. Thus, phasic dopamine release could be a signal that the learning of a task is incomplete. This description aligns closely with reinforcement models derived from machine learning, notably the temporal difference learning algorithm used to update value estimates from successive predictions (not just final outcomes) via the reward prediction error signal[74–76].

In the first trials of an extinction study, a reward prediction error is crucial because the conditioned cue suddenly ceases to predict reward delivery, which creates a strong difference between what is expected and what occurs. Thus, the reliability of the conditioned stimulus becomes ambiguous. According to one evolutionary and functional view, organisms might start to shift their attention from the conditioned stimulus to the context as they search for a reason why their prediction failed[43,77]. This mechanistic theory assumes that the onset of extinction creates a prediction error that results in an attentional switch to the context, which results in context-specific learning[5,72,77]. In the wild, using context cues to decide whether (and where) to repeat a behaviour is an optimal way to explore and exploit the resources available in an unpredictable environment – trying again does not cost much but might turn out to be highly profitable.

In summary, relapses of behaviour occur after a time (spontaneous recovery), when the post-extinction context differs from the extinction context (renewal) or when the unconditioned stimulus is given again after extinction (reinstatement). Although relapses might not seem functionally adaptive in the limited environment of a Skinner box, their significance becomes obvious when transferring these specific situations into the wild. When food resources are unavailable here and now, the appropriate behaviour is not inhibition and rest but, rather, the exploration of other places and/or revisiting the same place later.

Behavioural amplifications

Three idiosyncratic behavioural amplifications can accompany the onset of extinction: extinction burst, increased behavioural variability and the partial reinforcement extinction effect (Table 1). These invigorating (extinction burst), lengthening (resistance to extinction) and randomization of responses (behavioural variability) arise in both laboratory and naturalistic settings. Here, we characterize these phenomena and their assumed evolutionary conditions.

Extinction burst

When extinction begins, many things change abruptly. There is a sudden increase in the intensity, frequency or duration of the operant response – a behaviour known as an extinction burst (Fig. 2a). This burst most often occurs after continuous reinforcement (when each response is rewarded) and a high reinforcement rate (for instance, six food pellets versus one food pellet per trial). The burst stops after trying repeatedly for a period of time and gives way to a gradual reduction in responses and a shift to alternative behaviours[78].

Explaining this behaviour through learning theory is not simple[79,80]. A classic interpretation is that negative emotion results from the sudden interruption of an expected reward and invigorates the animal's responses[81]. Whatever the exact causal explanation, the extinction burst seems to depend on the animal's ability to predict the near future. Animals that experience partial reinforcement (frequent non-rewarded trials) do not show extinction bursts[82]. Also, children at high risk for autism spectrum disorders do not show extinction bursts, compared with age-matched healthy peers[83]. Neurobiological findings in mice suggest that the reward-associated firing patterns of ventral tegmental dopaminergic neurons have a key role in extinction bursts[84]. In mice in which these dopaminergic neurons were genetically modified and highly sensitive to the rewarding outcomes of the organism's own actions, these cells showed high activity during initial acquisition and low activity during the onset of extinction. These mice learned the operant task very quickly and showed a high extinction burst. In mice in which the dopaminergic neurons were less sensitive to response-related rewards, the cellular activity patterns between initial learning and extinction were similar, and an extinction burst was almost completely absent. Thus, the extent of the extinction burst is likely related to the perceived value of the action[84].

Extinction burst-like behaviour is common in the wild. For example, the European badger digs at different locations for various food sources, possibly attracted by olfactory or visual cues. When food is not rapidly found, badgers switch from using only one foreleg at a low rate to digging with both forelegs at a higher rate[85] (Fig. 2a). This pattern resembles psychological findings that a stronger reward expectation leads to a stronger extinction burst, whereas a lower reward reduces or suppresses this effect[80,82].

As another example, Australian foxes prey on endangered pygmy bluetongue lizards by identifying their locations and digging into their burrows. The foxes try increasingly hard to find the lizards, but are not always successful and have to give up at some point[86]. Similarly, operant responses cease after an extinction burst[78]. Overall, these examples demonstrate an essential foraging strategy of 'try harder' after failure[87]. After continuous failures, animals usually switch to behavioural alternatives. In the laboratory, a similar pattern is observed when the availability of alternative reward sources abolishes the extinction burst, causing a more rapid suppression of ongoing behaviour[88].

Increase of post-extinction behavioural variability

Extinction learning often drives the emergence of novel, previously non-reinforced behaviours[89]. Because extinction research has focused mostly on the cessation of responses, the onset of behavioural variability was often neglected in research. However, behavioural variability can be exploited to shape novel behaviour. For example, when problematic actions (hitting behaviour) during social encounters are extinguished in young boys, novel socially acceptable behaviour, such as toy play, can emerge that can be reinforced to replace the undesired ones[90]. In pigeons, behavioural variability after ABA renewal (Fig. 2b) can be simply accounted for by a computational associative network that uses the principles of associative learning, applied to the trial-by-trial dynamics of the animal's behaviour[91].

Psychologists rarely give animals a chance to show such behaviour in the laboratory – most studies involve only very limited response options. One exception is resurgence, another relapse phenomenon. Resurgence is the reappearance of an extinguished response to a first reward-predictive stimulus during the extinction of another response to a second stimulus[92]. Resurgence is usually shown by first conditioning a target response that is then extinguished. Next, a new response is reinforced and acquired. If this second response is then extinguished, the animal starts responding to the first target again – it resurges. Resurgence resembles an ABC extinction procedure in which the operant response comes back when the extinction context vanishes[93].

In the wild, animals have plenty of response alternatives, such as food options to pursue. According to optimal foraging theory, animals should switch between food types to maximize intake based on a trade-off between benefits and costs[94]. For instance, honey badgers quickly switched to other food resources when search patterns yielded no returns. By continuous food switching, the animals were able to maintain their intake level despite seasonal changes and important differences in prey availability[95] (Fig. 2b).

In the wild, behavioural post-extinction variability is also seen in transitions to other food patches, as food distribution in the environment is not homogeneous. These transitions can be described as relocations in the environment through long steps in a random direction (Lévy walks) that relocate foragers away from a place in which they were seeking food in vain. Following relocation, organisms start a different movement pattern: smaller random steps within a small area (Brownian walks). Whereas Brownian walks enable foragers to maximally exploit a patch, Lévy walks relocate the forager far from the patch. Brownian walks within a patch will eventually be extinguished again after a time due to food rarefication, giving rise to distancing through Lévy walks[96]. Thus, Lévy walks can be interpreted as a form of exploratory behaviour that prevents immediate revisitation of the inspected area[97]. Their alternation with Brownian walks, as well as the variability in their orientation

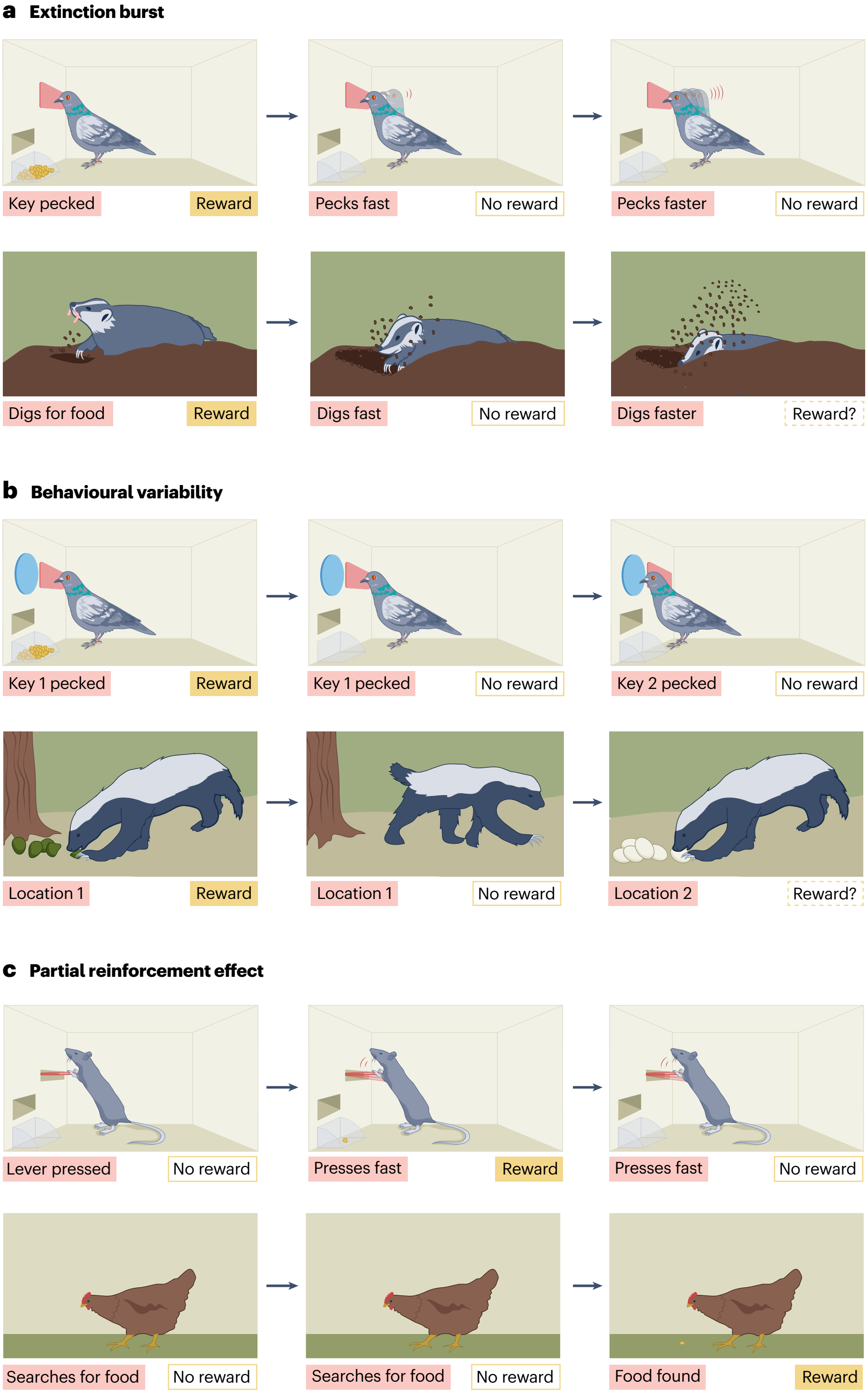

Fig. 2 | Behavioural amplifications in the laboratory and similar behaviours in the wild. **a**, Extinction bursts in a conditioning task can be observed at the onset of extinction as a strong increase in the frequency and force of operant behaviour in a pigeon (upper panels). Similar observations are common in the wild. For example, European badgers increase their digging speed and type when looking for food resources that do not immediately materialize (lower panels). **b**, Extinction learning also increases the variability of responses. During extinction a pigeon switches to pecking a key that was never rewarded or had been extinguished before (upper panels). Similarly, honey badgers swiftly look out for other patches and resources when food is depleted in one location (lower panels). **c**, The partial reinforcement extinction effect describes the observation that rats which work for random reward (upper left and centre panels) take a long time to stop showing the operant response during extinction (upper right panel). Similarly, chickens that search a long time for small pieces of food, and thus are used to not giving up, continue to search even when food is not available for a long time (lower panels).

and length, maximizes exploration of a large foraging area. The alternation of Lévy and Brownian walks was observed in animals as diverse as bacteria, mussels, honeybees, albatrosses, sharks, monkeys and human hunter-gatherers[98,99]. Because Lévy patterns extend the search area, foragers that show those patterns in unpredictable environments outperform foragers that use Brownian movement patterns only[100]. In computer simulations, a lower density of randomly distributed food items was associated with a significantly higher probability that the agents exhibit Lévy walks, as well as a higher chance of 'survival' within the fixed number of steps of the simulation[101,102].

Partial reinforcement extinction effect

Animals that were trained under partial reinforcement and then subjected to extinction show greater resistance to extinction compared with animals that received continuous reinforcement[103] (Fig. 2c). This robust effect occurs even when there are no differences in response rates before the start of extinction[104,105]. From an emotional perspective, it is often assumed that resistance to extinction is a consequence of learning to tolerate unrewarded trials in the training phase[103]. However, resistance to extinction might also result from reduced attention paid to context: the conditioned stimulus becomes less ambiguous during extinction for animals that were partially reinforced compared with those that were continuously reinforced. Thus, although partial reinforcement increases attention to the context compared with continuous reinforcement[106,107], in extinction the animals partially reinforced at training should pay less attention to contextual cues than the animals continuously reinforced. With a smoother transition to extinction due to pre-exposure to non-reinforced trials in partially reinforced animals, they should maintain their responses to the conditioned stimulus for longer and remain more focused on the task.

In the wild, 'non-rewarded trials' are frequent. For example, the peregrine falcon has a successful hunting rate of 47%[108], the spotted hyena of 30%[109] and the leopard of 14–38%[110] (Fig. 2c). Response persistence despite these failures is therefore crucial to collect enough food to survive. Persistent pheasant chicks are more effective in solving problems[111], and, overall, animals allocate more time to food searching when the food density is lower than when it is higher (such as in winter versus summer)[112–114]. When rewarded and unrewarded trials are randomly distributed (reward uncertainty), foragers overharvest food patches that have initially low resource yields, compared with food patches with high resource yields[115,116]. Thus, from a naturalistic perspective, resistance to extinction is not mysterious but an adaptation to harsh environmental conditions.

In summary, reward omission can cause perseverance instead of context-dependent relapses of extinguished behaviour. Invigorating, lengthening or randomizing a response during extinction is useless in a controlled laboratory setting because no more rewards can be obtained. But these effects are highly adaptive behaviours when the animal is challenged by unpredictable environments, in which working harder is often necessary to survival.

An evolutionary perspective on extinction learning

Overall, extinction phenomena studied by psychologists and ecologists overlap in many details, which suggests that they are governed by similar mechanisms. We have developed the extinction learning in the wild framework to integrate mechanistic and functional perspectives into extinction research. According to this framework, the so-called paradoxes observed in experimental extinction conditions are evolutionarily determined attempts at resumption or persistence within the – typically restricted – laboratory context (Fig. 3a). When animals are restricted to a single response option in a Skinner box, relapses and behavioural amplifications seem maladaptive because they cannot lead to renewed access to rewards. However, these same behaviours lose their paradoxical character when viewed from a functional perspective (Fig. 3b). Reward loss is not the end of learning but the starting point of exploration: it motivates organisms to try harder, return later or switch strategies to exploit resources in a changing environment. In ecological terms, 'failure of extinction' in the laboratory is a conserved survival strategy that promotes flexibility and persistence.

Our framework redefines extinction as an adaptive search process shaped by natural selection. Humans and other animals behave as they do because their evolutionary history has forced them to adapt to changes in resource availability in similar ways. Forgetting old associations would have been the wrong approach, as the extinguished behaviour or a variant of it could be successful again after some time or in a new location. Four conclusions can be drawn from this framework.

Firstly, extinction activates an evolutionarily conserved set of neural and behavioural mechanisms that lead to a strategy of 'try harder, try later again, try differently'. Extinction is not only about associative learning but also about motivation and exploration. Behaviour reappears or changes after extinction and therefore persists during extinction because the loss of reward motivates exploratory activities related to the extinguished action. Motivation refers to the fact that behaviour becomes incentivized by other reward cues to be approached when available[117], or by signals of adversity (uncertainty) that lead animals to seek reward or information in other areas or with greater investment[102]. Incentive motivation might not be part of the extinction process but is assumed to strongly interact with it.

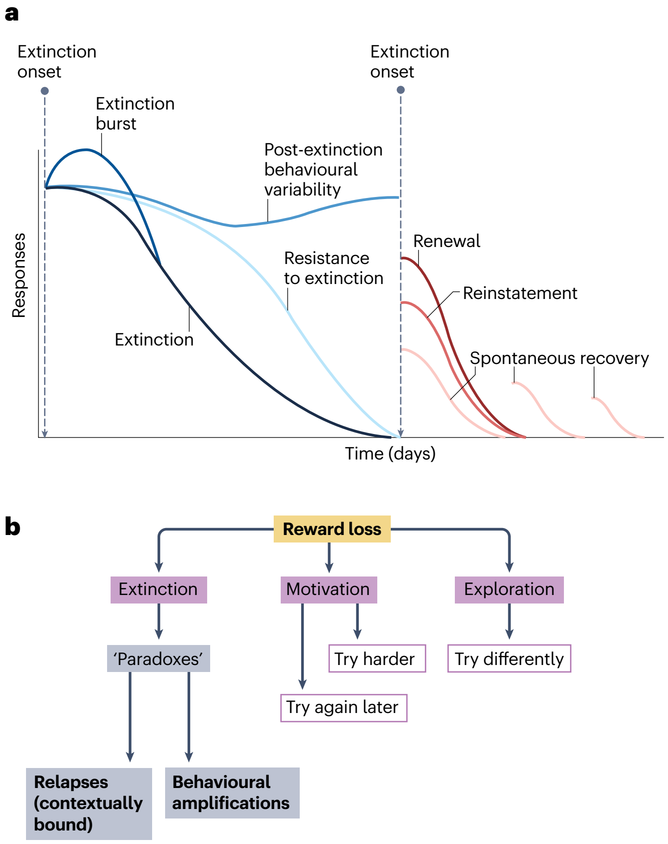

Fig. 3 | Extinction learning in the laboratory and the wild. a, Typical extinction-related phenomena shown in laboratory conditions during and after extinction of a response. These phenomena are often observed across several extinction sessions (days). **b**, The extinction learning in the wild framework posits that behaviour in the wild can reappear again or differently after extinction or persist during extinction because reward loss motivates exploratory activities related to the action being extinguished. Thus, 'paradoxes' shown in a Skinner box are interpreted as attempts to re-engage in reward seeking when the previous behaviour failed.

This view is supported by neurobiological data. For example, it might seem counterintuitive that dopamine, a neurotransmitter associated with reward seeking[117], is necessary for aversive extinction[118]. Similarly, norepinephrine is relevant to appetitive extinction, although it is more associated with the mobilization of effort than with the abandonment of tasks[119,120]. We assume that the involvement of these neurotransmitters in the extinction process is necessary because extinction primarily prepares the organism to resume new activities. Thus, extinction makes new opportunities possible rather than disengaging motivation and behaviour. If extinction simply ended behaviour — as happens in a Skinner box — animals would be forced to passively wait for a new opportunity to act. But even if animals are waiting for reward in the wild, they do not remain passive. For example, the black phoebe adopts a sit-and-wait foraging strategy, but uses active head movements to improve depth perception, motion detection and prey tracking[121]. Neurotransmitters and hormones involved in cue attraction (dopamine) and energy expenditure (norepinephrine and/or glucocorticoids) are therefore expected to play a role during extinction, as they contribute to the preparation of effortful and more variable responses to reward uncertainty in general[122]. In this view, dopamine is released during aversive extinction because the suppression of a negative event might create an expectation that prepares animals to behave under better conditions. By contrast, norepinephrine is released during appetitive extinction because the suppression of a positive event might induce an expectation that prepares animals to compensate behaviourally for difficult times. This opportunity to explore alternatives could actively direct attention to contextual cues and therefore be involved in context-sensitive inhibitory learning. In parallel, this focus on alternatives favours the search for new locations and the expression of new behaviours by preventing an immediate resumption in the extinction context. Functionally, extinction learning could therefore be seen as a form of inhibition of return, in which the loss of a reward in one location facilitates the processing of other stimuli in the vicinity of that location — a phenomenon related to visual search and exploration[123].

Secondly, extinction is in keeping with dynamic adjustments of animals to their local environment. For example, studies on behavioural ecology show that when a prey is leaving a place with intense predation, this behaviour is often accompanied by behavioural adaptations in which the prey engages in strategic prey–predator interactions[49,124]. Similarly, leaving an unprofitable area is often followed by a well-timed return to replenished resources[32–35]. These behaviours involve complex cognitive properties that might go beyond the classical assumptions of associative learning. Neurobiological findings provide a mechanism for this cognitive shift. The occurrence of a reward prediction error is associated with a change in the firing rate of dopaminergic neurons in the midbrain[125]. As learning progresses, this error term shifts back to the time of the conditioned stimulus presentation[125,126]. A later interpretation of this effect assumes that a reward prediction error triggers a causality-seeking mechanism based on the premise that causes must precede outcomes and that organisms learn associations simply by looking back in their memory to identify what caused the reward[127]. A series of experiments showed that this explanation of the dopaminergic effect provides better predictions than the temporal difference learning model[127]. Most importantly, changes in dopamine release not only establish associations between stimuli but also enable a cognitive understanding of the reasons for the perceived consequences. Although this study has been criticized[128,129], it has been confirmed in further experiments that show that rats learn reciprocal associations between causes and effects[130]. Further studies suggest that rats, birds and humans draw causal conclusions during associative learning[131–133]. A study also showed that pigeons in an extinction learning study might draw conclusions about the causes of the unexpected absence of food[134]. Thus, an integrated perspective of associative learning and behavioural ecology could pave the way for a cognitive understanding of extinction learning.

The reward prediction error signal supports motivation for exploration through the ambiguity-induced attentional shift. According to our functional perspective, a reward prediction error is not only a teaching signal ('learn that') but also a general message saying 'explore that!' In a Skinner box, various options for behavioural alternatives are usually not available. As a consequence, psychologists observe that animals disengage gradually from the task over the course of extinction. Disengagement without re-engagement is therefore a laboratory artefact. In the wild, attentional shift is therefore likely to shorten extinction in one location, which enables the individual to repeat (again or differently) the extinguished behaviour elsewhere many times a day. The frequent opportunities to re-express extinguished behaviour when time passes or conditions change in the wild suggest that there are no selective pressures for definitive behavioural suppression. Animals do not encounter such conditions in a natural setting, so total extinction is a counter-adaptive situation that is hard to learn: hundreds of extinction trials are necessary in laboratory conditions to fully extinguish a behaviour[135]. By contrast, what is called an 'extinction deficit' (that is, failure to diminish a conditioned response during extinction) likely reflects the necessity to remain vigilant and exhibit perseverance in harsh or threatening environments[136]. For example, ants learn quickly and show strong resistance to the extinction of learned associations because worker ants operate in highly stochastic environments and must often switch from one task to a previously learned one[137]. These and similar findings might indicate that the reward prediction error signal can easily be reactivated, which enables animals to jump on any opportunity to re-engage behaviour: disengagement makes room for re-engagement.

Thirdly, we conclude that relapses and other seemingly paradoxical behaviours have been positively selected by evolution. We therefore predict that species with different ecological backgrounds would exhibit systematic and predictable differences in extinction. Animals such as bees or hummingbirds, which feed on renewable resources, might have developed the ability to predict the speed and timing of replenishment[28]. By contrast, animals that feed on unpredictable resources, such as desert rodents that search for wind-borne seeds[138], should be less inclined to engage in recursive movement behaviour. Of course, controlled laboratory conditions are necessary to isolate specific processes that otherwise would occur in the noisy background of other phenomena. But providing more degrees of freedom to behaviour is also necessary to establish connections between behavioural aspects that may seem unrelated in the first place. For example, allowing animals in extinction to choose between the acquired response and a response to a novel schedule, or between the depleted food and another food type or a non-food reward, would tell us about the animal's motivation to explore alternative options. We predict that re-engagement in an alternative activity during extinction is more closely related to an animal's propensity to seek new sources of stimulation than to intolerance of non-rewarded delays, as identified by steeper extinction curves or faster temporal discounting[139]. Also, extinguishing a food-related behaviour should facilitate seeking behaviour for other hidden food resources or even non-food resources, signalled by a cue that they might be available elsewhere. If extinction depends on basic motivational (incentive) processes, these predictions should be confirmed in mammals and birds but also in phylogenetically more distant species such as insects. Thus, the wealth of species-specific behaviours studied by behavioural ecologists could provide researchers who study extinction with new animal models in which some textbook aspects of extinction learning might differ. Opening the Skinner box could offer opportunities to investigate both the learning-related and neural mechanisms of extinction learning in these animal models. However, this exchange of insights also works in reverse. Learning theory and neuroscience offer a wealth of knowledge for overlapping scientific questions in behavioural ecology.

Last, our framework sheds new light on the translational challenges of extinction-based therapies for anxiety and addiction in humans. A critical factor that promotes a post-therapeutic return of fear is the repeated avoidance of feared objects[140]. From an evolutionary perspective, avoidance is a natural form of self-protection by which prey animals circumvent feared areas that have an abundance of predators[141]; in these 'landscapes of fear'[24], prey animals often sacrifice foraging options for safety[142] and only briefly visit risky areas to harvest urgently needed food resources[143]. Unfortunately, this avoidance tendency in humans maintains fear by precluding the possibility to learn fear extinction[144]. Indeed, adults whose fear is reduced after consistently choosing to avoid an aversive object experience a strong return of fear when the option to avoid is taken away[145]. Although conducting exposure therapy without options for avoidance certainly promotes fear extinction, it hardly resembles the reality of the patient's life, which usually provides plenty of opportunities for avoidance. For instance, a child who is afraid to go down to the basement to look for a game might decide to do something else, such as drawing in the living room or playing in the garden. Thus, we agree with other scholars[145,146] that avoiding aversive situations as an integral part of exposure therapies could enhance the external validity and increase therapeutic success.

Our approach also explains core problems of relapse in appetitive instrumental conditioning, such as for addiction. Even after long periods of absence of drug use, individuals can experience a sudden relapse[147]. Studies on addiction in humans show that repeated consumption of potentially addictive substances or behaviours can amplify the incentive salience of these events by sensitizing the mesolimbic dopamine system[148]. Cues with such high incentive salience are then experienced as attractive and consequently elicit behavioural approaches in a context-dependent manner[149]. This effect persists: relapse can happen after years of discontinuation of drug use, driven by unconscious bias or fleeting attention to drug-related contextual cues[150]. For animals in the wild, such persistence makes sense, because often once-rewarding patches might bloom again when conditions change. Indeed, animals often revisit previously abandoned areas[35–38] and reinvigorate search behaviour after finding a single piece of food[58]. These returns to previously rewarding areas are often elicited by specific and/or contextual cues that signal a prospective option for replenished resources. In humans, drug-related cues and subsequent craving for those cues reliably predict relapse[151]. However, the discriminative context in which these cues occur and addiction develops also has a crucial role[152]. Thus, these studies suggest that therapies should avoid using drug cues as treatment targets but should focus on contextual cues that can elicit craving[153]. Taken together, by reframing extinction as exploration, researchers can better understand both relapse occurrence and therapeutic limitations in humans.

In summary, researchers must combine the dynamics of learning theory with the complexity of ecological demands to understand behaviour in humans and non-human animals.

Conclusions

In this Perspective, we have argued that the behavioural effects of extinction learning – long considered paradoxical in the laboratory – are adaptive strategies shaped by evolution to maximize survival and reproductive success in dynamic environments. Extinction should not be conceptualized only as inhibition of prior associations but also as an exploratory process that mobilizes motivation, attention and behavioural flexibility in the face of uncertainty.

Testing our extinction learning in the wild framework requires research that bridges ecological, psychological and neuroscientific approaches. Several directions are particularly promising. First, comparative studies should examine how species with different ecological niches exhibit distinct extinction dynamics. For example, nectar-feeding animals that rely on renewable resources might display strong spontaneous recovery or renewal, whereas desert foragers relying on stochastic food sources might show attenuated forms of these behaviours. These cross-species differences would provide direct evidence that ecological demands shape extinction patterns.

Second, laboratory paradigms should be enriched to give animals more than a single response option. Experiments that include multiple strategies, alternative rewards or changing resource landscapes would enable researchers to capture this adaptive dimension. Embedding ecological features such as patch depletion and replenishment into conditioning tasks could reveal how extinction guides foraging and risk management in realistic contexts and provide a closer approximation of the selective pressures under which these mechanisms evolved.

Third, neuroscientific studies should explore how brain systems that process reward loss also energize exploration. Rats would be an appropriate animal model, because they are known to be curious with high activity levels. Signals from dopamine and norepinephrine, often associated with motivation and effort, might help shift attention towards the context and trigger new behaviours. If extinction is indeed an exploratory process, then these neuromodulatory systems should weaken old associations by promoting variability and persistence. Modern tools – such as optogenetics, neuroimaging and computational models – make it possible to test these predictions directly.

Fourth, our approach provides a possible answer to why mental disorders are often so resilient and prone to relapse after initially successful psychotherapeutic treatment. These insights do not necessarily lead to novel therapies but connecting the wild and the clinic could improve psychotherapy to readjust the focus of clinical strategies to evolutionary mechanisms that maintain fear and addiction. Future research should insist on the positive (therapeutic) effects of the opportunities to perform alternative behaviours instead of trying to reduce inappropriate actions in a context-independent manner.

In conclusion, our framework is supported by numerous findings and is empirically testable. This framework would be disconfirmed if it appeared that the ecological demands in which species evolved did not shape the landscape of relapse and amplification effects, or that these effects were not reduced by opportunities to produce other behaviours. The framework would also be strongly weakened if blockade of dopamine and norepinephrine did not prevent re-engagement in new activities when options are available. In light of the behavioural, clinical and neurobiological evidence reviewed here, we propose that research efforts that address both the mechanisms and the functions

of extinction learning provide an evolutionary perspective to learning theory and neuroscientific explanations to behavioural ecology. Doing so opens the Skinner box and places it into the wild, where it belongs.

References

1. Fernández, R. S., Boccia, M. M. & Pedreira, M. E. The fate of memory: reconsolidation and the case of prediction error. *Neurosci. Biobehav. Rev.* **68**, 423–441 (2016).
2. Bouton, M. E., Todd, T. P., Vurbic, D. & Winterbauer, N. E. Renewal after the extinction of free operant behavior. *Learn. Behav.* **39**, 57–67 (2011).
3. Bouton, M. E., Maren, S. & McNally, G. P. Behavioral and neurobiological mechanisms of Pavlovian and instrumental extinction learning. *Physiol. Rev.* **101**, 611–681 (2021).
4. Nic Dhonnchadha, B. A. et al. D-Cycloserine deters reacquisition of cocaine self-administration by augmenting extinction learning. *Neuropsychopharmacology* **35**, 357–367 (2010).
5. André, M. A. E. & Manahan-Vaughan, D. Involvement of dopamine D1/D5 and D2 receptors in context-dependent extinction learning and memory reinstatement. *Front. Behav. Neurosci.* **9**, 372 (2015).
6. Lanters, L. R. et al. Disease-specific alterations in central fear network engagement during acquisition and extinction of conditioned interoceptive fear in inflammatory bowel disease. *Mol. Psychiatry* **29**, 3527–3536 (2024).
7. Gao, M., Lengersdorf, D., Stüttgen, M. C. & Güntürkün, O. NMDA receptors in the avian amygdala and the premotor arcopallium mediate distinct aspects of appetitive extinction learning. *Behav. Brain Res.* **343**, 71–82 (2018).
8. Eisenberg, M. & Dudai, Y. Reconsolidation of fresh, remote, and extinguished fear memory in medaka: old fears don't die. *Eur. J. Neurosci.* **20**, 3397–3403 (2004).
9. Lewis, V., Laberge, F. & Heyland, A. Transcriptomic signature of extinction learning in the brain of the fire-bellied toad, *Bombina orientalis*. *Neurobiol. Learn. Mem.* **184**, 107502 (2021).
10. Stollhoff, N., Menzel, R. & Eisenhardt, D. Spontaneous recovery from extinction depends on the reconsolidation of the acquisition memory in an appetitive learning paradigm in the honeybee (*Apis mellifera*). *J. Neurosci.* **25**, 4485–4492 (2005).
11. Zhang, Y., Zhou, Y., Zhang, X., Wang, L. & Zhong, Y. Clock neurons gate memory extinction in *Drosophila*. *Curr. Biol.* **31**, 1337–1343.e4 (2021).
12. Cavallo, J. S., Hamilton, B. N. & Farley, J. Behavioral and neural bases of extinction learning in *Hermissenda*. *Front. Behav. Neurosci.* **8**, 277 (2014).
13. Bukalo, O. et al. Prefrontal inputs to the amygdala instruct fear extinction memory formation. *Sci. Adv.* **1**, e1500251 (2015).
14. Fullana, M. A. et al. Fear extinction in the human brain: a meta-analysis of fMRI studies in healthy participants. *Neurosci. Biobehav. Rev.* **88**, 16–25 (2018).
15. Bouton, M. E. Conditioning, remembering, and forgetting. *J. Exp. Psychol.: Anim. Behav. Process.* **20**, 219–231 (1994).
16. Penninx, B. W., Pine, D. S., Holmes, E. A. & Reif, A. Anxiety disorders. *Lancet* **397**, 914–927 (2021).
17. Quirk, G. J. Memory for extinction of conditioned fear is long-lasting and persists following spontaneous recovery. *Learn. Mem.* **9**, 402–407 (2002).
18. Vervliet, B., Craske, M. G. & Hermans, D. Fear extinction and relapse: state of the art. *Annu. Rev. Clin. Psychol.* **9**, 215–248 (2013).
19. Labrenz, F., Woud, M. L., Elsenbruch, S. & Icenhour, A. The good, the bad, and the ugly—chances, challenges, and clinical implications of avoidance research in psychosomatic medicine. *Front. Psychiatry* **13**, 841734 (2022).
20. Craske, M. G. (ed.) *Fear and Learning. From Basic Processes to Clinical Implications* (American Psychological Association, 2006).
21. Goulson, D., Hawson, S. A. & Stout, J. C. Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. *Anim. Behav.* **55**, 199–206 (1998).
22. Milad, M. R. & Quirk, G. J. Fear extinction as a model for translational neuroscience: ten years of progress. *Annu. Rev. Psychol.* **63**, 129–151 (2012).
23. Rescorla, R. A. Spontaneous recovery. *Learn. Mem.* **11**, 501–509 (2004).
24. Laundré, J. W. Behavioral response races, predator–prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology* **91**, 2995–3007 (2010).
25. Katz, M. W. et al. Optimal foraging of little egrets and their prey in a foraging game in a patchy environment. *Am. Naturalist* **181**, 381–395 (2013).
26. English, M. et al. Foraging site recursion by forest elephants *Elphas maximus borneensis*. *Curr. Zool.* **60**, 551–559 (2014).
27. Bar-David, S. et al. Methods for assessing movement path recursion with application to African buffalo in South Africa. *Ecology* **90**, 2467–2479 (2009).
28. Berger-Tal, O. & Bar-David, S. Recursive movement patterns: review and synthesis across species. *Ecosphere* **6**, 149 (2015).
29. Possingham, H. P. The distribution and abundance of resources encountered by a forager. *Am. Nat.* **133**, 42–60 (1989).
30. Ohashi, K., Leslie, A. & Thomson, J. D. Trapline foraging by bumble bees: V. Effects of experience and priority on competitive performance. *Behav. Ecol.* **19**, 936–948 (2008).
31. Ohashi, K., Leslie, A. & Thomson, J. D. Trapline foraging by bumble bees: VII. Adjustments for foraging success following competitor removal. *Behav. Ecol.* **24**, 768–778 (2013).
32. Gilbert, F. et al. Individually recognizable scent marks on flowers made by a solitary bee. *Anim. Behav.* **61**, 217–229 (2001).
33. Burke, D. & Fulham, B. J. An evolved spatial memory bias in a nectar-feeding bird? *Anim. Behav.* **66**, 695–701 (2003).
34. Boisvert, M. J., Veal, A. J. & Sherry, D. F. Floral reward production is timed by an insect pollinator. *Proc. Biol. Sci.* **274**, 1831–1837 (2007).
35. Mailly, J., Riotte-Lambert, L. & Lihoreau, M. How pollinator movement patterns emerge from the interaction between cognition and the environment. *Proc. Biol. Sci.* **292**, 20242271 (2025).
36. Denniston, J. C., Chang, R. C. & Miller, R. R. Massive extinction treatment attenuates the renewal effect. *Learn. Motiv.* **34**, 68–86 (2003).
37. Haberlandt, K., Hamsher, K. & Kennedy, A. W. Spontaneous recovery in rabbit eyelid conditioning. *J. Gen. Psychol.* **98**, 241–244 (1978).
38. Charnov, E. L., Orians, G. H. & Hyatt, K. Ecological implications of resource depression. *Am. Nat.* **110**, 247–259 (1976).
39. Bouton, M. E., Westbrook, R. F., Corcoran, K. A. & Maren, S. Contextual and temporal modulation of extinction: behavioral and biological mechanisms. *Biol. Psychiatry* **60**, 352–360 (2006).
40. Gershman, S. J., Monfils, M.-H., Norman, K. A. & Niv, Y. The computational nature of memory modification. *eLife* https://doi.org/10.7554/eLife.23763 (2017).
41. Peschken, J., Hahn, L. A., Pusch, R. & Rose, J. Extinction context is learned by pigeons, not given by the environment. *Commun. Psychol.* **3**, 83 (2025).
42. Starosta, S. et al. Context specificity of both acquisition and extinction of a Pavlovian conditioned response. *Learn. Mem.* **23**, 639–643 (2016).
43. Rosas, J. M., Todd, T. P. & Bouton, M. E. Context change and associative learning. *Wiley Interdiscip. Rev. Cogn. Sci.* **4**, 237–244 (2013).
44. Packheiser, J., Güntürkün, O. & Pusch, R. Renewal of extinguished behavior in pigeons (*Columba livia*) does not require memory consolidation of acquisition or extinction in a free-operant appetitive conditioning paradigm. *Behav. Brain Res.* **370**, 111947 (2019).
45. Packheiser, J., Donoso, J. R., Cheng, S., Güntürkün, O. & Pusch, R. Trial-by-trial dynamics of reward prediction error-associated signals during extinction learning and renewal. *Prog. Neurobiol.* **197**, 101901 (2021).
46. Seghers, B. H. Geographic variation in the responses of guppies (*Poecilia reticulata*) to aerial predators. *Oecologia* **14**, 93–98 (1974).
47. Mitchell, W. A. Multi-behavioral strategies in a predator–prey game: an evolutionary algorithm analysis. *Oikos* **118**, 1073–1083 (2009).
48. Vijayan, S. et al. Time to revisit? A predator's previous successes and failures in prey capture determine its return time to patches. *Oecologia* **190**, 387–397 (2019).
49. Lima, S. L. Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.* **17**, 70–75 (2002).
50. Stephens, D. W. & Krebs, J. R. *Foraging Theory* (Princeton Univ. Press, 1986).
51. Maren, S. Nature and causes of the immediate extinction deficit: a brief review. *Neurobiol. Learn. Mem.* **113**, 19–24 (2014).
52. Charnov, E. L. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136 (1976).
53. Wajnberg, E., Bernhard, P., Hamelin, F. & Boivin, G. Optimal patch time allocation for time-limited foragers. *Behav. Ecol. Sociobiol.* **60**, 1–10 (2006).
54. Houston, A. The matching law applies to wagtails' foraging in the wild. *J. Exp. Anal. Behav.* **45**, 15–18 (1986).
55. Kacelnik, A. & Todd, I. A. Psychological mechanisms and the marginal value theorem: effect of variability in travel time on patch exploitation. *Anim. Behav.* **43**, 313–322 (1992).
56. Kacelnik, A. & Todd, I. A. Psychological mechanisms and the marginal value theorem: dynamics of scalar memory for travel time. *Anim. Behav.* **46**, 765–775 (1993).
57. Pavlov, I. P. *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex* (Oxford Univ. Press, 1927).
58. Kelamangalath, L. & Wagner, J. J. Effects of abstinence or extinction on cocaine seeking as a function of withdrawal duration. *Behav. Pharmacol.* **20**, 195–203 (2009).
59. Symes, L. & Wheatley, T. Random isn't real: how the patchy distribution of ecological rewards may generate "incentive hope". *Behav. Brain Sci.* **42**, e53 (2019).
60. Arditi, R. & Dacorogna, B. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am. Naturalist* **131**, 837–846 (1988).
61. Raichlen, D. A. et al. Evidence of Levy walk foraging patterns in human hunter-gatherers. *Proc. Natl Acad. Sci. USA* **111**, 728–733 (2014).
62. Blaich, C. F. & Miller, D. B. Alarm call responsivity of mallard ducklings (*Anas platyrhynchos*). IV. Effects of social experience. *J. Comp. Psychol.* **100**, 401–405 (1986).
63. Shaham, Y., Shaleev, U., Lu, L., de Wit, H. & Stewart, J. The reinstatement model of drug relapses: history, methodology and major findings. *Psychopharmacology* **168**, 3–20 (2003).
64. Haaker, J., Golkar, A., Hermans, D. & Lonsdorf, T. B. A review on human reinstatement studies: an overview and methodological challenges. *Learn. Mem.* **21**, 424–440 (2014).
65. Schmidt, K. et al. Enhanced neural reinstatement for evoked facial pain compared with evoked hand pain. *J. Pain.* **20**, 1057–1069 (2019).
66. Bernal-Gamboa, R., Gámez, A. M. & Nieto, J. Reducing spontaneous recovery and reinstatement of operant performance through extinction-cues. *Behav. Process.* **135**, 1–7 (2017).
67. Uengoer, M., Thorwart, A., Lucke, S., Wöhr, M. & Lachnit, H. Adding or removing context components equally disrupts extinction in human predictive learning. *Behav. Process.* **179**, 104216 (2020).
68. LaBar, K. S. & Phelps, E. A. Reinstatement of conditioned fear in humans is context dependent and impaired in amnesia. *Behav. Neurosci.* **119**, 677–686 (2005).

69. Icenhour, A. et al. When gut feelings teach the brain to fear pain: context-dependent activation of the central fear network in a novel interoceptive conditioning paradigm. *NeuroImage* **238**, 118229 (2021).
70. Walther, T. et al. Context-dependent extinction learning emerging from raw sensory inputs: a reinforcement learning approach. *Sci. Rep.* **11**, 2713 (2021).
71. Kappel, D. & Cheng, S. Global remapping emerges as the mechanism for renewal of context-dependent behavior in a reinforcement learning model. *Front. Comput. Neurosci.* **18**, 1462110 (2024).
72. Dolón-Vera, L., Donoso, J., Cheng, S. & Manahan-Vaughan, D. *Place cell activity and behaviour during task acquisition and extinction learning predict renewal outcome* (2025).
73. Schultz, W. Predictive reward signal of dopamine neurons. *J. Neurophysiol.* **80**, 1–27 (1998).
74. Lerner, T. N., Holloway, A. L. & Seiler, J. L. Dopamine, updated: reward prediction error and beyond. *Curr. Opin. Neurobiol.* **67**, 123–130 (2021).
75. Niv, Y., Duff, M. O. & Dayan, P. Dopamine, uncertainty and TD learning. *Behav. Brain Funct.* **1**, 6 (2005).
76. Schultz, W., Dayan, P. & Montague, P. R. A neural substrate of prediction and reward. *Science (N. Y.)* **275**, 1593–1599 (1997).
77. Rosas, J. M. & Callejas-Aguilera, J. E. Context switch effects on acquisition and extinction in human predictive learning. *J. Exp. Psychol. Learn. Mem. Cogn.* **32**, 461–474 (2006).
78. Nist, A. N. & Shahan, T. A. The extinction burst: impact of reinforcement time and level of analysis on measured prevalence. *J. Exp. Anal. Behav.* **116**, 131–148 (2021).
79. Lattal, K. M. & Lattal, K. A. Facets of Pavlovian and operant extinction. *Behav. Process.* **90**, 1–8 (2012).
80. Shahan, T. A. & Avellaneda, M. The extinction burst: effects of reinforcement magnitude. *J. Exp. Anal. Behav.* **123**, 312–323 (2025).
81. Thomas, B. L. & Papini, M. R. Adrenalectomy eliminates the extinction spike in autoshaping with rats. *Physiol. Behav.* **72**, 543–547 (2001).
82. Torres, C., Glueck, A. C., Conrad, S. E., Morón, I. & Papini, M. R. Dorsomedial striatum lesions affect adjustment to reward uncertainty, but not to reward devaluation or omission. *Neuroscience* **332**, 13–25 (2016).
83. Northrup, J. B., Libertus, K. & Iverson, J. M. Response to changing contingencies in infants at high and low risk for autism spectrum disorder. *Autism Res.* **10**, 1239–1248 (2017).
84. Juarez, B. et al. Temporal scaling of dopamine neuron firing and dopamine release by distinct ion channels shape behavior. *Sci. Adv.* **9**, eadg8869 (2023).
85. Pigozzi, G. Digging behaviour while foraging by the European badger, *Meles meles*, in a Mediterranean habitat. *Ethology* **83**, 121–128 (1989).
86. Nielsen, T. P. & Bull, C. M. Impact of foxes digging for the pygmy bluetongue lizard (*Tiliqua adelaidensis*). *Trans. R. Soc. South. Aust.* **140**, 228–233 (2016).
87. Brown, J. S. & Kotler, B. P. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* **7**, 999–1014 (2004).
88. Shahan, T. A. A theory of the extinction burst. *Perspect. Behav. Sci.* **45**, 495–519 (2022).
89. Tinsley, M. R., Timberlake, W., Sitomer, M. & Widman, D. R. Conditioned inhibitory effects of discriminated Pavlovian training with food in rats depend on interactions of search modes, related repertoires, and response measures. *Anim. Learn. Behav.* **30**, 217–227 (2002).
90. Grow, L. L., Kelley, M. E., Roane, H. S. & Shillingsburg, M. A. Utility of extinction-induced response variability for the selection of mands. *J. Appl. Behav. Anal.* **41**, 15–24 (2008).
91. Donoso, J. R. et al. Emergence of complex dynamics of choice due to repeated exposures to extinction learning. *Anim. Cogn.* **24**, 1279–1297 (2021).
92. Winterbauer, N. E. & Bouton, M. E. Mechanisms of resurgence II: response-contingent reinforcers can reinstate a second extinguished behavior. *Learn. Motiv.* **42**, 154–164 (2011).
93. Winterbauer, N. E. & Bouton, M. E. Mechanisms of resurgence of an extinguished instrumental behavior. *J. Exp. Psychol. Anim. Behav. Process.* **36**, 343–353 (2010).
94. Krebs, J. R. *An Introduction to Behavioural Ecology* (Blackwell Scientific, 1987).
95. Begg, C. M., Begg, K. S., Du Toit, J. T. & Mills, M. G. L. Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger (*Mellivora capensis*). *J. Zool.* **260**, 301–316 (2003).
96. Jager, M. et al. *How Superdiffusion Gets Arrested. Ecological Encounters Explain Shift from Lévy to Brownian Movement* (KOPS Universität Konstanz, 2014).
97. Schlesinger, M. F. & Klafter, J. in *Growth and Form* (eds Stanley, H. E. & Ostrowski, N.) 279–283 (Martinus Nijhof, 1986).
98. Bartumeus, F. Lévy processes in animal movement: an evolutionary hypothesis. *Fractals* https://doi.org/10.1142/S0218348X07003460 (2007).
99. Reynolds, A. M. Current status and future directions of Lévy walk research. *Biol. Open.* **7**, bio030106 (2018).
100. Viswanathan, G. M. et al. Optimizing the success of random searches. *Nature* **401**, 911–914 (1999).
101. Anselme, P., Otto, T. & Güntürkün, O. Foraging motivation favors the occurrence of Lévy walks. *Behav. Process.* **147**, 48–60 (2018).
102. Anselme, P. & Güntürkün, O. How foraging works: uncertainty magnifies food-seeking motivation. *Behav. Brain Sci.* **42**, e35 (2019).
103. Amsel, A. *Frustration Theory. An Analysis of Dispositional Learning and Memory* Vol. 11 (Cambridge Unive. Press, 1992).
104. Fuentes-Verdugo, E. et al. Effects of partial reinforcement on autoshaping in inbred Roman high- and low-avoidance rats. *Physiol. Behav.* **225**, 113111 (2020).
105. Rescorla, R. A. Within-subject partial reinforcement extinction effect in autoshaping. *Q. J. Exp. Psychol.* **52**, 75–87 (1999).
106. Abad, M. J. F., Ramos-Alvarez, M. M. & Rosas, J. M. Partial reinforcement and context switch effects in human predictive learning. *Q. J. Exp. Psychol.* **62**, 174–188 (2009).
107. Bouton, M. E. & Sunsay, C. Contextual control of appetitive conditioning: influence of a contextual stimulus generated by a partial reinforcement procedure. *Q. J. Exp. Psychol. B* **54**, 109–125 (2001).
108. Buchanan, J. B., Herman, S. G. & Johnson, T. M. Success rates of the peregrine falcon (*Falco peregrinus*) hunting dunlin (*Calidris alpina*) during winter. *J. Raptor Res.* **20**, 130–131 (1986).
109. Holekamp, K. E., Smale, L., Berg, R. & Cooper, S. M. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *J. Zool.* **242**, 1–15 (2009).
110. Bothma, J. P. & Coertze, R. J. Motherhood increases hunting success in southern Kalahari leopards. *J. Mammal.* **85**, 756–760 (2004).
111. van Horik, J. O. & Madden, J. R. A problem with problem solving: motivational traits, but not cognition, predict success on novel operant foraging tasks. *Anim. Behav.* **114**, 189–198 (2016).
112. Daunt, F., Afanasyev, V., Silk, J. R. D. & Wanless, S. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behav. Ecol. Sociobiol.* **59**, 381–388 (2006).
113. Lovette, I. J. & Holmes, R. T. Foraging behavior of American redstarts in breeding and wintering habitats: implications for relative food availability. *Condor* **97**, 782–791 (1995).
114. Kramer, D. L. & Weary, D. M. Exploration versus exploitation: a field study of time allocation to environmental tracking by foraging chipmunks. *Anim. Behav.* **41**, 443–449 (1991).
115. Anselme, P., Wittek, N., Oeksuez, F. & Güntürkün, O. Overmatching under food uncertainty in foraging pigeons. *Behav. Process.* **201**, 104728 (2022).
116. Kilpatrick, Z. P., Davidson, J. D. & El Hady, A. Uncertainty drives deviations in normative foraging decision strategies. *J. R. Soc. Interface* **18**, 20210337 (2021).
117. Berridge, K. C. The debate over dopamine's role in reward: the case for incentive salience. *Psychopharmacology* **191**, 391–431 (2007).
118. Abraham, A. D., Neve, K. A. & Lattal, K. M. Dopamine and extinction: a convergence of theory with fear and reward circuitry. *Neurobiol. Learn. Mem.* **108**, 65–77 (2014).
119. Sara, S. J. & Bouret, S. Orienting and reorienting: the locus coeruleus mediates cognition through arousal. *Neuron* **76**, 130–141 (2012).
120. Lui, S., Brink, A. K. & Corbit, L. H. Optogenetic stimulation of the locus coeruleus enhances appetitive extinction in rats. *eLife* **12**, RP89267 (2024).
121. Gall, M. D. & Fernández-Juricic, E. Visual fields, eye movements, and scanning behavior of a sit-and-wait predator, the black phoebe (*Sayornis nigricans*). *J. Comp. Physiol. A, Neuroethol. Sensory Neural Behav. Physiol.* **196**, 15–22 (2010).
122. Anselme, P. Unconscious will as a neurobehavioral mechanism against adversity. *Neurosci. Biobehav. Rev.* **169**, 105985 (2025).
123. Klein, R. M. Inhibition of return. *Trends Cogn. Sci.* **4**, 138–147 (2000).
124. Hugie, D. M. The waiting game: a "battle of waits" between predator and prey. *Behav. Ecol.* **14**, 807–817 (2003).
125. Schultz, W. Dopamine reward prediction-error signalling: a two-component response. *Nat. Rev. Neurosci.* **17**, 183–195 (2016).
126. Sutton, R. S. *Reinforcement Learning. An Introduction* (MIT Press, 1998).
127. Jeong, H. et al. Mesolimbic dopamine release conveys causal associations. *Science* **378**, eabq6740 (2022).
128. Amo, R. Prediction error in dopamine neurons during associative learning. *Neurosci. Res.* **199**, 12–20 (2024).
129. Gershman, S. J. et al. Explaining dopamine through prediction errors and beyond. *Nat. Neurosci.* **27**, 1645–1655 (2024).
130. Navarro, V. M., Dwyer, D. M. & Honey, R. C. Prediction error in models of adaptive behavior. *Curr. Biol.* **33**, 4238–4243.e3 (2023).
131. Blaisdell, A. P., Sawa, K., Leising, K. J. & Waldmann, M. R. Causal reasoning in rats. *Science (N. Y.)* **311**, 1020–1022 (2006).
132. Waldmann, M. R., Hagmayer, Y. & Blaisdell, A. P. Beyond the information given: causal models in learning and reasoning. *Curr. Directions Psychol. Sci.* **15**, 307–311 (2006).
133. Sharp, P. B. & Eldar, E. Humans adaptively deploy forward and backward prediction. *Nat. Hum. Behav.* **8**, 1726–1737 (2024).
134. Longán, A. & Blaisdell, A. P. Pigeons (*Columba livia*) distinguish between absence of events and lack of evidence in contingency learning. *Int. J. Comp. Psychol.* **36**, 1–9 (2023).
135. Blaisdell, A. P., Gunther, L. M. & Miller, R. R. Recovery from blocking achieved by extinguishing the blocking CS. *Anim. Learn. Behav.* **27**, 63–76 (1999).
136. Perogamvros, L., Castelnovo, A., Samson, D. & Dang-Vu, T. T. Failure of fear extinction in insomnia: an evolutionary perspective. *Sleep. Med. Rev.* **51**, 101277 (2020).
137. Piqueret, B., Sandoz, J.-C. & d'Ettorre, P. Ants learn fast and do not forget: associative olfactory learning, memory and extinction in *Formica fusca*. *R. Soc. Open. Sci.* **6**, 190778 (2019).
138. Ben-Natan, G., Abramsky, Z., Kotler, B. P. & Brown, J. S. Seeds redistribution in sand dunes: a basis for coexistence of two rodent species. *Oikos* **105**, 325–335 (2004).
139. Mazur, J. E. & Biondi, D. R. Delay–amount tradeoffs in choices by pigeons and rats: hyperbolic versus exponential discounting. *J. Exp. Anal. Behav.* **91**, 197–211 (2009).
140. Krypotos, A.-M., Effting, M., Kindt, M. & Beckers, T. Avoidance learning: a review of theoretical models and recent developments. *Front. Behav. Neurosci.* **9**, 189 (2015).
141. Sih, A. in *Ecology of Predator–Prey Interactions* (eds. Barbosa, P. & Castellanos, I.) 240–255 (Oxford Univ. Press, 2005).
142. Brown, J. S. Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* **1**, 49–71 (1999).

143. Hernández, L. & Laundré, J. W. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildl. Biol.* **11**, 215–220 (2005).
144. Lovibond, P. F., Mitchell, C. J., Minard, E., Brady, A. & Menzies, R. G. Safety behaviours preserve threat beliefs: protection from extinction of human fear conditioning by an avoidance response. *Behav. Res. Ther.* **47**, 716–720 (2009).
145. Vervliet, B. & Indekeu, E. Low-cost avoidance behaviors are resistant to fear extinction in humans. *Front. Behav. Neurosci.* **9**, 351 (2015).
146. Pittig, A. & Wong, A. H. K. Reducing the return of avoidance and fear by directly targeting avoidance: comparing incentive-based and instructed extinction of avoidance to passive fear extinction. *J. Exp. Psychopathol.* **13**, 20438087221136424 (2022).
147. Sinha, R. New findings on biological factors predicting addiction relapse vulnerability. *Curr. Psychiatry Rep.* **13**, 398–405 (2011).
148. Robinson, T. E. & Berridge, K. C. The incentive-sensitization theory of addiction 30 years on. *Annu. Rev. Psychol.* **76**, 29–58 (2025).
149. Anselme, P. & Robinson, M. J. F. From sign-tracking to attentional bias: implications for gambling and substance use disorders. *Prog. Neuropsychopharmacol. Biol. Psychiatry* **99**, 109861 (2020).
150. Tommaso, M. de & Turatto, M. Testing reward–cue attentional salience: attainment and dynamic changes. *Br. J. Psychol.* **113**, 396–411 (2022).
151. Vafaie, N. & Kober, H. Association of drug cues and craving with drug use and relapse: a systematic review and meta-analysis. *JAMA Psychiatry* **79**, 641–650 (2022).
152. Ndiaye, N. A. et al. Relapse after intermittent access to cocaine: discriminative cues more effectively trigger drug seeking than do conditioned cues. *Psychopharmacology* **241**, 2015–2032 (2024).
153. Wray, J. M., Gass, J. C. & Tiffany, S. T. A systematic review of the relationships between craving and smoking cessation. *Nicotine Tob. Res.* **15**, 1167–1182 (2013).

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