

When and why are motivational trade-offs evidence of sentience?

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Simon Alexander Burns Brown (ORCID: 0000-0002-5606-6979)

Jonathan Birch (ORCID: 0000-0001-7517-4759)

Correspondence: simonabbrown@gmail.com

London School of Economics and Political Science

Abstract

Motivational trade-off behaviours, where an organism behaves as if flexibly weighing up an opportunity for reward against a risk of injury, are often regarded as evidence that the organism has valenced experiences like pain. This type of evidence has been influential in shifting opinion regarding crabs and insects. Critics note that (i) the precise links between trade-offs and consciousness are not fully known; (ii) simple trade-offs are evinced by the nematode worm *Caenorhabditis elegans*, mediated by a mechanism plausibly too simple to support conscious experience; (iii) pain can sometimes interfere with rather than support making trade-offs rationally. However, rather than undermining trade-off evidence in general, such cases show that the nature of the trade-off, and its underlying neural substrate, matter. We investigate precisely how.

Keywords: sentience, pain, motivational trade-offs, animal consciousness, marker approach

1. Introduction

We are sentient beings, undergoing conscious experiences which feel good or bad, such as pleasure and pain. Other animals have such experiences too—but which animals exactly?

Attributions of sentience to other mammals, though once controversial, are now widely accepted. Controversy in recent years has centred on taxa that are further from humans in evolutionary terms: especially fishes [1,2] and invertebrates such as insects [3,4], crustaceans [5], and octopuses [6]. Substantial uncertainty remains in all these cases, reflecting deep methodological disagreement and a lack of conclusive, well-validated tests of sentience [7–9].

Faced with this uncertainty, several authors advocate testing for a wide range of behavioural and neural ‘markers’ [5,10–21]. Each marker is regarded, if found, as strengthening the evidence for some species’ capacity to feel pain. While practical applications of this approach have so far simply sought evidence for whether species have markers from pre-determined lists [4-6], theoretical discussions have emphasised that such lists should not be treated as *static*. Instead we should investigate as many potential markers as possible, combining

this investigation with theoretical work that iteratively *improves* the list of markers [8-21]. The list is always a work in progress, subject to regular revision and updating.

According to this approach, if any test has some face validity—if it is plausible that it provides at least *some* evidence of pain—and is practically applicable, then, as a starting point, it should be attempted. No single test will be conclusive. But with enough investigations, we will be able to study the emerging patterns in the test results, and with luck a picture will emerge that supports greater confidence than any one test could. We will see how the results of this test cluster with those of others (e.g. do we tend to find that species passing tests A, B, and C, also tend to pass test D?) and improve our understanding of the mechanisms supporting performance on the tests and ways in which they might relate to sentience. That is, we will find the ‘natural kinds’ that our initial definition of pain pointed loosely towards. All the while, our rational degree of belief as to whether various species experience pain will be shifted upwards or downwards by the new evidence, helping us make better decisions.

Methodological strategies of this general shape (that is: no initial commitment to a single theory, a pluralistic search for markers, iterative improvement of the list of markers and their theoretical basis, and the goal of identifying natural kinds and underlying mechanisms) have been advocated by a wide range of authors under various labels [10–21]. An important idea for all these authors is that subjectively experienced states are not so special and mysterious as to be beyond the reach of normal scientific methods: we should approach them like we would approach any poorly understood natural kind. Some have argued that this downplays the special methodological issues raised by subjective experience [22–24]. In this article we will assume the soundness of the basic strategy in order to focus on issues raised by one specific family of tests—tests for *motivational trade-offs*—and consider how critiques of trade-off experiments can be used to help iteratively improve the marker and our use of it.

Motivational trade-offs occur when animals make flexible decisions that take into account *multiple conflicting motivations*—how much of an unpleasant stimulus to withstand for a certain reward, how much of an opportunity for one kind of reward to give up for another, and so on. This behaviour appears in several lists of markers of pain/sentience [5,25,26]. However, various critiques have been offered of trade-offs as an indicator of pain. We review some prominent examples of trade-off behaviours (without aspiring to be exhaustive), then discuss three lines of criticism. We argue that the criticisms fail to motivate *abandoning* trade-offs as a marker, but do motivate *refining* it. More precision is needed about trade-offs in question and the mechanisms that support them. These refinements could inspire a new generation of trade-off experiments that will allow further iterative improvements.

2. What are motivational trade-offs?

A major upshot of this paper will be that details about how specific trade-offs are achieved matter to the implications for sentience. In this vein, it is important to be clear from the outset that only some trade-offs are motivational trade-offs. No one has claimed that *all* trade-offs are evidence for sentience. Natural selection makes many trade-offs for us. Some are unrelated to cognition: body plans, for example, reflect trade-offs between factors like mobility,

robustness, nutritional requirements and so forth. Others pertain to cognitive architecture: for example, chickadee populations in harsher climates appear to have been selected for stronger spatial memory at the expense of lower cognitive flexibility [43]. Sometimes developmental plasticity supports flexible adjustment to an environmental trade-off without relying on sentience or requiring the organism to represent the trade-off. For example, zebra finch chicks' begging behaviour and growth pattern both adjust to fit their particular nest temperature thanks to their parents acoustically signalling the temperature to their embryos, but the mechanism in this case is developmental plasticity, not sentience [44].

In other cases, what is selected for are simple heuristics, behavioural strategies, or even fixed action patterns triggered by specific sensory inputs [45]. These may produce behaviour that appears to reflect a balancing of different evolutionary costs and benefits without requiring the animal to represent the costs and benefits. For example, parasitoid wasps lay their eggs in hosts such as caterpillars or aphids, and need to determine how long to stay laying eggs in any given patch before moving off to find another one, trading off being sure of laying eggs in a suitable patch now with the possibility of laying them in a better patch later. In principle, wasps could make this trade-off using affective experiences (e.g. a growing urge to move as time passes, dependent on patch quality). However, they seem to solve the problem in a different way. They have developed specialised, likely inflexible decision rules, which produce behaviour that, on average, approximates the optimal trade-off for specific species in their particular environments. One example of such a rule in some species is leaving any given patch in any given period with a probability that depends on how many hosts they have encountered in that patch [46]. Such mechanisms do not seem to rely on *feeling* the patches to be good or bad.

Motivational trade-offs are different; they are behaviours that plausibly result from balancing different *motivations*. In these cases, a process of representing and balancing options forms part of the *proximate mechanism* supporting the behaviour. This can be contrasted with any case in which talk of 'trade-offs' merely describes competition between evolutionary pressures that shaped the proximate mechanism. When the organism is resolving motivational conflicts flexibly in real time, it becomes more reasonable to posit that sentience might be part of the mechanism through which the conflict is resolved.

3. Motivational trade-offs: the story so far

Motivational trade-offs have been shown in a wide variety of species, with corresponding variety in experiments testing for them.

In the 1980s and 1990s, Cabanac and colleagues studied trade-offs in an attempt to show that a 'common currency' of valenced experience enabled animals to choose between competing motivations across very different domains. In an early experiment, they showed that when rats had to traverse a cold tunnel to access food, they responded by having larger but less frequent meals [27]. In later work, they found behaviours showing smooth, continuous changes in the amount of one resource subjects were willing to sacrifice to attain another. Balasko and Cabanac

made water-deprived rats choose how much of a liquid to consume, with two different variables affecting this decision: the ambient temperature of the tunnel the rats had to traverse to get to the liquid and the sweetness (saccharine concentration) of the liquid. Incrementally higher temperature and incrementally higher sweetness both caused incrementally higher liquid consumption, and Balasko & Cabanac were able to construct a trade-off surface predicting how much liquid a rat would consume at a novel temperature-concentration combination [28]. The smooth trade-off shows a balancing or weighing process: it was not that rats simply stopped caring about saccharine at a certain temperature level or vice versa, a pattern found with much earlier studies on the effects of electric shocks on eating [29].

These smooth trade-offs, together with neural evidence that certain kinds of brain stimulation could provide a reward that does not show satiety (suggesting it signals reward in general rather than the satisfaction of any specific need [30]), were used by Cabanac and colleagues to argue that rats were making such decisions by converting disparate motivations into the common currency of affective experience, in line with their earlier theoretical suggestions about the importance of such a common currency to all decision-making [31]. The cold felt bad, the sweetness felt good, and the rats carried on feeding for as long as the experience as a whole felt good on balance.

This approach was applied not just in rats, but in a wide array of species, such as iguanas [32], goldfish, and trout [33,34]. Two bodies of work have subsequently investigated trade-offs in invertebrates.

Elwood and colleagues pursued a somewhat different line of investigation into hermit crabs (reviewed in [35]). They took advantage of a natural behaviour: hermit crabs select shells to live in. They therefore face decisions that involve weighing up advantages and disadvantages of different options. They have to make decisions like: Should I choose this shell or that shell? Should I leave my current shell to enter that one? Is it worth attempting to fight the current occupant of that shell to try to get it for myself? Elwood showed that crabs make these decisions in ways which are sensitive to their current levels of fatigue; the properties of the different shells in question, including colour (i.e. camouflage potential in a specific environment), fit, weight, size (and they can base their estimate of these properties on memory, vision or touch, depending on whether they are currently inside a given shell or looking at it from the outside); a potential opponent's likely fighting performance; and numerous contextual factors, such as chemical cues or the presence of predators, the kind of predators they are likely to face (defending against shell-crushers vs. shell-peelers calls for shells of different properties), and the potential need and opportunity to fit through small gaps [36–38]; and further evidence of similar trade-offs has been found by other labs [39,40] and in other crab species [41].

Perhaps these factors suggest complex decision-making, but do they suggest sentience? The key experiments here involve crabs' behaviour following small electric shocks. This produces various behaviours independently suggestive of pain: wound-tending behaviour, investigation of the shell (as if to see what caused the pain), and an increased willingness to investigate and choose other shells for 24 hours afterwards. The aspects of their behaviour that

most directly imply a trade-off relate to how likely they are to leave immediately: higher-voltage shocks make them more likely to leave, with a higher voltage required to make them leave if the shell is more desirable or if they sense a predator odour.

Gibbons *et al.* [42] investigated trade-off behaviours in bumblebees. Bees chose between feeders at which they could either receive a high-value reward (high sucrose concentration) or a lower-value reward. In some conditions, access to the high-value reward would require sitting on a surface heated to an aversive temperature. As an alternative, they could go to a room-temperature feeder where they received the lower-value reward. When the feeders had the same level of reward, bees overwhelmingly chose the room-temperature feeder. When rewards in the aversive temperature were much higher, most bees chose to tolerate the higher temperature in order to get them. For intermediate differences in reward level, the observed choices were more finely balanced, with some bees choosing aversive heat and intermediate reward and others choosing lower-value reward and room temperature. Importantly, the trade-off was evident in where the bees chose to land, a choice that must have been based on memories or on learned associations, given that they would not experience the pros and cons of each feeder until after landing. In a follow-up experiment reported in [4], Gibbons and colleagues modified the setup so that, in the test phase, the feeders did not have any reward, and they found (admittedly with a sample size of only 10) that bees still chose to land at the feeders in the same pattern, using their past experience as a guide. In this respect this study resembled one of the experiments on shore crabs, which tested whether subjects retained evaluative information from past experiences [41].

As with other experiments in comparative cognition, some of these specific findings have not been directly or extensively replicated. While this work is valuable, therefore, it is important to not put excessive weight on any single finding. However, our focus here will be on three major criticisms targeting the very idea that such behaviour, when reliably present, is indicative of sentience. The following sections review these, arguing that the right response is more precision about the idea of a trade-off and more experimental investigation, not abandoning trade-offs as a relevant line of evidence. This will also allow us to uncover relevant differences in details between experimental designs.

4. First problem: Missing evidence (so far) of a link to conscious experience

One common complaint about motivational trade-offs is that there is a lack of strong justification for thinking that trade-offs could not result from wholly unconscious processing—processing that does not feel like anything from the animal’s point of view. After all, as Sec. 2 showed, sentience is not required for other kinds of trade-off. Why are motivational trade-offs different?

When explaining why motivational trade-off tests have face validity as a marker of pain, authors cite several considerations. One is that they imply that the animal in question is not merely relying on a reflex: they require centralised processing in the brain (e.g. “These responses are not mere nociceptive reflexes; rather they are consistent with the predictions of a pain experience and, hence, sentience” [35]; “What is important here is ... they do suggest that what

is going on is not just a bodily reflex” [47]; see also [48]). Some also highlight that they involve information integration [49], flexibility, intelligence, and suggest deliberation in light of seeing different possibilities as good and bad [47].

However, it is questionable whether any of these properties is both clearly implied by the behaviours surveyed and strongly linked to conscious experience. Granted, it is very plausible that one *necessary* condition for a painful conscious experience of a noxious stimulus is that the stimulus is centrally processed. Yet it is not a *sufficient* condition. Plenty of brain processing involves integrating information yet remains unconscious, such as processing of retinal input very early in the visual hierarchy, or cerebellar control of posture. So, finding centralised integrative processing of nociceptive information may raise the probability of pain; but that probability might remain low. Positing deliberation and intelligence of a kind that implies consciousness, meanwhile, seems to go beyond the available evidence.

When evaluating the evidence, it is important to understand that trade-offs do refute some outdated, yet still widely held, positions. Insects are sometimes dismissed as ‘reflex machines’ whose behaviour is *entirely* inflexible. Proponents of this view point to what appears to be strikingly inflexible behaviour, such as the alleged tendency of digger wasps to repeatedly perform a stereotyped action of moving a cricket to the opening of their nest without noticing that it keeps being moved away, discussed famously by Dennett [50]. This view ignores examples of considerable flexibility even in digger wasps’ behaviour in similar scenarios [51], and trade-offs further undermine seeing insect behaviour as *generally* inflexible. Others have suggested that, while insects may have conscious visual experiences, they do not have experiences that feel bad or feel good. Both of these positions are hard to reconcile with the trade-off evidence. This evidence shifts the dial by forcing sceptics to acknowledge that at least some insects do show flexible behaviour guided by centralised processing that represents and evaluates options. Sceptics must then fall back on the line that it is the *wrong sort* of centralised processing. However, evidence can knock down views held by poorly informed sceptics without thereby providing strong evidence for pain in the eyes of well-informed neutrals, and we should aim for experiments that do the latter.

Two lines of evidence are currently missing for trade-offs. Firstly, the natural kind approaches discussed above advocate searching for correlations or clustering between different potential markers of sentience; it is currently unknown how far the ability to make trade-offs correlates across species with other potential markers like trace conditioning or reversal learning. Secondly, it is unclear whether a contrast between conscious and unconscious processing applies in the case of trade-offs. Most human consciousness research is aimed at using techniques such as masking and conditions such as blindsight to tease out which forms of visual processing can be carried out unconsciously and which imply consciousness. Such contrasts are particularly important to validating markers of sentience; yet it is unclear if anyone has even investigated whether consciousness facilitates making trade-offs, or if it is possible for humans or other animals to make trade-offs just as effectively without conscious experience [14,49,52]. The problem is that we currently lack reliable methods for disentangling conscious and unconscious

affective states. It is disputed whether unconscious affective states (or unconscious central states with affect-like motivational effects) are possible at all—on top of broader methodological issues with untangling conscious and unconscious processing even in the case of vision [23,53,54]. As such, perhaps we should not expect rapid progress on this front [9,14]. Nonetheless, at this stage, trade-offs' relationship to consciousness is a matter more of unknowns than of problems known to be intractable. The message should not be to abandon them as a marker, but to investigate further.

5. Second problem: The challenge from nematodes

Trade-off phenomena have been observed in the nematode worm *Caenorhabditis elegans*. Despite their diminutive size (including famously having only 302 neurons), these worms engage in behaviour that appears to balance different goods and bads quantitatively. When faced with a damaging barrier (composed of Cu^{2+} or fructose) between them and the source of diacetyl, an odorant that typically signals food, worms are more likely to cross the barrier if the odorant is more and the barrier less concentrated [55–57]. Furthermore, these trade-offs are modulated by factors like food deprivation: if a worm has not eaten in a few hours, they will be more likely to cross the barrier, results reminiscent not only of behaviour in animals like us, but also in the predatory snail *Pleurobranchaea californica* [58]. And not only food deprivation: previous encounters with harmful stimuli, osmotic stress, and bacterial pathogens, affect these trade-offs too [59]. Some have taken these results in an organism as simple as *C. elegans* to imply that trade-offs which look motivational can be achieved without conscious processing [60,61].

It would be wrong to abandon a test for sentience solely because *C. elegans* passes it: we are not in a position to rule out sentience in *C. elegans* conclusively enough for that.¹ Indeed, such findings might be taken as evidence of pain in *C. elegans* [62]; the authors of such studies typically advocate for using *C. elegans* as a model organism for studying cognitive and affective processes more broadly, such as 'rational' and 'irrational' decision-making [63,64], 'computation of odor value' [63], 'biased attention' [63], and even 'hedonic valence' [65]. The authors of a study in which *C. elegans* speed up their movement and ignore food for a period following an electric shock interpret this as suggesting 'a form of emotion, akin to fear' [66].

However, the sceptical interpretation receives support from the details of the mechanisms underlying *C. elegans*' behaviour in these cases.

In many decisions of this type, just one or two pairs of neurons detect each stimulus, such as the two AWA neurons for diacetyl, or ASH for fructose.² The worm's behaviour amounts to going forward, turning, or going backwards, and the decision of which of these to pursue is determined by a weighted sum of signals favouring each option (with attractive odours like

¹ Mason and Lavery [1] pursue a more sophisticated version of this strategy for criticising other potential markers, focusing on multiple systems that they expect to be unconscious.

² As the *C. elegans* nervous system has been entirely mapped, individual neurons (or pairs of neurons) are named, with three-letter sequences like 'AWA'.

diacetyl favouring going forward, and threats like fructose favouring reversing), with these ‘decisions’ often being taken in single neurons that receive inputs from the different competing streams of information. Much of the processing involved is feedforward, but there are important recurrent connections, particularly at later stages of processing [67,68], and even early on: for example, the effects of food deprivation seem to be achieved by suppression of a feedback loop between neurons ASH and RIM that in well-fed conditions uses a slowly changing tyramine signal to strengthen the signal from ASH (which, detecting the dangerous fructose, promotes turning around rather than going forward) [57], and by signals from downstream neurons changing the threshold or boosting the sensitivity of neurons like AWA which detect food odours [59].

A few features of this mechanism are noteworthy. Firstly, the number of neurons and connections involved is often very small: In some cases, only three neurons, with connections from two sensory neurons to one interneuron, are required for the decision. The number of neurons is not decisive: even single neurons can contain complex internal mechanisms [69]. But in this case the effect can be explained without appealing to such internal complexity: while the precise channels by which these neurons influence one another, and the genes controlling these channels, can be and have been uncovered in detail, all that we need to know of the mechanism to explain the trade-off behaviour can be captured in a very simple circuit diagram. Indeed, the simplicity of the mechanisms giving rise to trade-offs and the limits to the number of neurons introduce demonstrable limitations: *C. elegans* only has 12 pairs of chemosensory neurons for detecting a wide range of odours, including only two pairs (AWC and AWA) driving chemotaxis towards volatile odours specifically, and this can lead to interference between the detection of different odours, causing imperfect trade-offs which systematically violate rational choice theory in certain scenarios, although the authors of these studies are keen to emphasise that all animals violate the same axioms in many scenarios [63,64].

Secondly, there is no evidence of any internal model or representation of either the external world or the subject here. Rather, proximal stimulation—particular chemicals—is directly attractive or aversive, and the total plus and minus signals on either side are simply totted up. To be clear, odorants like diacetyl are not themselves food, and are attractive because they are typically associated with food in *C. elegans*’ natural distal environment; but there is no hint that the worms are sensitive to this distinction or represent the food itself. While contextual factors like food deprivation do affect the decisions, they do so by mechanically modulating simple mechanisms, not via being integrated into a representation of the ongoing state of the organism.³ This lack of representational sophistication has further consequences. One is a rather limited repertoire of behaviours in response to sensed stimuli, which amount more or less to going forward, slowing, reversing, turning (and some other actions like swallowing). Another is that while *C. elegans* can show forms of learning [71,72], these too seem rather limited and simple. Hermit crabs integrate many different variables at once in extremely context-sensitive

³ Potentially comparable results have been found in a more sophisticated animal than nematodes: leeches, where control of a choice was found to be governed by intermediate levels of a neural hierarchy [70].

ways to evaluate shell quality, incorporating memory across different modalities and dealing with novel shell-types thanks to the many combinations of distal features they are capable of representing (see Sec. 3). They seem to be weighing up an electric shock against a rather abstract representation incorporating many different aspects of shell quality, as part of a representation of the environment around them. Bees learn about feeders, associating reward and punishment with seemingly arbitrary visual stimuli and external locations (see Sec. 3). *C. elegans* do not seem to display a representation of the world in their trade-off mechanisms, beyond the immediate balance of attractive and aversive signals.

We cannot be certain that *C. elegans* is as simple as this characterisation suggests: they may be capable of a form of spatial associative learning [73], which Irvine suggests as a crucial feature of those trade-offs that can provide evidence of sentience, along similar lines to the suggestion here [60]. It may yet turn out that *C. elegans* are sentient. But the message is not about *C. elegans* per se, but about trade-offs: the marker for pain is not just *any* trade-off. It matters which mechanisms are involved. Features like *prospective weighing of risk and opportunity, integration of information from many different sources into an overall evaluation* connected to a *genuine representation of distal items in the world around the subject* raise the probability that a trade-off reflects sentience; straight competition between two or more reflexes may lead to adaptive solutions to simple problems but need not involve any internal representation at all.

6. Third problem: Does pain help or hinder trade-offs?

Cabanac's original rationale for studying trade-offs was an intuition about the function of valence as a common currency for comparing very different goods and bads. On this view, pain allows tissue damage of varying grades of severity to be assigned corresponding affective values, and pleasure allows different amounts of beneficial food to be assigned values in the same metric. This provides a way of balancing the costs of tissue damage against the benefits of nutrition, against any other goods and bads we experience: will 'pay more', in terms of nutrition, to stop more intense tissue damage, in a way that is ultimately adaptive. A third line of criticism questions how far this rationale takes us.

Brown points towards a very different intuition [74]: pain *captures our attention*, at least sometimes making careful trade-offs *harder*. The more intense the pain, the more difficult it is to even frame, let alone weigh up, different options, even including those that might lead to cessation of the pain. Put simply, pain stops us from thinking straight.

Think of stubbing your toe. On Cabanac's view, there is an element of your pain experience—its unpleasantness, how *bad* it feels—which you can compare to other priorities in order to decide whether to push through the pain to run to an appointment. Is this introspectively plausible? Or do you need willpower to overcome the pain's tendency to distract you from even considering your other goals? Or take a case where you are weighing the risks and benefits of a procedure to solve a medical problem. Will you be better able to make decisions if the problem

in your body is actively causing pain, or if you know about it solely via medical scans? Pain hardly seems helpful in this type of situation.

It has been shown that pain can hijack attention and disrupt performance in tasks like discriminating between high and low tones and reporting whether the current letter in a stream of letters presented on a screen matches the letter presented two letters ago [75–77], with the threat of greater pain enhancing some of these effects [78]. Even emotionally valenced images can induce a form of attentional ‘blink’, in which visual processing is diminished to the point that stimuli can be missed for a few hundred milliseconds later [79], although there is some uncertainty about how important valence per se is to this effect, and how much it is driven by salient stimuli in general (including very *unexpected* stimuli) [80]. Furthermore, while in pain, we tend to overweight the importance of stopping the pain we are currently feeling, even relative to other (potential) future pains, becoming more risk-taking and prone to value immediate over longer-term rewards [81].

Capturing our attention, causing us to fixate on one particular aspect of our situation to the *neglect* of others, may be a general feature of conscious states, not just pain: attentional capture effects are central to Morales’ recent account of the intensity of experience [82]. Such effects are also not unique to very intense experiences like *extreme* pain: even ‘microvalences’, such as one’s slight fondness for one coffee cup over another, can guide attention [83]. And in general, attention typically involves benefits to *some* processing paired with costs elsewhere [84,85].

Felt valence does not straightforwardly enhance our ability to make trade-offs.⁴ One reply is that pain may inhibit *some* ways of making trade-offs while still being indispensable to tradeoffs in general. One possibility is that we have two modes of decision-making: *rational, deliberative* decision-making, and a more ancient mode of decision-making driven directly by valenced experience. This more primitive mode does not depend on thinking straight but on being pushed around by feelings. For example, pain might directly cause us to stop pursuing a sugary reward and instead attend to the cold, and it might do this with more urgency and efficacy the more severe the cold becomes. Given that deliberative reasoning and executive control is often thought to be quite a late evolutionary development, perhaps only valenced experience can enable animals like invertebrates to make such trade-offs. But a deeper response to the objection requires consideration of different mechanisms that might support tradeoffs.

7. Possible Mechanisms Supporting Tradeoffs

It is plausible that there are ways of making trade-offs besides coolly rational deliberation. However, there is not a simple dichotomy between rational and affect-based decision-making: we can hypothesise *many* possible mechanisms (Table 1). At least four (Conscious Deliberation, Automatic Affective Competition, Attention Capture, and Affectively

⁴ Brown also raises a somewhat independent objection against Cabanac’s idea that we use a valence-based ‘common currency’ in our decision-making at all [86]; see also [87].

Learned Habits) imply sentience, but in other possible mechanisms (Unconscious Capture, Unconsciously Learned Habits, and Fixed Decision Rule) sentience plays no role.

Table 1. Possible mechanisms for producing tradeoffs with and without sentience

Mechanism	Short Description	Involves Sentience?
<i>Conscious Deliberation</i>	Subjects consider valenced experiences alongside other inputs in a fully explicit decision process.	✓
<i>Automatic Affective Competition</i>	Subjects consciously feel/imagine/remember multiple valenced experiences at once, with their relative strength in a common currency determining action.	✓
<i>Attention Capture</i>	The trade-off is achieved by pre-conscious competition for consciousness, resulting in only one valenced experience (that immediately drives action).	✓
<i>Affectively Learned Habits</i>	Subjects' trade-off decisions are shaped over time by sentience-based reinforcement learning. Valenced experience at the time of the decision itself is not required.	✓
<i>Unconscious Capture</i>	The trade-off is achieved by unconscious behaviour-driving states competing with and suppressing one another (e.g. food deprivation suppressing sensitivity to aversive stimuli in <i>C. elegans</i>)	×
<i>Unconsciously Learned Habits</i>	Subjects' trade-off decisions are shaped over time by reinforcement learning with an unconscious 'reward' signal.	×
<i>Fixed Decision Rule</i>	As in Sec. 3's parasitoid wasp example, innately determined, inflexible, and unconscious processing of specific inputs has been shaped by evolution to produce behaviour that balances different fitness costs and benefits.	×

These possible mechanisms do not exhaust the option space.⁵ Neither are these mechanisms mutually exclusive: indeed, such mechanisms probably interact. For example, attention is likely to affect what is encoded in memory; and rather than winner-takes-*all*, valenced experiences may *partially* suppress competitors, with different priorities still being simultaneously experienced and compared in a common currency, just one with distorted prices.

The point is that even this short menu of possible mechanisms shows great diversity, and some mechanisms are far more relevant to questions of sentience than others. Motivational trade-offs *per se* are not strong evidence of sentience, but *specific features* of particular trade-offs could provide considerable confidence about sentience or its absence by helping us select among these explanations.

Designing experiments that can tease apart these different mechanisms is challenging but not impossible. For example, effects on attention may be testable through studying interference with performance in cognitively demanding tasks; and such results can be better understood given other experiments revealing the extent of willpower or ability to maintain focus in general in the subject in question.

Different mechanisms in a single subject may show up in goods and bads being ‘exchanged’ at different rates in different contexts. For example, if remembered pain has a weaker influence on attention than current pain, the bees in a study like Gibbons *et al.*’s [42] might require more sugar to compensate for heat while *actually undergoing the heat* than when deciding using memory. Indeed, certain mechanisms may be especially beneficial in certain contexts: plausibly, pain leads to *faster* decisions than more deliberative modes of centralised decision-making, while still going beyond a reflex to produce a coordinated, flexible, whole-animal response; and habits often kick in when the situation has been experienced many times before. Knowledge of the neural mechanisms can also help: for example, while *C. elegans* have individual neurons suppressing one another so that food deprivation leads to more tolerance of dangerous chemical gradients, there is evidence for a more elaborate kind of downregulation of nociception by centralised positively-valenced states in insects [48].

None of these suggestions should be treated as a prediction of the effects of sentience across all contexts. For example, humans sometimes prefer to take more pain now in order to avoid the dread of a smaller amount of future pain [88], so it cannot be that imagined or remembered pain is *always* less influential on decision-making than currently felt pain. Rather, they are a starting point for further clarifying mechanistic details in specific contexts.

8. Future Directions

Are motivational trade-offs a useful marker of sentience? This depends on how high a bar we set for useful markers. Motivational trade-offs are not, at present, strong evidence in isolation. They can nonetheless be a valuable part of the overall picture when combined with other forms of

⁵ For example, further distinctions between non-conscious mechanisms are discussed in [89], which also develops an elaborate version of the common currency account based around the idea that a system for autonomously making decisions would use self-modeling of a kind that would imply the subjective experience of pain.

evidence and when they have the right features. The relevance to sentience is strongest when the trade-off is supported by integration of valence with representations of the world, by integration across multiple sense modalities and/or time, by dynamic interactions with attention and memory, and by a distinctive kind of fast, centralised decision-making that takes over from other slower or less centralised decision-making mechanisms, becoming more dominant as the intensity of the stimulus increases. The trade-offs found so far in rats, iguanas, fishes, hermit crabs and bees have some but not all of the relevant features, whereas trade-offs in nematodes have none of them. So in the first five examples the trade-offs provide some evidence while being far from conclusive.

Taken as a whole, the motivational trade-off literature illustrates the advantages of an iterative strategy based on starting with plausible, loosely defined markers and learning more about them and their underlying mechanisms in a range of different species. This leads naturally to proposals about which specific kinds of trade-off are better indicators, bringing new research directions into view.

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References

1. Mason GJ, Lavery JM. 2022 What Is It Like to Be a Bass? Red Herrings, Fish Pain and the Study of Animal Sentience. *Front. Vet. Sci.* **9**. (doi:10.3389/fvets.2022.788289)
2. Zacks O, Jablonka E. 2023 The evolutionary origins of the Global Neuronal Workspace in vertebrates. *Neurosci. Conscious.* **2023**, niad020. (doi:10.1093/nc/niad020)
3. Barron AB, Klein C. 2016 What insects can tell us about the origins of consciousness. *Proc. Natl. Acad. Sci.* **113**, 4900–4908. (doi:10.1073/pnas.1520084113)
4. Gibbons M, Crump A, Barrett M, Sarlak S, Birch J, Chittka L. 2022 Chapter Three - Can insects feel pain? A review of the neural and behavioural evidence. In *Advances in Insect Physiology* (ed R Jurenka), pp. 155–229. Academic Press. (doi:10.1016/bs.aiip.2022.10.001)
5. Crump A, Browning H, Schnell A, Burn C, Birch J. 2022 Sentience in decapod crustaceans: A general framework and review of the evidence. *Anim. Sentience* **7**. (doi:10.51291/2377-7478.1691)
6. Birch J, Burn C, Browning H, Schnell AK, Crump A. 2021 *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*. Department for Environment, Food & Rural Affairs (Defra).
7. National Research Council. 2009 Pain in Research Animals: General Principles and Considerations. In *Recognition and Alleviation of Pain in Laboratory Animals*, National Academies Press (US).

8. Birch J. 2024 *The Edge of Sentience: Risk and Precaution in Humans, Other Animals, and AI*. Oxford University Press.
9. Browning H, Birch J. 2022 Animal sentience. *Philos. Compass* **17**, e12822. (doi:10.1111/phc3.12822)
10. Brown SAB, Paul ES, Birch J. 2024 To test the boundaries of consciousness, study animals. *Trends Cogn. Sci.* (doi:10.1016/j.tics.2024.06.003)
11. Bayne T *et al.* 2024 Tests for consciousness in humans and beyond. *Trends Cogn. Sci.* **28**, 454–466. (doi:10.1016/j.tics.2024.01.010)
12. Bayne T *et al.* 2024 Animals and the iterative natural kind strategy. *Trends Cogn. Sci.* , S1364–6613(24)00196–7. (doi:10.1016/j.tics.2024.07.009)
13. Bayne T, Shea N. 2020 Consciousness, Concepts and Natural Kinds. *Philos. Top.* **48**, 65–83. (doi:10.5840/philtopics20204814)
14. Birch J. 2022 The search for invertebrate consciousness. *Nous* **56**, 133–153. (doi:10.1111/nous.12351)
15. Shea N. 2011 Methodological Encounters with the Phenomenal Kind. *Philos. Phenomenol. Res.* **84**, 307–344. (doi:10.1111/j.1933-1592.2010.00483.x)
16. Allen C. 2009 Animal Consciousness. In *The Stanford Encyclopedia of Philosophy* (eds EN Zalta, U Nodelman), Metaphysics Research Lab, Stanford University.
17. Andrews K. 2020 *How to Study Animal Minds*. Cambridge: Cambridge University Press. (doi:10.1017/9781108616522)
18. Shea N, Bayne T. 2010 The Vegetative State and the Science of Consciousness. *Br. J. Philos. Sci.* **61**, 459–484. (doi:10.1093/bjps/axp046)
19. Shevlin H. 2021 Non-human consciousness and the specificity problem: A modest theoretical proposal. *Mind Lang.* **36**, 297–314.
20. Whiteley C. 2022 Kinds and classification in consciousness science. phd, London School of Economics and Political Science. See <https://etheses.lse.ac.uk/4444/>.
21. Mckilliam A. 2024 Natural kind reasoning in consciousness science: An alternative to theory testing. *Nous* **n/a**. (doi:10.1111/nous.12526)
22. Michel M. 2018 Fish and Microchips: On Fish Pain and Multiple Realization. *Philos. Stud.* **176**, 2411–2428. (doi:10.1007/s11098-018-1133-4)
23. Phillips I. 2018 The methodological puzzle of phenomenal consciousness. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **373**, 20170347. (doi:10.1098/rstb.2017.0347)
24. Taylor H. 2023 Consciousness as a Natural Kind and the Methodological Puzzle of Consciousness. *Mind Lang.* **38**, 316–335. (doi:10.1111/mila.12413)
25. Dung L, Newen A. 2023 Profiles of animal consciousness: A species-sensitive, two-tier account to quality and distribution. *Cognition* **235**, 105409. (doi:10.1016/j.cognition.2023.105409)
26. Sneddon LU, Elwood RW, Adamo SA, Leach MC. 2014 Defining and assessing animal pain. *Anim. Behav.* **97**, 201–212. (doi:10.1016/j.anbehav.2014.09.007)
27. Johnson KG, Cabanac M. 1982 Homeostatic competition between food intake and temperature regulation in rats. *Physiol. Behav.* **28**, 675–679. (doi:10.1016/0031-9384(82)90050-6)
28. Balasko M, Cabanac M. 1998 Motivational conflict among water need, palatability, and cold discomfort in rats. *Physiol. Behav.* **65**, 35–41. (doi:10.1016/S0031-9384(98)00090-0)
29. Warden CJ. 1931 *Animal Motivation: Experimental Studies on the Albino Rat*. Columbia University Press.
30. Shizgal P, Conover K. 1996 On the neural computation of utility. *Curr. Dir. Psychol. Sci.* **5**, 37–43. (doi:10.1111/1467-8721.ep10772715)
31. Cabanac M. 1992 Pleasure: the common currency. *J. Theor. Biol.* **155**, 173–200. (doi:10.1016/s0022-5193(05)80594-6)
32. Balasko M, Cabanac M. 1998 Behavior of Juvenile Lizards (*Iguana iguana*) in a Conflict between Temperature Regulation and Palatable Food. *Brain. Behav. Evol.* **52**, 257–262. (doi:10.1159/000006570)
33. Millsopp S, Laming P. 2008 Trade-offs between feeding and shock avoidance in goldfish (*Carassius*

- auratus*). *Appl. Anim. Behav. Sci.* **113**, 247–254. (doi:10.1016/j.applanim.2007.11.004)
34. Dunlop R, Millsopp S, Laming P. 2006 Avoidance learning in goldfish (*Carassius auratus*) and trout (*Oncorhynchus mykiss*) and implications for pain perception. *Appl. Anim. Behav. Sci.* **97**, 255–271. (doi:10.1016/j.applanim.2005.06.018)
 35. Elwood RW. 2022 Hermit crabs, shells, and sentience. *Anim. Cogn.* (doi:10.1007/s10071-022-01607-7)
 36. Arnott G, Elwood RW. 2007 Fighting for shells: how private information about resource value changes hermit crab pre-fight displays and escalated fight behaviour. *Proc. Biol. Sci.* **274**, 3011–3017. (doi:10.1098/rspb.2007.1196)
 37. Appel M, Elwood RW. 2009 Motivational trade-offs and potential pain experience in hermit crabs. *Appl. Anim. Behav. Sci.* **119**, 120–124. (doi:10.1016/j.applanim.2009.03.013)
 38. Magee B, Elwood RW. 2016 Trade-offs between predator avoidance and electric shock avoidance in hermit crabs demonstrate a non-reflexive response to noxious stimuli consistent with prediction of pain. *Behav. Processes* **130**, 31–35. (doi:10.1016/j.beproc.2016.06.017)
 39. Gorman D, Barros F, Turra A. 2015 What motivates hermit crabs to abandon trapped shells? Assessing the influence of shell value, olfactory attractants, and previous experience. *Hydrobiologia* **743**, 285–297. (doi:10.1007/s10750-014-2047-6)
 40. Briffa M, Twyman C. 2011 Do I stand out or blend in? Conspicuousness awareness and consistent behavioural differences in hermit crabs. *Biol. Lett.* **7**, 330–332. (doi:10.1098/rsbl.2010.0761)
 41. Barr S, Elwood RW. 2024 Trade-Offs between Avoidance of Noxious Electric Shock and Avoidance of Bright Light in Shore Crabs Are Consistent with Predictions of Pain. *Animals* **14**, 770. (doi:10.3390/ani14050770)
 42. Gibbons M, Versace E, Crump A, Baran B, Chittka L. 2022 Motivational trade-offs and modulation of nociception in bumblebees. *Proc. Natl. Acad. Sci.* **119**, e2205821119. (doi:10.1073/pnas.2205821119)
 43. Tello-Ramos MC, Branch CL, Kozlovsky DY, Pitera AM, Pravosudov VV. 2019 Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. *Anim. Behav.* **147**, 129–136. (doi:10.1016/j.anbehav.2018.02.019)
 44. Mariette MM, Buchanan KL. 2016 Prenatal acoustic communication programs offspring for high posthatching temperatures in a songbird. *Science* **353**, 812–814. (doi:10.1126/science.aaf7049)
 45. Gigerenzer G, Todd PM. 1999 Fast and frugal heuristics: The adaptive toolbox. In *Simple heuristics that make us smart*, pp. 3–34. New York, NY, US: Oxford University Press.
 46. Wajnberg É. 2006 Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. *Behav. Ecol. Sociobiol.* **60**, 589–611. (doi:10.1007/s00265-006-0198-9)
 47. Godfrey-Smith P. 2020 *Metazoa: Animal Minds and the Birth of Consciousness*. HarperCollins UK.
 48. Gibbons M, Sarlak S, Chittka L. 2022 Descending control of nociception in insects? *Proc. R. Soc. B Biol. Sci.* **289**, 20220599. (doi:https://doi.org/10.1098/rspb.2022.0599)
 49. Dung L. 2022 Assessing tests of animal consciousness. *Conscious. Cogn.* **105**, 103410.
 50. Dennett DC. 1973 Mechanism and Responsibility. In *Essays on Freedom of Action* (ed T Honderich), pp. 157–84. Routledge.
 51. Keijzer F. 2013 The SpheX Story: How the Cognitive Sciences Kept Repeating an Old and Questionable Anecdote. *Philos. Psychol.* **26**, 502–519. (doi:10.1080/09515089.2012.690177)
 52. Paul ES, Sher S, Tamietto M, Winkielman P, Mendl MT. 2020 Towards a comparative science of emotion: Affect and consciousness in humans and animals. *Neurosci. Biobehav. Rev.* **108**, 749–770. (doi:10.1016/j.neubiorev.2019.11.014)
 53. Phillips IB. 2021 Blindsight is qualitatively degraded conscious vision. *Psychol. Rev.* **128**, 558–584. (doi:10.1037/rev0000254)
 54. Irvine E. 2013 *Consciousness as a Scientific Concept: A Philosophy of Science Perspective*. Dordrecht: Springer Netherlands. (doi:10.1007/978-94-007-5173-6)
 55. Shinkai Y *et al.* 2011 Behavioral choice between conflicting alternatives is regulated by a receptor

- guanylyl cyclase, GCY-28, and a receptor tyrosine kinase, SCD-2, in AIA interneurons of *Caenorhabditis elegans*. *J. Neurosci. Off. J. Soc. Neurosci.* **31**, 3007–3015. (doi:10.1523/JNEUROSCI.4691-10.2011)
56. Ishihara T, Iino Y, Mohri A, Mori I, Gengyo-Ando K, Mitani S, Katsura I. 2002 HEN-1, a secretory protein with an LDL receptor motif, regulates sensory integration and learning in *Caenorhabditis elegans*. *Cell* **109**, 639–649. (doi:10.1016/s0092-8674(02)00748-1)
 57. Ghosh DD, Sanders T, Hong S, McCurdy LY, Chase DL, Cohen N, Koelle MR, Nitabach MN. 2016 Neural Architecture of Hunger-Dependent Multisensory Decision Making in *C. elegans*. *Neuron* **92**, 1049–1062. (doi:10.1016/j.neuron.2016.10.030)
 58. Gillette R, Huang R-C, Hatcher N, Moroz LL. 2000 Cost-benefit analysis potential in feeding behavior of a predatory snail by integration of hunger, taste, and pain. *Proc. Natl. Acad. Sci. U. S. A.* **97**, 3585–3590.
 59. McLachlan IG, Kramer TS, Dua M, DiLoreto EM, Gomes MA, Dag U, Srinivasan J, Flavell SW. 2022 Diverse states and stimuli tune olfactory receptor expression levels to modulate food-seeking behavior. *eLife* **11**, e79557. (doi:10.7554/eLife.79557)
 60. Irvine E. 2020 Developing Valid Behavioral Indicators of Animal Pain. *Philos. Top.* **48**, 129–154.
 61. Zalucki O, Brown DJ, Key B. 2023 What if worms were sentient? Insights into subjective experience from the *Caenorhabditis elegans* connectome. *Biol. Philos.* **38**, 34. (doi:10.1007/s10539-023-09924-y)
 62. Andrews K. 2024 “All animals are conscious”: Shifting the null hypothesis in consciousness science. *Mind Lang.* **39**, 415–433. (doi:10.1111/mila.12498)
 63. Cohen D, Teichman G, Volovich M, Zeevi Y, Elbaum L, Madar A, Louie K, Levy DJ, Rechavi O. 2019 Bounded rationality in *C. elegans* is explained by circuit-specific normalization in chemosensory pathways. *Nat. Commun.* **10**, 3692. (doi:10.1038/s41467-019-11715-7)
 64. Iwanir S, Ruach R, Itskovits E, Pritz CO, Bokman E, Zaslaver A. 2019 Irrational behavior in *C. elegans* arises from asymmetric modulatory effects within single sensory neurons. *Nat. Commun.* **10**, 3202. (doi:10.1038/s41467-019-11163-3)
 65. Khan M, Hartmann AH, O’Donnell MP, Piccione M, Pandey A, Chao P-H, Dwyer ND, Bargmann CI, Sengupta P. 2022 Context-dependent reversal of odorant preference is driven by inversion of the response in a single sensory neuron type. *PLoS Biol.* **20**, e3001677. (doi:10.1371/journal.pbio.3001677)
 66. Tee LF, Young JJ, Maruyama K, Kimura S, Suzuki R, Endo Y, Kimura KD. 2023 Electric shock causes a fleeing-like persistent behavioral response in the nematode *Caenorhabditis elegans*. *Genetics* **225**, iyad148. (doi:10.1093/genetics/iyad148)
 67. Kaplan HS, Nichols ALA, Zimmer M. 2018 Sensorimotor integration in *Caenorhabditis elegans*: a reappraisal towards dynamic and distributed computations. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **373**, 20170371. (doi:10.1098/rstb.2017.0371)
 68. Brittin CA, Cook SJ, Hall DH, Emmons SW, Cohen N. 2021 A multi-scale brain map derived from whole-brain volumetric reconstructions. *Nature* **591**, 105–110. (doi:10.1038/s41586-021-03284-x)
 69. Gershman SJ. 2023 The molecular memory code and synaptic plasticity: A synthesis. *Biosystems* **224**, 104825. (doi:10.1016/j.biosystems.2022.104825)
 70. Shaw BK, Kristan Jr. WB. 1997 The Neuronal Basis of the Behavioral Choice between Swimming and Shortening in the Leech: Control Is Not Selectively Exercised at Higher Circuit Levels. *J. Neurosci.* **17**, 786–795. (doi:10.1523/JNEUROSCI.17-02-00786.1997)
 71. S H, Y I. 2022 The redundancy and diversity between two novel PKC isoforms that regulate learning in *Caenorhabditis elegans*. *Proc. Natl. Acad. Sci. U. S. A.* **119**. (doi:10.1073/pnas.2106974119)
 72. Zhang Y, Lu H, Bargmann CI. 2005 Pathogenic bacteria induce aversive olfactory learning in *Caenorhabditis elegans*. *Nature* **438**, 179–184. (doi:10.1038/nature04216)
 73. Gourgou E, Adiga K, Goettmoeller A, Chen C, Hsu A-L. 2021 *Caenorhabditis elegans* learning in a structured maze is a multisensory behavior. *iScience* **24**, 102284. (doi:10.1016/j.isci.2021.102284)
 74. Brown S. 2022 How much of a pain would a crustacean “common currency” really be? *Anim.*

- Sentience* **7**. (doi:10.51291/2377-7478.1749)
75. Crombez G, Eccleston C, Baeyens F, Eelen P. 1996 The disruptive nature of pain: an experimental investigation. *Behav. Res. Ther.* **34**, 911–918. (doi:10.1016/s0005-7967(96)00058-7)
 76. Eccleston C, Crombez G. 1999 Pain demands attention: a cognitive-affective model of the interruptive function of pain. *Psychol. Bull.* **125**, 356–366. (doi:10.1037/0033-2909.125.3.356)
 77. Moore DJ, Keogh E, Eccleston C. 2012 The interruptive effect of pain on attention. *Q. J. Exp. Psychol.* **2006** **65**, 565–586. (doi:10.1080/17470218.2011.626865)
 78. Crombez G, Eccleston C, Baeyens F, Eelen P. 1998 Attentional disruption is enhanced by the threat of pain. *Behav. Res. Ther.* **36**, 195–204. (doi:10.1016/s0005-7967(97)10008-0)
 79. McHugo M, Olatunji BO, Zald DH. 2013 The emotional attentional blink: what we know so far. *Front. Hum. Neurosci.* **7**, 151. (doi:10.3389/fnhum.2013.00151)
 80. Santacroce LA, Swami AL, Tamber-Rosenau BJ. 2023 More than a feeling: The emotional attentional blink relies on non-emotional “pop out,” but is weak compared to the attentional blink. *Atten. Percept. Psychophys.* **85**, 1034–1053. (doi:10.3758/s13414-023-02677-6)
 81. Koppel L, Andersson D, Morrison I, Posadzy K, Västfjäll D, Tinghög G. 2017 The effect of acute pain on risky and intertemporal choice. *Exp. Econ.* **20**, 878–893. (doi:10.1007/s10683-017-9515-6)
 82. Morales J. 2023 Mental strength: A theory of experience intensity. *Philos. Perspect.* **37**, 248–268. (doi:10.1111/phpe.12189)
 83. Lebrecht S, Bar M, Barrett LF, Tarr MJ. 2012 Micro-Valences: Perceiving Affective Valence in Everyday Objects. *Front. Psychol.* **3**. (doi:10.3389/fpsyg.2012.00107)
 84. Carrasco M. 2011 Visual attention: The past 25 years. *Vision Res.* **51**, 1484–1525. (doi:10.1016/j.visres.2011.04.012)
 85. Wu W. 2014 *Attention*. Routledge.
 86. Hayden BY, Niv Y. 2021 The case against economic values in the orbitofrontal cortex (or anywhere else in the brain). *Behav. Neurosci.* **135**, 192–201. (doi:10.1037/bne0000448)
 87. Garcia B, Lebreton M, Bourgeois-Gironde S, Palminteri S. 2023 Experiential values are underweighted in decisions involving symbolic options. *Nat. Hum. Behav.* **7**, 611–626. (doi:10.1038/s41562-022-01496-3)
 88. Story GW, Vlaev I, Seymour B, Winston JS, Darzi A, Dolan RJ. 2013 Dread and the disvalue of future pain. *PLoS Comput. Biol.* **9**, e1003335. (doi:10.1371/journal.pcbi.1003335)
 89. Farnsworth KD, Elwood RW. 2023 Why it hurts: with freedom comes the biological need for pain. *Anim. Cogn.* **26**, 1259–1275. (doi:10.1007/s10071-023-01773-2)