



Differences in the Intensity of Valenced Experience across Species

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Key Highlights

- Differences in the intensity range of valenced experience across species may affect how we ought to allocate resources to help different types of animals
- Humans and other mammals likely share a roughly similar intensity range
- It is unlikely that any species of animal possesses an intensity range that is exclusively extraordinarily mild
- Some aspects of cognitive sophistication appear to be positively correlated with intensity range; other aspects of cognitive sophistication appear to be negatively correlated with intensity range
- Affective complexity generally appears to be positively correlated with intensity range
- There is as yet no good objective measure of valence intensity, though there is much interesting work ongoing in this area

1. First, I explored what, if anything, theoretical evolutionary biology could tell us about the function of valenced experience.
2. Next, I explored how different aspects of intellectual and emotional complexity might affect the characteristic intensity of valenced experience.
3. Finally, I explored potential neurobiological, behavioral, and physiological markers of the intensity of valenced experience in humans and nonhuman animals.

Broadly speaking, the evolutionary function of valenced experience is to promote fitness-improving behaviors. It's plausible that natural selection would not produce animals for whom valenced experiences were always extraordinarily weak because subjective experiences that were so faint as to be almost imperceptible would appear to do a poor job motivating behavior. Conversely, it appears unlikely that evolution would select for animals with a non-contiguous range that was exclusively extraordinarily strong because extremely intense experiences are distracting in a way that appears likely to reduce fitness.

Executive Summary

This post is the fifth in [Rethink Priorities'](#) moral weight series. In this report, I explain why it would matter if different sorts of animals possessed characteristically different intensity ranges of valenced experience, what factors might affect the intensity range of valenced experience, and how we might begin to measure differences in the intensity of valenced experience.

Animals differ in their perceptual abilities, their physiology and neural architecture, and their cognitive, affective, and social complexity. Given these differences, it would be surprising if the intensity range of valenced experience were uniform across species. To investigate differences in the intensity range of valenced experience across species, I adopted a three-stage methodology:

'Cognitive sophistication' is a nebulous term that may refer to any of a constellation of mostly independent traits. Many of these traits plausibly affect the intensity of valenced experience, but the sign of the effect is often unclear. 'Affective complexity' refers to the diversity and depth of emotional sensations an animal can experience. Increased affective complexity may unlock qualitatively unique emotional states—such as fear, depression, or love—that by themselves or in combination with physical states increase the intensity range of experience.

There are currently no good cross-species measures of the intensity of valenced experience, though there is intriguing recent evidence that neural oscillations in the gamma band may track differences in pain intensity in both humans and nonhuman mammals.



Humans and nonhuman mammals possess neurologically and behaviorally similar affective systems, suggesting that most mammals are capable of experiencing roughly the same base set of emotions. It's unclear how stark the differences in cognitive sophistication are across mammalian species and how these differences might affect the intensity of valenced experience. Given these facts, it would appear that we are more justified in thinking that humans possess an intensity range roughly similar to other mammals than we are in thinking that humans possess a much wider range than other mammals. It is unclear how mammals compare to other groups of animals, in part because there is a much sparser scientific literature on the capabilities of non-mammals and in part because it is unclear how increasing phylogenetic distance ought to influence reasoning-by-analogy about subjective experience.

Intensity of Valenced Experience and Its Range

Valenced experiences are those experiences that take on a positive or negative phenomenal affect.¹ That is, valenced experiences are those experiences that *feel good* or *feel bad* to the subject.²

1 In this report I assume a unidimensional analysis of valence. There is not sufficient space to adjudicate the appropriateness of that assumption here. The interested reader is encouraged to consult §7.2 of [Browning 2019](#). She outlines four reasons to endorse a unidimensional analysis of valence: common usage/intuition, introspection, trade-offs and decision-making, and functional and structural similarities between affects.

2 As such, only creatures that are sentient are capable of valenced experiences. However, experiences need not be valenced: some experiences, like tying one's shoes or checking the mail, may be perfectly neutral. Thus, the class of sentient creatures is not necessarily coextensive with the class of creatures capable of valenced experience. Some animals might be sentient but incapable of experiencing positive or negative affects.

3 Experiences can be valuable for reasons beyond their duration and valenced intensity. An unpleasant experience might be instrumentally valuable because it teaches one a valuable life lesson. On some non-hedonistic theories of welfare, experiences can even be *morally* valuable beyond their duration and valenced intensity, if they instantiate some non-instrumental good (the appreciation of artistic beauty, say). I take such value to be outside the intrinsic nature of the experience, however.

4 In this context, 'intensity' refers exclusively to *valence* intensity. That is, the intensity of an experience is the measure of how good or bad the experience feels. In this sense, non-valenced experiences do not have an intensity. Of course, there is another sense of 'intensity' in which non-valenced experiences can be more or less intense (e.g., the experience of a red ripe tomato may be more or less *vivid*), but I won't be concerned with that sense in this report.

5 Importantly, intensity is a synchronic rather than diachronic notion. That is, when I refer to the intensity of an experience, I mean the intensity-at-a-time of the experience. When I speak loosely of the intensity of an experience that is extended in time, I normally mean something like the average intensity-at-a-time of the experience. There is a sense in which the pain of a broken leg is strong because it lasts so long and the pleasure of a Facebook like is weak because it is so fleeting. I won't use 'intensity' in that sense in this report.

6 In discussing potential cross-species differences, I often focus on differences in the intensity of painful experiences. This bias isn't because I endorse suffering-focused ethics, negative utilitarianism, or any value asymmetry between positive and negative experiential states. The bias in this post merely reflects a bias in the relevant literature. As one review explains, "The traditional approach to animal welfare was that pain, suffering, distress, and other negative physical or mental experiences should be minimized. Consequently, there is a bias in the science of animal welfare toward the study of negative experiences at the expense of positive ones" ([Webb et al. 2019](#): 62). The authors add that "there has been very little work to date done on assessing affective happiness in animals" ([Webb et al. 2019](#): 71).

7 What one means by an individual's possible range depends on how one understands the 'possible' in 'possible intensity range of valenced experience.' We are interested in differences in the ranges of intensity of valenced experience across species. To define the intensity range of an animal's possible experiences, we look at the animal's most intense experiences across some subset of possible worlds. How we carve up modal space—that is, which possible worlds make it into the defining set—will affect the range we assign to each animal. If we make the defining set the set of all physically possible worlds, each animal's range will be larger than we want it to be. (The set of all physically possible worlds includes worlds where a mad scientist genetically engineers the animal to maximize its pain or pleasure.) If we restrict the set to the actual world, each animal's range will be smaller than we want it to be. (Just because an animal is effectively

The intrinsic value of an experience is the product of its (possibly [subject-relative](#)) duration and valenced intensity.³ Just as the duration of experiences varies, so too does the valenced intensity of experiences.⁴ Some pains hurt worse than others: a sprained wrist is typically less wrenching than a broken femur. Some pleasures are better than others: an evening watching television typically engenders less joy than the birth of one's first child.⁵

Human life contains an assortment of valenced experiences.⁶ Some experiences, like the birth of one's child, may be profoundly positive. Other experiences, like breaking one's femur, may be acutely negative. Taking the difference of one's best experience and one's worst experience gives us one's *realized intensity range of valenced experience*. Of course, the average human probably doesn't experience the highest possible highs and lowest possible lows. Most of us do not have the misfortune of, say, suffering torture in a prisoner-of-war camp. Neither, though, do most of us taste the pure jubilation of, say, scoring the winning point in a sports championship. Taking the difference of the best experience one might undergo and the worst experience one might undergo gives us one's *possible intensity range of valenced experience*.⁷

Characteristic Range vs. Possible Range

In addition to *realized* range and *possible* range, there is a third conception of valenced intensity range that is useful for our purposes. An animal's *characteristic intensity range of valenced experience* is defined by those experiences that are common for a member of the animal's species at a particular point in the history of the species.⁸ Characteristic range is still a modal notion because it is independent of an animal's *actual* experiences. (It's possible that an animal's *actual* experiences exclusively fall outside the characteristic range.)

One potential reason to be more concerned about characteristic range than possible range is that animals might differ much more in their characteristic than their possible range, which would be especially concerning if inducing intensities outside the characteristic range were much more challenging⁹ than inducing intensities within the characteristic range. If this is the case, then for practical purposes, when deciding how to allocate resources to different species, it might be more informative to look at characteristic rather than possible range.

An example will illustrate the point. Suppose it's possible (though very difficult) for both pigs and chickens to reach intensities as low as -100 and as high as +100. Suppose as well that the characteristic range of pigs is -90 to +90 and the characteristic range of chickens is -10 to +10. Suppose finally that moving an animal one point outside its characteristic range is ten times as costly as moving an animal one point inside its characteristic range. In this scenario, focusing too much on possible as opposed to characteristic range might lead us to allocate equal resources to pigs and chickens even though, given the assumptions and all else equal, it will usually be more cost-effective to help pigs rather than chickens in this scenario. More generally, differences in possible range that are rarely realized may matter less than differences in character-

istic range that are often realized.

The features and considerations I explore below are sometimes more relevant to possible range than characteristic range, sometimes more relevant to characteristic range than possible range, and sometimes equally relevant to both. At the level of generality with which I discuss the topic, the distinction is not usually important. However, a more fine-grained and detailed examination of these issues would need to pull apart the effects on possible range from characteristic range. In so doing, we might discover that one type of range is more important or more variable than the other.

Why Variation in the Intensity Range of Valenced Experience Matters

Theories of welfare agree: experiences matter, morally.¹⁰ If animals differ in the intensity ranges of their valenced experience, such differences could affect the magnitude of welfare changes we create by helping (or harming) different sorts of animals. Suppose, for instance, the valence intensity of honey bees only vacillates between mildly positive experiences and mildly negative experiences. That is to say, the worst a honey bee might expect to suffer could be the equivalent of a human stubbing her toe; conversely, the best a honey bee might expect to enjoy could be the equivalent of a human eating a decent banana. In that case, improving the experiential states of honey bees would not generate large improvements in welfare. On the other hand, suppose that the valenced experiences of honey bees reach extreme intensities.¹¹ A typical honey bee pain might be worse than the worst human migraine; a typical honey bee pleasure might be better than the best human orgasm. In that case, improving the experiential states of honey bees could lead to large gains in welfare.

Humans exploit an incredibly phylogenetically diverse group of

tortured its whole life on a factory farm doesn't mean it couldn't have experienced genuine pleasures.)

8 Obviously, as stated this is an underspecification. What counts as 'characteristic' will depend on how we operationalize 'common.' But for the sake of the conceptual point at issue here, we need not precisify the notion any more than I have in the main text.

9 For example, to reach the maximum of an individual's characteristic range, it might be sufficient to give the individual her/his favorite food. But to reach the maximum of the *possible* range, one might have to first develop a drug that is personally tailored to the individual's neural architecture such that the drug maximally activates the hedonic hotspots of the individual's brain.

10 Consider the three main kinds of theories of welfare: (1) hedonistic theories, according to which welfare is the balance of experienced pleasure and pain, (2) desire-fulfillment theories, according to which welfare is the degree to which one's desires are satisfied, and (3) objective list theories, according to which welfare is the extent to which one attains non-instrumental goods like happiness, virtue, wisdom, friendship, knowledge, and love. According to hedonism, experiences are all that ultimately matter morally. Experiences are also relevant to desire-fulfillment accounts of welfare. We generally desire pleasurable experiences and desire to avoid painful experiences. (And painful experiences often get in the way of our non-experiential desires.) Objective list theories maintain that there are a variety of intrinsic goods, but all plausible objective list theories include goods either constituted by our experiences (such as pleasure) or for which our experiences are directly relevant (such as life satisfaction or happiness).

11 In these examples, I assume that the intensity range is symmetric between positive and negative valences. But the intensity ranges of valences need not be symmetric. There is modest evidence that humans don't have a symmetric range.

animals.¹² An exponentially greater diversity of animals suffer in the wild. But animal advocates have limited resources. Thus, hard choices must be made. Knowing that we can't help all animals simultaneously, we must choose where to invest our scarce resources. There are, of course, many considerations that must be examined when deciding how to allocate time and money to different groups of animals. But to fully judge interventions and policies, we need to be able to evaluate (at least roughly) welfare gains and losses across many species.¹³

Animals differ with respect to their neurobiological makeup,¹⁴ their cognitive and affective complexity,¹⁵ and their experiential capabilities.¹⁶ These differences make plausible the idea that there are characteristic differences in the intensity range of valenced experience across species.^{17,18} Moreover, it appears that pain sensitivity varies among humans. Humans exposed to the same sort of stimuli often report different subjective experiences. One review observes, "Pain perception varies widely among individuals. Even in controlled experimental settings, the same mild nociceptive stimulus can elicit unpredictably intense sensations in one individual, yet be barely perceived by another. In real-world settings, equally serious injuries often result in remarkably different painful per-

cepts. What drives such dramatic variability of pain perception across individuals remains elusive" (Hu & Iannetti 2019: 1782).¹⁹ Given such differences among humans, who broadly share social, affective, intellectual, behavioral, and neurobiological characteristics, it's not hard to imagine more profound differences among nonhuman animals. This possibility is sometimes explicitly raised in the literature: "The apparent occurrence of intra-specific variation in individuals' pain experiences raises the hypothesis that there might be inter-specific variation in individuals' pain experiences, i.e., individuals of different species may have different capacities for pain experiences" (Yeates 2012: 25).²⁰

How to Discern Differences in the Intensity Range of Valenced Experience

Discerning differences in the intensity range of valenced experience across species is not easy. As I detail below, the limited evidence currently available suggests extreme uncertainty. When researching the topic, I adopted the following three-step methodology, which also serves as a useful conceptual framing for this report.

12 See [this spreadsheet](#) for an accounting of the phylogenetic diversity of the animals humans exploit. Counting somewhat conservatively, there are at least 51 taxonomic families of animals, across 33 orders, 13 classes and 6 phyla, that humans directly exploit in large numbers. Through habitat destruction, environmental degradation, and anthropogenic climate change, humans indirectly affect almost all animals on the planet.

13 Ideally, we would also like to know *the location* of an animal's intensity range on the valence scale. According to many plausible theories, there is a moral prohibition on bringing into existence creatures whose intensity range is wholly negative. Conversely, under some circumstances we might wish to promote the propagation of creatures whose intensity range is wholly positive, especially if the range were on the high end of the positive side.

14 Although almost all animals possess nociceptors, the specialized cells that detect noxious stimuli, the types and thresholds of these nociceptors vary widely. (For example, the nociceptors of temperate species of fish are more sensitive to heat damage than the nociceptors of tropical fish [Sneddon 2019: 4].) And given differences in neural architectures across taxonomic orders, it would not be surprising if the way in which nociception was processed differed as well. Such differences could plausibly give rise to differences in the range of valenced experience.

15 Some animals can experience the pain of losing a friend or the joy of raising a child. Some animals can become depressed or traumatized; others can be amused or hopeful. Some animals can rationalize current suffering and anticipate future pleasure. Differences in these sorts of capacities could plausibly affect the intensity range of experiences.

16 Many bat and dolphin species navigate using echo-location. Wolves, bears, and elephants have extraordinarily rich olfactory experiences. Rats, hamsters, and shrews learn about the world through [whisking](#). Expanding our consideration to birds, fish, or insects would multiply this kind of diversity. Given these sorts of differences in sensorial capabilities, it's plausible that the perception of pains and pleasures differs across species in a way that affects intensity range.

17 One way to argue that intensity range is invariable is to adopt a subject-relative, deflationary account of valence intensity. If the intensities of experience supervene on, or are otherwise grounded in, individual preferences, then valence intensity won't correspond to an objective measure that can be compared across individuals. (To say that pain 1 hurts worse than pain 2 is just to express one's preference for pain 2 over pain 1.) Depending on the details, intensity range would either be incomparable across individuals or exactly equal. However, I don't find such an account plausible because it gets the order of explanation wrong. If pain 1 hurts worse than pain 2, then, all else equal, the *reason* I prefer pain 2 to pain 1 is *because* the experience will be less intense. If the intensity of pains is grounded in preferences, we lose this natural explanation.

18 Strictly speaking, *intensity range of valenced experience* is a property of individuals, not of species. Nevertheless, for simplicity's sake, it will often be useful to compare the intensity range of, say, chickens, rainbow trout, and honey bees. For some species, intensity range might change with life stage. The pupal or larval stage of an insect might have a broader or narrower range than the adult form, for example. For these animals, we will have to specify 'species member at life stage x.'

19 See also: "The personal experience of pain is highly variable among individuals even if the underlying noxious stimulation is similar" (Furman et al. 2018: 204).

20 See also: "We do not have good reason to think that these similarities hold between quite dissimilar species; for example, it is not likely that the scope of welfare intensity for a lion is anything like that for a lungfish" (Browning 2019: 156).

1. Start with considerations from theoretical evolutionary biology. The evolutionary function of valenced experience may place some general constraints on the scope and location of intensity ranges. Thinking about how selection pressures are likely to operate on valenced experience in various conditions may help us identify some rough principles for broad groups of animals.
2. Next, consider how intensity range is likely to vary with characteristics like cognitive sophistication, affective complexity, and sociality.²¹
3. Finally, try to identify various neurobiological and behavioral markers of valenced experience and see how these vary across species. The proxies ought to be validated in humans first and in the right conditions extended to some nonhuman animals.

I address these three steps in turn below.

The Evolutionary Role of Valenced Experience

²¹ During this stage we need to be wary of combination effects. For example, an animal's degree of cognitive sophistication (in all its heterogeneous variety) could interact with the animal's degree of affective complexity (in all its heterogeneous variety) to influence the intensity of valenced experience in unexpected ways. Analyzing traits in isolation makes the project conceptually more manageable, but the complexity we sweep under the rug by doing so could hide the majority of the intensity range variance across species. A more thorough treatment of the topic would thus confront the problem of combination effects head-on, rather than sidestepping the issue, as I have mostly done here.

²² Of course, there's no *guarantee* that animals with the capacity for valenced experience accrued a fitness advantage in virtue of that capacity. Valenced experience might merely be the byproduct of unrelated evolutionary forces.

²³ In what follows I remain neutral between the view that valenced experience evolved only once in the ancestors of those animals with the capacity for valenced experience and the view that the capacity for valenced experience is the product of convergent evolution in multiple lineages.

²⁴ In what follows I assume that valenced experience plays roughly the same role for all animals with the capacity for valenced experience. This assumption seems to be widely shared in the literature. (e.g., "The basic function of pain is likely to be common to all vertebrates, or perhaps all mobile animals, causing an individual to stop traumatic activities or attempt to escape damaging situations. Posttrauma, pain reminds animals to avoid further injury and encourages rest and recuperation as far as the requirements of survival allow" [Finlay & Syal 2014: 615].) However, if the capacity for valenced experience evolved multiple times, it's possible that valenced experience plays different roles in different lineages. Even if the capacity for valenced experience only evolved once, it may have been co-opted for different purposes by different lineages.

²⁵ "Animals which have shared evolutionary history, as well as sharing the structures and function of their brains and bodies, also have shared selection pressures. If we take subjective experience, and the behavioural and physiological responses it produces, as being the products of selective processes (e.g. Ginsburg & Jablonka, 2019; Godfrey-Smith, 2017), then it makes sense that shared selection pressures will have led to similar experience and responses. Animals with shared evolutionary history (most particularly those of the same species) will have brains adapted to the same biological challenges, and it makes sense to infer that they will share similar psychology, with the same scope for welfare experience" (Browning 2019: 153).

²⁶ When discussing the biological function of valenced experience there are two questions we might ask. The first is *etiological*: in virtue of what was the capacity for valenced experience selected for in the past? The second is *consequentialist* (in this sense, unrelated to the normative theory): how does the capacity for valenced experience currently contribute to the interests of animals with that capacity? The questions are logically independent because evolution might have selected for valenced experience for one function but later animals may have co-opted the system for a different purpose. See Casser 2020 (especially §2.2) for discussion.

²⁷ "pain and other negative affects evolved to guard us from danger, and equally important are the positive affects that evolved to attract us to things that will probably improve our lives" (Phillips 2008: 291).

²⁸ "Pain, like everything about life, we presume, is a Darwinian device, which functions to improve the sufferer's survival. Brains are built with a rule of thumb such as, 'If you experience the sensation of pain, stop whatever you are doing and don't do it again'" (Dawkins 2009: 393).

²⁹ Iteroparous animals are animals that can reproduce multiple times over the course of their lives. The contrast to iteroparous is *semelparous*. Semelparous animals only mate once. Virtually all mammals and birds are iteroparous. Many fish, arthropods, and molluscs are semelparous.

³⁰ The frequency of sexual interactions varies dramatically by species. If given the opportunity, roosters are known to copulate several times a day. On the

If valenced experiences—pleasures and pains, broadly defined—are relatively widespread throughout the animal kingdom, there is probably an evolutionary story that explains why animals with the capacity for valenced experience accrued a fitness advantage over animals without that capacity.^{22,23,24} The quality and intensity of valenced experience has, like aspects of animal behavior and physiology, been shaped by selection pressures (Browning 2019: 153).²⁵ By examining the evolutionary role of valenced experience, we may be able to identify some rough bounds on the likely variation in intensity of valenced experience across species. By taking an evolutionary lens to certain properties, we may even be able to estimate relative differences in the intensity range of valenced experience among some broad groups of animals.²⁶

According to many evolutionary biologists, valenced experience is adaptive because it motivates fitness-improving actions (Phillips 2008: 291)²⁷ and discourages fitness-reducing actions (Dawkins 2009: 393).²⁸ Orgasm feels good to iteroparous²⁹ animals, so those animals are motivated to sexually reproduce.³⁰ Tissue damage feels bad, so animals are motivated to avoid physical

harm. Juvenile care feels good to altricial³¹ animals, so those animals are motivated to ensure the bearers of their genes survive to adulthood. Rotten fruit looks, smells, and tastes bad (to some animals), so those animals are motivated to avoid what for them would be unhealthy food. And so on.

To motivate fitness-improving actions, valenced experience is thought to play three roles. First, valenced experience represents, in at least a loose sense, fitness-relevant information. Second, valenced experience serves as a common currency for decision-making. Third, valenced experience facilitates learning.

Representation and Information-Gathering

We can think of the felt goodness or badness of an experience as a direct, intrapersonal representation of potentially fitness-relevant information.³² For example, an animal might feel a lance of pain when it moves its injured leg in a certain way. This pain can be thought to represent both the disturbance to the leg (including its location, shape, and quality) and the fact that this sort of disturbance is apt to harm the animal to a certain degree (Cutter & Tye 2011: 99).³³ This information motivates the animal to rest until the injury has healed. Animals that lack access to such intrapersonal representation are often at a severe fitness-disadvantage.³⁴

other hand, Pacific salmon mate only once and die shortly thereafter (Gallup, Towne, & Stolz 2018: 52). Among species that mate only once, reproduction is thought to be “hedonically neutral” (Gallup, Towne, & Stolz 2018: 53). It has also been theorized that “the frequency of sex ought to be proportional to the magnitude of sexual pleasure that organisms derive from sex” (Gallup, Towne, & Stolz 2018: 53). Thus: “sexual pleasure across different species ought to be inversely proportional to reproductive rate. Species that have the capacity to produce hundreds or even thousands of descendants on a single occasion, such as salmon, do not need to engage in sex very often to insure that their genes will be represented in subsequent generations. But in the case of mammals, and more so in the case of primates as a mammalian subcategory, the number of offspring produced on any given occasion is far more limited” (Gallup, Towne, & Stolz 2018: 53-54). If this view is right, then “humans would be expected to approach the upper end of the distribution when it comes to sexual gratification and sexual pleasure” (Gallup, Towne, & Stolz 2018: 54).

31 Altricial animals produce young that are unable to care for themselves after birth. In contrast, the young of *precocial* species are relatively mature and independent at birth.

32 See Tye 1995, Cutter & Tye 2011, and Cutter 2017 for more on representational theories of consciousness, especially as applied to painful experiences. See Bain 2017 for a helpful overview and history of this literature.

33 An alternative view is that the representational content of the pain is *imperative* rather than indicative. According to imperativist accounts of pain, pain does not represent information about the body; rather, pain represents a *command* to do or not do something (in general, a command to protect the body). See Klein 2015 and Martínez 2011.

34 I mean to restrict this claim to animals belonging to a species that normally represents fitness-relevant information via subjective experience in this way. Nematodes may not be capable of any subjective experience, but given the evolutionary niche they have carved for themselves, this inability does not induce a fitness disadvantage.

35 “The ability to sense pain protects us from harm and is thus an essential aspect of our well-being. Patients suffering from channelopathies that eliminate the ability to feel pain have very high rates of early mortality, largely due to self-mutilation and repetitive fractures” (Peirs & Seal 2016: 578).

36 “The adaptive value of pain lies in the actions it motivates (Goubert et al., 2005; Wall, 1999; Wiech & Tracey, 2013). On the one hand, there are the actions of the sufferer, such as escaping a painful situation and adopting a relieving posture. On the other hand, there are the actions of observers, namely, assistance, care, and treatment” (Steinkopf 2016: 1).

37 This is known as the *pain of altruism hypothesis*.

38 Their primary example is childbirth: “We suggest that cervical dilation has become rivetingly painful to induce help seeking and all of its subsequent cultural elaborations in our social species. The offspring of those who sought help are more likely to be (with) us” (Finlay & Syal 2014: 616). They add that our “human ancestors motivated to ask for help survived in greater numbers than either the thick-skinned or the stoic” (Finlay & Syal 2014: 615).

For instance, humans with congenital analgesia (a condition that prevents the experience of pain) almost always die young (Peirs & Seal 2016: 578).³⁵

In many species, valenced experience also induces outward changes that represent fitness-relevant information to observers, especially conspecifics. The outward signs of disgust after ingesting a poisonous berry warn other members of the species to avoid that food. In social species (such as humans), grunts and wincing of pain may elicit offers of assistance (Steinkopf 2016: 1).³⁶ In fact, some researchers have theorized that highly social animals suffer characteristically worse pains than non-social animals.³⁷ For instance, Barbara Finlay and Supriya Syal argue that “over evolutionary time, several stimuli and situations that are painful in neither mammals generally nor in our primate relatives particularly have come to be experienced as pain in humans, accompanied by obvious distress that serves to elicit help from others. In humans, our domesticated species, and perhaps other highly social animals, soliciting help may allow survival in otherwise fatal situations” (Finlay & Syal 2014: 615).³⁸

Reflecting on the representation of valenced experience, especially painful experience, may help us recognize differences in the intensity of valenced experience in certain groups. Predators have

evolved to detect evidence of injury in their prey. Predators display a clear preference for injured prey, and this preference can be explained by the fitness benefit of maximizing energy expenditure to consumption efficiency ([Butler & Finn 2009](#)). In response, prey species have evolved mechanisms to minimize the outward expressions of pain that would alert a predator to injury ([Mogill 2009](#): 290; [McLennan 2018](#): 1).³⁹ This feat might have been accomplished in two (non-exclusive) ways: (1) individuals better at hiding their pain may have outcompeted conspecifics worse at hiding their pain or (2) individuals with a higher pain tolerance may have outcompeted conspecifics with lower pain tolerance. If the latter strategy predominated in particular species, we should expect that members of that species to experience characteristically less intense pains than members of a comparable species that did not face predation pressures of this kind.^{40,41}

Decision-Making

Another proposed purpose of valenced experience is to serve as a common currency for complex decision-making ([Ginsburg & Jablonka 2019](#): 374).⁴² Animals face many competing demands. They must forage for food, avoid predators, care for juveniles, seek reproductive mates, and shelter from environmental hazards. Animals need a process to weigh, say, the fear of predatory attack with the pang of an empty stomach and make the appropriate tradeoff. Valenced experiences, as representations of

fitness-relevant information, may allow animals to compare and evaluate disparate risks and rewards.⁴³

Reflecting on the role that valenced experience plays in decision-making may help us put rough bounds on the likely variation in intensity ranges across species. In particular, evolutionary considerations may give us reason to rule out both intensity ranges that are exclusively extraordinarily weak and intensity ranges that are exclusively extraordinarily strong.⁴⁴

Some activists have suggested that animals with relatively simple nervous systems are only capable of extraordinarily weak valenced experiences. For instance, Matt Ball [writes](#), “So even if insects can have any subjective experience, their most intense sensation would be the palest hint of a feeling—a tiny fraction of the worst suffering we can experience.” The motivation for this view seems to be the idea that the intensity of an animal’s valenced experience should scale with the complexity of the animal’s nervous system.⁴⁵ However, it’s hard to square this idea with the evolutionary function of valenced experience. It’s unclear what fitness advantage the palest hint of a feeling could convey. Pain motivates animals to do things like avoid bodily damage; pleasure motivates animals to do things like reproduce. Subjective experiences so faint as to barely register would do a poor job motivating anything.

39 “It is not surprising that the task of recognizing pain in rodents is difficult, given their ecological niche as prey animals. A rat or mouse too obviously advertising any injury makes a tempting target for predators” ([Mogill 2009](#): 290). See also: “Farm animals are prey species which tend not to overtly express pain or weakness, making recognizing and evaluating pain incredibly difficult” ([McLennan 2018](#): 1).

40 It seems to me that the best way to hide a pain is not to feel it in the first place, which is perhaps a (weak) reason to prefer the latter hypothesis. Of course, there is a fitness limit to the usefulness of pain reduction. As noted above, humans incapable of pain perception do not usually survive to reproductive age.

41 Experimental evidence could help us choose between the hypotheses. Suppose the same putatively painful stimulus is applied to both a sheep and a wolf while the animals are restrained in an MRI scanner. Suppose the wolf howls in pain while the sheep is stoically silent. If the sheep brain lights up in just the way the wolf brain does, that’s plausible evidence the sheep feels but conceals the pain. More generally, we could look at the pain behavior of prey animals both in the presence and absence of their predators. If their reactions are similar in both situations, that’s evidence for the reduced pain sensitivity hypothesis.

42 “The animal must therefore have a ‘common (value) currency’ for consistently evaluating types of world and body states in spite of their inevitable variations and for preferring one type of state over another type according to its value, which is context dependent” ([Ginsburg & Jablonka 2019](#): 374).

43 For example, in a laboratory setting, hermit crabs will abandon their shells if they are subjected to a mild shock. Initially, such behavior was thought to be purely reflexive. However, recent experiments show the crabs are significantly less likely to abandon their shells after shock if the odor of a predator is present ([Magee & Elwood 2016](#)). The fact that the crabs remain in their shells when the odor of a predator is present suggests that the behavior is *not* reflexive. A natural explanation is that the crabs weigh the pain of the shock against the fear of a predator, thus incorporating different interests and demands into a unified utility function.

44 By ‘exclusively extraordinarily weak’ intensity ranges, I mean ranges in which the animal’s valenced experience only vacillates between extremely mild endpoints. The human equivalent of such a range might put the ‘pain’ of a gentle muscle spasm as the worst possible suffering and the ‘pleasure’ of eating unseasoned lentils as the best possible joy. By ‘exclusively extraordinarily strong’ intensity ranges, I mean ranges in which the animal’s valenced experience only ever occupies the extreme endpoints of the valence scale. (Such a range would be non-contiguous.) The human equivalent of such a range might be a lifetime in which valenced experience alternates between Jhana-like ultimate bliss and the pure torture of an intense cluster headache, with never a mild pleasure or pain in between. (As before, the range need not be symmetric. An animal only capable of extraordinary pain would still count as possessing an exclusively strong intensity range.)

45 In what follows I set aside the difficulty of measuring the relative complexity of nervous systems. In point of fact, I think the relative simplicity of insect nervous systems compared to mammalian nervous systems is often overstated.

One possible reply to this line of argument is to suggest that motivational requirements vary by taxa. Perhaps mammals require intense experiences in order to motivate actions, but insects only require weak experiences to motivate similar actions. The thought is plausible if you think that motivation depends on the relative strengths of one's experiences. If all an insect's experiences are faint, then competition for the insect's motivational resources will not be fierce. So long as the experiences are still ordered by intensity, the insect will be motivated to pursue pleasures at the top end of the scale more than pleasures at the bottom end of the scale and motivated to avoid pains at the top end of the scale more than pains at the bottom end of the scale.

Here, though, we tread on conceptually precarious ground. If one adopts a subject-relative account of intensity, then it follows that insects do *not* have characteristically less intense experiences than other animals. So the position must be that insects have objectively faint experiences but subject-relative motivational requirements. But it's unclear if that is a coherent position. There appears to be *some* sort of connection between motivation and intensity. It would be strange if there were an individual in extreme pain that, all else equal, were not motivated to escape the pain. Conversely, if an individual were extremely motivated to avoid mild pains, such an aversion would, all else equal, be regarded as pathological. The connection between intensity and motivation may not be conceptual, but if the evolutionary function of valenced experience is to motivate actions, it's plausible that intensity and motivation generally co-vary under normal circumstances. Anyone who claims that insects have extraordinarily faint experiences faces a dilemma: either deny that insects are motivated to act (which seems empirically false) or deny the connection between intensity and motivation. One who adopts the latter horn of the dilemma owes us an evolutionary story about how the connection between intensity and motivation was severed.⁴⁶

On the other hand, others have speculated that animals with simpler nervous systems have characteristically much more intense experiences than humans. For example in his blog post "[Is Brain Size Morally Relevant?](#)" Brian Tomasik explores the idea that "to a tiny brain, an experience activating just a few pain neurons

could feel like the worst thing in the world from its point of view." Insofar as this notion is plausible, it depends on two ideas: (1) that pain intensity depends, at least roughly, on the proportion of total "pain neurons" that are firing at a given time and (2) that small brains are more likely to have a total proportion of their pain neurons firing at once. As far as I can tell, there is little empirical evidence to support either (1) or (2).

Moreover, there may be theoretical reasons to regard this notion with suspicion. There appears to be a limit to how intense experiences can be before they lose the fitness advantage for which they were selected in the first place. In humans the conscious sensation of pain is distracting ([Chan et al. 2012](#)). Mild pain can be an annoyance, and intense pain can be so overwhelming that it effectively incapacitates the sufferer. (A similar story is probably true of pleasures.) If an animal's experiences were exclusively extremely strong, it seems the animal's decision-making would be impaired.

Learning

It seems that one of the most important evolutionary functions of valenced experience is to facilitate learning ([Damasio & Carvalho 2013](#): 145).⁴⁷ Behaviors which improve evolutionary fitness, such as mating, tend to have a positive valence, while behaviors which reduce evolutionary fitness, such as eating spoiled meat, tend to have a negative valence. When these valences are paired with the appropriate behaviors often enough, an animal learns to pursue fitness-boosting behaviors and avoid fitness-reducing behaviors. Lynne Sneddon and her collaborators argue that the "key function [of pain] appears to be that the aversive experience of pain creates a strong and lasting motivation that enables the animal to avoid getting into a similar situation in the future" ([Sneddon et al. 2014](#): 202).⁴⁸

Animals less likely to benefit from long-term learning may be less likely to benefit from valenced experiences. This idea has led some researchers to speculate that animals with a shorter lifespan are less sensitive to pain than animals with a longer lifespan ([Wal-](#)

⁴⁶ Alternatively, one could deny that the evolutionary function of valenced experience is to motivate action.

⁴⁷ "Given that body states are necessarily valenced — they are either good or bad from the point of view of homeostasis — feelings are powerful proxies of ongoing biological value and natural guides of adaptive behaviour. Feelings along a range that includes pain and pleasures at its extremes force the organism to attend to its current conditions. Feelings also facilitate learning of the circumstances surrounding a change in body state and the subsequent application of this knowledge to the prediction of future situations, resulting in an increase in behavioural flexibility" ([Damasio & Carvalho 2013](#): 145).

⁴⁸ Mere nociception is unlikely to be an efficient response to noxious stimuli in the long-term. Nociception is fast and reflexive, but it is not normally associated with a lasting memory. Conversely, conscious pain experiences, with their attendant felt badness, tend to leave a memorial imprint ([Bisaz, Travaglia, & Alberini 2014](#)). Because pain experiences are often stored in long-term memory, pain can induce long-term behavioral and motivational changes. For long-lived animals in complex environments, pain is potentially more effective at protecting the animal from damage than mere nociception. Again in the words of [Sneddon et al. 2014](#): "while nociception typically allows for an immediate reduction of tissue damage, pain typically allows for longer-term protection" (202).

ters 2018: 12).⁴⁹ The basic idea is that the reproduction-survival tradeoff will push some animals to occupy an evolutionary niche that favors traits that increase early reproductive success, even at the expense of traits that promote long-term survival (Stearns 2012: 4309).⁵⁰ One important function of painful experiences is to teach an animal which stimuli to avoid in order to promote long-term survival. Short-lived animals that won't be around long enough to benefit from such learning may be unlikely to invest in costly fine-grained nociceptive systems (Finlay 2019: 6).⁵¹ These animals would still benefit from a nociceptive system that alerted the animals to a threat of imminent death, but they would be less likely to benefit from a system that, say, induced an unpleasant sensation when the animals ate foods that were only slightly bad for them.

Similar reasoning may be applied to animals (again, like many insects) that produce large numbers of offspring that don't survive to adulthood and that change drastically between life stages. If most individuals in the larval or pupal stage are likely to benefit less from valenced experience than adult members of the species,⁵² then the intensity range of adults might be characteristically larger than the range for juveniles.⁵³ This consideration may be especially important for invertebrate species welfare prioritization. Some invertebrate species, such as mealworms and black soldier flies, are slaughtered before they reach adulthood; other species, such as crickets, are farmed to adulthood. However, recent research suggests (or perhaps merely assumes) that fruit fly larvae process noxious stimuli in the same way as adult flies (Lopez-Bellido et al. 2019).⁵⁴

Finally, the didactic role of valenced experience may make differences in [the subjective experience of time](#) relevant to differences in the intensity of valenced experience. Suppose it's the case that for some range of values, x seconds of valenced experience at intensity n is as effective a teaching tool as $2x$ seconds of valenced

experience at intensity $0.5n$. If animal A has a [rate of subjective experience](#) twice that as animal B, A could learn the same lesson as B in either half the time or at *half the intensity*.

Cognitive Sophistication and Intensity of Valenced Experience

There are two ways in which an animal's degree of cognitive sophistication could plausibly affect the intensity range of its valenced experiences. Certain types of cognitive sophistication may directly alter valenced states, amplifying or diminishing the intensity of certain pains and pleasures. Other types of cognitive sophistication may alter intensity range by unlocking new states that characteristically accompany certain pains and pleasures, the combination of which serves to reduce or magnify the overall intensity of the combined experiences. As we'll see below, the means by which an animal's level of cognitive sophistication affects its experiences do not all cut in the same direction. Some types of cognitive sophistication appear to increase intensity range, while other types of cognitive sophistication appear to decrease intensity range.

The primary reason for this tension is that—as I hope is independently plausible—cognitive sophistication is not a single, unidimensional characteristic. Instead, the thing we somewhat nebulously refer to as 'cognitive sophistication' is actually a loose, heterogeneous bundle of independent traits. These various traits affect the intensity of valenced experience in various ways. Thus, the claim that *cognitive sophistication* affects the intensity of valenced experience, while true, is conceptually too simple for our purposes. We need a more fine-grained analysis that recognizes the different ways that different elements of cognitive sophistication are apt to influence the intensity of valenced experience.⁵⁵

49 "It would not be surprising for adults of short-lived species like most insects to maximize reproductive activities at the expense of behavior (such as nociceptive sensitization) that promotes survival of the adult but diverts energy and time away from mating and reproduction" (Walters 2018: 12).

50 An alternative hypothesis is that the pleasure of reproduction is much higher for animals with shorter lifespans. If that were the case then, all else equal, animals with shorter lifespans would have larger intensity ranges than animals with longer lifespans. Some combination of the hypotheses (increased pleasure sensitivity and decreased pain sensitivity) may also be true, with the possible result an asymmetric skewing of the range toward positive states but no overall lifespan-dependent difference in range size. Empirical experiments may be able to distinguish increased pleasure sensitivity from decreased pain sensitivity.

51 "Moreover, we know very little about how species might differ in pain and illness calculations. For example, long-lived species might be considerably more conservative in risk, and willing to invest more energy in long-term maintenance, which could have relevance for pain sensitivity, but to my knowledge, there is no real literature in this subject" (Finlay 2019: 6).

52 This might occur if juvenile survival is largely a matter of luck, but adult reproductive success is not.

53 This includes the possibility that for species in which juvenile survival is raw luck, the capacity to experience valenced states at all in pre-adult stages might be selected against.

54 See also: "examination of larvae of *Drosophila* and *Manduca* has revealed specialized nociceptors that cover the entire body wall, and these larvae show strong, relatively long-lasting (hours or days) nociceptive sensitization of defensive behaviors evoked by mechanical or heat stimulation" (Walters 2018: 12).

55 To put these insights into practice, we need an equally fine-grained empirical taxonomy of the ways in which animals of interest differ with respect to the different dimensions of cognitive sophistication.

A further complication is that different elements of cognitive sophistication may affect different types of valenced experience in different ways. This multitude of relationships between different elements of cognitive sophistication and different types of valenced experience makes for a complicated web of effects (Yeates 2012: 33).⁵⁶ Great care must be taken to untangle this web. We should thus be wary of claims that report a clear and general relationship between the intensity of valenced experience and cognitive sophistication.⁵⁷

Mental Time Travel

The capacity to remember past events and imagine future events may influence the intensity of valenced experiences. Psychologists call this ability *mental time travel*. Evidence of mental time travel is currently limited to birds and mammals (Cheke & Clayton 2010), though any attribution of the ability to nonhuman animals is at least somewhat controversial.⁵⁸ Like many of the other cognitive traits discussed in this section, mental time travel seems to reduce the intensity of experiences in some circumstances and amplify the intensity of experiences in other circumstances. It is thus unclear whether animals that possess this ability have characteristically more or less intense valenced experiences overall.

For animals experiencing acute pain with a fixed endpoint, mental time travel may reduce the intensity of pain. Sahar Akhtar writes, “Greater time horizons in either direction might lessen the intensity of one’s pain: being able to think about the past can allow us to recollect and take comfort in painless past experiences. Similarly, by thinking about future periods we may be able to take relief in the thought of future periods without pain and we are ca-

pable of recognizing that the pain will end. An animal may not be able to remember times without pain or imagine future periods without the pain” (Akhtar 2011: 507). In addition to remembering pain-free moments in the past, if the current painful experience is of a type that an animal has undergone in the past, reflecting on that past painful experience may diminish the intensity of the current experience. In humans, familiarity with a pain reduces the intensity of the pain (Reichert et al. 2017: 544),⁵⁹ and it’s plausible that nonhuman animals with sufficient memorial skills experience a similar reduction in intensity. Animals unable to become familiar with a repeated painful stimulus may experience the pain at its peak intensity every time. Akhtar concludes that animals “that have a limited temporal sense would seem to be unable to escape, or get outside of, their present mental state, including a present painful state” (Akhtar 2011: 507).⁶⁰

On the other hand, the ability to recall past suffering and anticipate future suffering adds an additional dimension to experience. Some authors have thus argued that mental time travel increases rather than decreases the intensity range of valenced experience. Huub Brouwer and Willem van der Deijl write, “Also, while animals, especially lower animals [sic] such as mice and rattlesnakes, may not be capable of experiencing as high levels of wellbeing as humans, they might also not have the capacity to suffer as much as humans can. One reason to think that this is so, is that humans can remember past suffering and anticipate future suffering to a much greater extent than, for instance, mice and rattlesnakes can” (Brouwer & van der Deijl 2020: 353). In humans the anticipation of certain (especially psychological) stressors can induce anxiety-driven hyperalgesia (enhanced pain sensitivity) (Reichert et al. 2017: 551).⁶¹ James Yeates summarizes

56 “Based on this conceptual analysis and review of empirical evidence, there are reasons to consider that the capacity to experience pain may be increased or decreased by increased cognitive capacities. Cognition appears to increase pain in some cases but decrease it in others, and the multiple relationships cannot be generalised into a single overall statement that different animals experience more or less pain per se as an overall net effect (which fits with our popular belief that less intelligent humans do not thereby experience less pain)” (Yeates 2012: 33).

57 For instance, in humans, childhood intelligence is negatively correlated with chronic widespread pain (CWP) in middle age (Gale et al. 2012). (That is, more intelligent children are less likely to develop CWP as adults.) This correlation is explained in part (but only in part) by the negative correlation between intelligence and body-mass index and socioeconomic status, two risk factors for CWP. The authors speculate that “people with lower intelligence may be less able to apply appropriate coping strategies when faced with pain, increasing the likelihood that it becomes chronic” (2342). I don’t think we should read too much into or try to generalize from this example.

58 Part of the problem is that there is disagreement about the definition of mental time travel. The ability probably comes in degrees, and it’s unclear if rudimentary displays of memory or future planning constitutes possession of the ability.

59 “the anticipation of an aversive event is supposed to cause heightened pain perception (Tracey and Mantyh, 2007). The predictability of the aversive event seems to be a crucial factor, as it was shown that the more unpredictable an upcoming aversive event the greater its pain augmenting effect (Ploghaus et al., 2003). In contrast, negative emotions can also result in a decrease of pain. This seemingly paradox effect was first established in animal research, showing that high levels of stress lead to so-called stress-induced analgesia (Butler and Finn, 2009). In human studies, decreased pain sensitivity was observed when participants were anticipating an aversive electrical shock, which they had experienced before (predictable threat). However, participants reported more pain when they were expecting an electrical shock they had never experienced before (unpredictable threat) (Rhudy and Meagher, 2000)” (Reichert et al. 2017: 544).

60 It is an open question whether similar considerations apply to pleasures, but there is no obvious reason why they should not.

61 “Over the past decades, it has become increasingly clear that the nature, duration and intensity of the stressor are key determinants of the effects of stress and threat on pain. While exposure to an acute, robust, intense stressor seems to induce a reduction in pain responding, a phenomenon described as stress-in-

the dual nature of mental time travel thusly: “The ability to temporally locate pain allows animals to know *when* pain will begin or end and *that* pain will begin, end or continue. The latter knowledge may help animals to cope, and higher animals that are able to anticipate pain’s end may therefore find pain experiences less unpleasant. Conversely, higher animals’ knowledge that pain is likely to continue may exacerbate their negative feelings” (Yeates 2012: 28).

Whether mental time travel increases or decreases the intensity of experience may depend on how fully developed the ability is in a given animal. Akhtar speculates that “beings with only a basic or rudimentary sense of time and of self may be at the greatest disadvantage from pain. They may possess enough self- and time-awareness to suffer from the anticipation and memory of pain, but not enough to be able to discount pain, choose to refrain from focusing on pain, form expectations about the cessation of pain, or to consider other interests or times without pain” (Akhtar 2011: 510). It’s unclear which animals fall into this category, but it plausibly encompasses many bird and nonhuman mammal species.

Rationalization and Normative Reasoning

The ability to rationalize valenced experiences may reduce their intensity. When one understands that the pain one endures is suffered for good cause (the fatigue of exercise or the prick of a flu shot, say), it’s plausible that the overall experience is less intense than comparable stimuli endured for no good cause. Rationalization may reduce the overall intensity of negative experience by removing other negative states. A dog receiving a parvovirus vaccination might feel alarm and betrayal that their best friend would subject them to such discomfort, whereas a human undergoing a similar procedure might only feel the physical pain of the shot. Alternatively (and non-exclusively), rationalization might reduce the overall intensity of negative experiences by introducing positively valenced states that counteract the negative state. Although a human might dislike the nature of a painful medical procedure, she might find solace in the fact that the procedure improves her health. Donald Broom argues that “more sophisti-

duced analgesia (Butler and Finn, 2009), exposure to repeated physical or psychological stressors, which may be more anticipatory and thus anxiogenic in nature, typically results in the phenomenon of stress-induced hyperalgesia in humans (Kuehl et al., 2010; Gibbons et al., 2012; Crettaz et al., 2013)” (Reicherts et al. 2017: 551).

62 On the other hand he also notes, “For some sentient animals, pain can be especially disturbing on some occasions because the individual concerned uses its sophisticated brain to appreciate that such pain indicates a major risk. [...] Therefore, in some circumstances, humans who experience a particular pain might suffer more than fish, whilst in other circumstances a certain degree of pain may cause worse welfare in fish than in humans” (Broom 2007: 103).

63 “Overall, although causality cannot be established from these data, we propose that beliefs about blame and loss in judging injustice may promote suffering or block adjustment to pain, whereas justice beliefs, in the form of the belief in a just world, may act as a personal resource that supports coping attempts in some circumstances of pain” (McParland & Eccleston 2013: 485).

64 It’s unclear if this ability also increases *possible* intensity range.

cated brain processing will also provide better opportunities for coping with some problems. For example, humans may have means of dealing with pain that fish do not, and may suffer less from pain because they are able to rationalise that it will not last for long” (Broom 2007: 103).⁶² Sahar Akhtar adds, “Without the belief that there are good reasons to endure their pain—even if there are good reasons, such as a painful but necessary veterinary procedure—animal pain would likely be more intense” (Akhtar 2011: 506).

On the other hand, the ability to recognize good reasons for an experience is probably a manifestation of a more general capacity to reason normatively about the world. In some circumstances, this capacity appears to increase rather than diminish the intensity of experience. For instance, witnessing or undergoing an event that one recognizes as unjust adds a moral dimension to the experience, and adding a moral dimension to an experience plausibly amplifies the intensity of the experience. Recent research suggests that pains perceived to be unjust or unfair are judged to be more severe (McParland & Eccleston 2013: 485),⁶³ though a causal explanation of the correlation has yet to be established. Still, it’s plausible that pains and pleasures perceived to be undeserved might feel worse, all things considered, than comparably evoked pains and pleasures without a normative component. Pains and pleasures perceived to be deserved might feel better, all things considered, than comparably evoked pains and pleasures without a normative component. If that is true, then, all else equal, creatures capable of forming normative judgments will possess a wider characteristic⁶⁴ intensity range than creatures incapable of forming such judgments.

It’s unclear whether nonhuman animals are capable of normative reasoning. For recent discussion of the question see Clement 2013, Johannsen 2019, and Andrews 2020.

Attention and Focus

The ability to consciously direct one's attention and focus may affect the intensity of valenced experience. Because valenced experiences evolved to make fitness-relevant information salient, they tend to grab our attention ([Bjekić et al. 2018](#): 587).⁶⁵ Many animals seem to lack the ability to deliberately redirect their attention and focus away from valenced experiences, and this inability may increase the intensity of the experiences. James Yeates speculates that “animals more able to divide attention would experience pain of lower intensity (because the attention is divided)” ([Yeates 2012](#): 29). Sahar Akhtar concurs, writing, “The facts, if they are facts, that many animals do not have many substitutes for focusing on their pain and cannot will themselves to focus on other things, cannot form expectations about the ending of pain, think about other times without pain, or consider more complex interests for which pain may be a necessary means, provide us with reasons for thinking that the overall pain experience caused by a given measure of pain might sometimes be worse for animals than it is for us” ([Akhtar 2011](#): 509).

Although Yeates and Akhtar appear to base their reasoning on *a priori* considerations, there is at least modest empirical evidence to support their position. Cognitive inhibition is the ability to disregard stimuli that are irrelevant to the task at hand. Recent research suggests that, in humans, “a higher level of cognitive inhibition is associated with lower experimental pain sensitivity” ([Bjekić et al. 2018](#): 580). Hence, it appears that humans that are better able to consciously redirect their focus also suffer characteristically less intense pains.⁶⁶

The extent to which nonhuman animals can consciously control their attention is unclear. Nonhuman primates are generally thought to be able to redirect their focus non-reflexively ([Scerif, Gomez, & Byrne 2004](#)), and recent research suggests rodents may also possess this ability ([Matzel, Wass, & Kolata 2011](#); [Lustig et al. 2013](#)). It appears this ability has not been widely studied in other nonhuman animals.

65 “Perception of pain is fast and uncontrolled—it interrupts attention and behavior and urges one to act” ([Bjekić et al. 2018](#): 587).

66 One might worry about the causal direction of this relationship. If less intense pains are less distracting, then those that experience less intense pains (for other reasons) will also be better able to ignore them. There are two responses to this worry. First, cognitive inhibition is not a measure of one's ability to ignore pains but a more general measure of one's ability to suppress prepotent responses to make task-relevant decisions. Second, evidence from brain-imaging studies suggest that the same brain region that suppresses irrelevant information during cognitive inhibition tasks is also more active in subjects that report less intense pain ([Bjekić et al. 2018](#): 587).

67 This variation can occur even among closely related species. For example, Katja Hoedjes and her collaborators write, “Recent research unveiled remarkable natural variation in learning rate and in the dynamics of memory formation between closely related parasitoid wasp species” ([Hoedjes et al. 2010](#): 889).

Learning Ability

As noted above, one of the main evolutionary functions of valenced experience is to facilitate the learning of fitness-improving behaviors. Pain teaches animals which stimuli are noxious, how to avoid those stimuli, and what to do to recover from injury. Pleasure teaches animals which foods are healthy and which activities increase the likelihood of gene propagation. Because extremely intense experiences are often distracting, animals that undergo characteristically extremely intense experiences appear to be at a selective disadvantage compared to conspecifics with less intense experiences. Thus, we might expect evolution to select for animals with experiences just intense enough (in general) to play the primary instructive role of pleasure and pain.

Animals differ with respect to the ease with which they are able to learn new information. In controlled settings, some species can be taught a new behavior in fewer trials than other species.⁶⁷ (The potential complexity of learned behavior also varies by species.) Some types of animals appear better equipped to pick up patterns in signals only weakly conveyed. In general, less cognitively sophisticated animals probably require stronger signals for pattern-learning. If valenced experience is the signal, then we might reasonably expect the intensity of valenced experience to correlate inversely with learning ability. That is, all else equal, the better an animal is at learning, the less intense its valenced experiences might normally be.

This line of reasoning is, however, entirely speculative. It's possible learning depends more on the statistical regularity of the pattern than the strength of the stimulus during trials, in which case we should not expect a relationship between learning ability and the intensity of valenced experience.

Self-Awareness

Self-awareness may influence the intensity of valenced experience. However, like many of the features described above, the direction of this influence is unclear. Some authors emphasize the ways self-awareness may unlock new states that increase intensity range. For instance, Gregory Berns writes, “An animal who is

aware of his or her own pain and suffering may well experience the existential fear associated with imminent death” (Berns 2017: 245). If self-awareness is a necessary condition on existential fear, and existential fear is one of the worst possible experiences, then, all else equal, it seems self-awareness extends both an animal’s possible intensity range of experience and, if existential fear is common enough, an animal’s characteristic intensity range. However, other authors have suggested that the *lack* of self-awareness increases the intensity of valenced experience. Sarah Akhtar argues that “the absence of self- and time-awareness may mean that the feeling of pain for animals is much worse in certain respects than has previously been thought. The absence of awareness may mean that in some cases pain is worse for animals than a comparable measure of pain for us” (Akhtar 2011: 499). Akhtar’s argument for this claim proceeds by way of mental time travel, for which she takes self-awareness to be a necessary condition. She writes, “Animals without an awareness of self and time would not be able to anticipate the cessation of the pain or take relief in the thought that it may or will end” (Akhtar 2011: 507).

Of course, what exactly constitutes self-awareness is also contentious. There is a philosophical tradition dating back at least to Kant that claims sophisticated language ability is the only hallmark of true self-awareness. More recently, empirical evidence has suggested that many nonhuman mammals, such as mice, appear to be self-aware (Wada et al. 2016). There is even controversial evidence for self-awareness in cleaner wrasse, a species of bony fish (Khoda et al. 2019). If metacognition is a type of self-awareness, then self-awareness is probably even more widespread. There is evidence of uncertainty monitoring, a type of metacognition, in bees (Perry & Barron 2013) and ants (Czaczkes & Heinze 2015).⁶⁸

Doxastic Capacity

A creature’s doxastic capacity refers to its ability to adopt doxastic attitudes (canonically: belief, disbelief, and suspension of judgment⁶⁹) toward various propositions. Some animals have a wide range of beliefs concerning a large variety of topics. Other animals have a limited set of beliefs concerning a narrow range of topics.

68 See Beran et al. 2010 for a (now somewhat dated) review of metacognition in nonhuman animals.

69 Credences are also a type of doxastic attitude.

70 Peter Singer has argued that cognitive capacities affect the characteristic intensity range of experience on similar grounds. For example, he writes, “There are many areas in which the superior mental powers of normal adult humans make a difference: anticipation, more detailed memory, greater knowledge of what is happening and so on. These differences explain why a human dying from cancer is likely to suffer more than a mouse” (Singer 2011: 52).

71 In experiencing sampling studies, subjects are generally prompted to record their current thoughts, feelings, or behaviors multiple times over the course of a day for several days. See Scollon, Prieto, & Diener 2009 for advantages and disadvantages of this method.

An ability to form beliefs about one’s valenced experiences may influence the intensity of those experiences. James Yeates writes, “Insofar as pain is ‘information,’ an animal’s doxastic reasoning abilities can affect how it processes painful stimuli. Higher animals may entertain beliefs about a pain’s cause, duration, permanence and the animal’s ability to control it” (Yeates 2012: 32).

This ability, however, may cut both ways. Knowing that a pain to come will be fleeting plausibly reduces the intensity of the pain. Animals that are unable to form such beliefs may suffer more from comparable stimuli. (Compare a routine medical procedure for humans with a routine veterinary procedure for dogs.) On the other hand, knowing that, say, a migraine could strike at any moment induces a dread that would be absent if one were unable to entertain beliefs about future pain states.⁷⁰ Yeates summarizes the relationship thusly: “Higher doxastic capacities may be beneficial for animals who experience predictable, controllable and impermanent pain, whereas animals experiencing pain that appears unpredictable, uncontrollable and permanent may suffer more from knowing this” (Yeates 2012: 33).

Affective Complexity and Intensity of Valenced Experience

Affective complexity is a measure of the potential diversity and depth of emotional states that an animal can experience. In humans, emotional states are a pervasive and universal component of experience. In experience-sampling studies,⁷¹ humans report the presence of some emotion virtually every waking moment, and these emotions almost always have a valence (Lucas & Diener 2008: 471-472). It’s plausible that affective complexity is, in general, positively correlated with intensity range of valenced experience. That is, species that experience a greater variety and/or greater complexity of emotional states are, all else equal, capable of more intense positive and negative experiences.

There are two ways in which affective complexity might increase the possible intensity range of valenced experience. Different degrees of affective complexity might unlock qualitatively different kinds of pleasures and pains that are emotional rather than physical in nature. If these emotional states can be more intense than

mere physical states,⁷² then adding them to an animal's valence repertoire increases the possible intensity range. Even if the emotional states by themselves are not more intense than mere physical states, they might combine with physical states to produce valences that are overall more intense than emotional or physical states alone.⁷³

Combination may take different forms. Distinct valence types may be roughly additive, such that the combination of a physical pain and an emotional pain generates greater overall suffering than the physical or emotional pain alone. Alternatively (but not exclusively), the different valence types may interact in some way, with emotional states amplifying or reducing the intensity of physical states. There is a rich literature documenting the effect of emotional states on physical pain in humans. Summarizing this literature, Philipp Reicherts and his collaborators write, "Emotions have tremendous influence on the perception of pain. In general, pain is diminished by positive while it is increased by negative emotions" (Reicherts et al. 2017: 544). Unfortunately, the literature on emotional states in nonhuman animals is much sparser. Elodie Briefer explains, "Because the emotions of non-human animals have long been considered as unobservable processes that could not be objectively studied, scientific interest in this topic is relatively recent" (Briefer 2018: 1).

Even if affective complexity doesn't affect an animal's *possible* intensity range, it still may affect an animal's *characteristic* intensity range in important ways. There may be some physical pains and pleasures that are so intense they effectively crowd out all other feelings, such that layering an emotional state on top of the physical state doesn't alter the overall valence.⁷⁴ Nonetheless, if such physical states are rare, and if emotional states often exacerbate the intensity of common experiences, then animals with greater affective complexity will tend to experience a greater intensity

range in their everyday lives.

Notably, some of the differences in affective complexity are plausibly the result of differences in *social* complexity. As such, the question of how affective complexity affects the intensity of valenced experience is inextricably connected to the question of how differences in sociality affect the intensity of valenced experience.

Fear and Anxiety

Although basically all animals react to perceived danger, it appears only some animals are capable of conscious fear and anxiety. Genuine⁷⁵ fear and anxiety may be among the worst emotional states an animal can experience. The negative effects of fear and anxiety on human welfare are well-documented.⁷⁶ The experience of fear is associated with certain physiological and behavioral responses. Behavioral markings of fear include fleeing, hiding, freezing, and suspending unnecessary bodily functions. Physiological reactions to fear can include elevated heart rate, hyperventilation, increased muscle tension, constriction of blood vessels, nausea, and dizziness. Insofar as other animals display relevantly similar physiological and/or behavioral responses, that is evidence that they too experience conscious fear.⁷⁷

Anxiety is related to but distinct from fear. Anxiety is sometimes said to be the result of danger that is perceived to be unavoidable (Öhman 2008) or situations in which the threat is ambiguous or unknown (Belzung & Philippot 2007). Anxiety is often considered a secondary emotion, that is, an emotion in response to another emotion. For example, in humans, generalized fear often leads to anxiety. Physiological and behavioral signs of anxiety include elevated heart rate, rapid breathing, increased perspiration, increased motor tension, changes in sleeping patterns, and/or

72 At least some authors appear to endorse this claim, e.g., "The most intense affective experiences humans ever have are during emotional episodes. All other mammals exhibit similar types of emotional arousals" (Panksepp 2011a: 1). (Note that Panksepp is using the term 'affective' the way I use the term 'valenced'.)

73 For instance, in humans, the combination of physical and emotional pain plausibly generates the possibility of greater overall suffering than physical pain alone. Conversely, the combination of physical and emotional intimacy plausibly generates the possibility (whether typically realized or not) of greater overall pleasure than physical intimacy alone.

74 Or, it could be that emotional additions to intense experiences continue to be additive but that the additions continually diminish as the extremes are reached such that there's an asymptotic curve created by the impact of emotions on physical suffering. If this were the case, then even if affective complexity in fact extended the possible range of intensity it could be a rather trivial extension to the range of experiences.

75 There is a large literature in the philosophy of art that seeks to explain why, if fear is such a negative emotion, many people actively seek out seemingly fear-inducing fiction (e.g., scary movies, haunted houses). (This issue is normally discussed under the more general term *the paradox of tragedy*.) Although the details are complicated, the most plausible response, in my view, is that what people seek out in fiction, while closely related to fear, is not actually *genuine* fear.

76 Chronic fear and anxiety often lead to depression and significantly increase the risk of suicide. See the American Psychiatric Association's *Diagnostic and Statistical Manual of Mental Disorders* (DSM-5) for more details.

77 For discussion of the negative effects of predation fear on feeding, breeding, and cognition across vertebrates, as well as a discussion of the ecosystem-level importance of predation fear, see Ogden 2016.

changes in food intake.⁷⁸ In addition to physiological and behavioral reactions, anxiety is also associated with certain cognitive changes. For example, anxiety increases general apprehension and is correlated with pessimistic cognitive biases ([Anderson and Adolphs 2014](#)). Anxiety tends to amplify physical pain in both humans and (at least some) nonhuman animals ([Rhudy & Meagher 2000](#)).

It's plausible that many nonhuman animals also experience these effects. There is evidence that exposure to fear- or anxiety-producing stimuli reduces the lifespan of domestic dogs ([Dreschel 2010](#)). Other researchers have argued, on empirical grounds, that predator-induced fear commonly causes post-traumatic stress disorder-like symptoms in wild mammals and birds and perhaps other animals ([Zanette et al. 2019](#)).

Two worries are worth noting with respect to the detection of fear and anxiety in nonhuman animals. The first is that applying emotional terms to nonhuman animals, especially phylogenetically distant animals, may result in problematic anthropomorphizing. Both crayfish ([Fossat et al. 2014](#)) and honeybees ([Bateson et al. 2011](#)) exhibit many of the behaviors associated with human fear and anxiety, but, because those terms come loaded with anthropocentric connotations, applying those terms to those animals may inevitably be misleading.

The other worry runs in the opposite direction. Because the lifestyle and environment of some animals is so alien to us, we should not expect negative emotional states to be expressed in precisely the same manner. William Gibson and his collaborators remind us that “distantly related species may express emotion states through behaviors that have no obvious homology to human behaviors” ([Gibson et al. 2015](#): 1401). They advocate for an “alternative approach to identifying instances of emotional expression, which does not depend on anthropocentric homologies” by establishing “general features of emotion states, or ‘emotion primitives,’ which apply both to different emotions in a species and to

emotions across phylogeny. One can then search for behaviors that exhibit evidence of such emotion primitives in model organisms” (*ibid.*).⁷⁹

Depression

All else equal, animals that are capable of becoming depressed may generally possess wider intensity ranges than animals that are not capable of becoming depressed. In humans, severe depression appears to be one of the very worst valenced states. One 2011 study reported that, on average, subjects with severe depression lost about 80% of their wellbeing, nearly twice the wellbeing loss associated with extreme pain/discomfort ([Graham, Higuera, & Lora 2011](#)).⁸⁰ A 2012 study found similar results: severe depression had a bigger effect on life satisfaction and day affect than extreme pain/discomfort ([Dolan & Metcalfe 2012](#)).⁸¹ A 2013 study found that depression had a bigger impact on the self-reported frequency of happy states than physical pain did ([Mukuria & Brazier 2013](#)). And in the United States, among individuals who die by suicide, mental health problems are about twice as common as physical health problems ([Karch, Logan, & Patel 2011](#)).⁸² If nonhuman animals experience depression in a similar way, it appears plausible that the ability to experience severe depression extends a creature's intensity range in many circumstances.

Components of depression include sadness, anhedonia, and learned helplessness. Each of these components has been detected in nonhuman animals.

Monkeys, elephants, whales, bears, buffalo, cats, dogs, rabbits, goats, and horses display behavior reminiscent of sadness ([King 2013](#)). In fact, the capacity for sadness appears to be adaptive. In humans, sadness increases the accuracy of some types of memory and generally improves decision-making and problem-solving ([Bonanno, Goorin, & Coifman 2008](#): 799).⁸³ In social mammals, including humans, displays of sadness also tend to invoke offers of assistance from others (*ibid.*).⁸⁴ When sadness slides into

78 There are many different types of anxiety (e.g., acute versus chronic) and different types of anxiety produce different symptoms.

79 The authors add that “such emotion primitives may include the following features or dimensions: persistence following stimulus cessation, scalability (a graded nature of the response), valence, generalization to different contexts, and stimulus degeneracy (different stimuli can evoke the same behavior by induction of a common emotion state).” According to the authors, many of these emotion primitives have been identified in fruit flies.

80 Note, however, that the error bars for many conditions, including severe depression and extreme pain, are quite wide.

81 Note, however, that the sample size of this study was relatively small.

82 Of course, if mental health problems are more common in general than physical problems, then this statistic may merely reflect the differing frequencies of the conditions. The percentage of people with intense mental/physical health problems who kill themselves would be a more relevant figure. In any event, note that depression may involve catastrophizing and hopelessness that make suicide look more attractive, even if the degree of suffering isn't as intense as extreme pain.

83 “An extensive body of experimental data has associated sadness with more detail-oriented information processing, more accurate performance appraisals, and less overall reliance on heuristics and stereotyping for decision making” ([Bonanno, Goorin, & Coifman 2008](#): 799).

84 “From a social-functional perspective, expressions of emotion in mammals are evolutionary adaptations to social environments related to the creation

depression, however, these benefits dissipate. The decrease in motivation wipes out the cognitive gains, and prolonged depression tends to hurt relationships, reducing assistance from others (Bonanno, Goorin, & Coifman 2008: 800-801). Thus, whereas sadness appears to play an evolutionarily useful role, depression looks to be maladaptive.

Anhedonia is a loss of interest in activities previously found to be rewarding (Willner, Muscat, & Pap 1992). In nonhuman animals, external symptoms of anhedonia may include “behavioral deficits consistent with a loss of responsiveness to reward, such as decreased sucrose consumption, decreased ability to associate rewards with a distinctive environment, and decreased sensitivity to rewarding electrical brain stimulation” (Moreau 2002: 351). Anhedonia-like behavior can be induced in fruit flies by exposing them to aversive, uncontrollable vibrations over several days. The shaken flies show reductions in various voluntary behaviors, although reflexive behavior remains unchanged. In particular, shaken flies consume much less glycerol (commonly used as a reward in fruit fly studies) than non-shaken controls, suggesting that the shaken flies have lost their taste for sweets (Ries et al. 2017).

Learned helplessness is a condition in which a human or non-human animal adopts an overly passive reaction profile that disrupts important voluntary behavior.⁸⁵ A creature in the throes of learned helplessness will often neglect basic survival needs, ignoring food, water, predators, and potential mates. Learned helplessness is triggered by repeated, uncontrollable exposure to traumatic stimuli, and it can be reliably reproduced in a number of nonhuman animals. For example, if dogs are subjected to repetitive and unavoidable electric shocks, the dogs will eventually stop trying to evade the shocks, sitting passive and still even if later explicitly given the opportunity to escape (Seligman 1968).⁸⁶

Given the prevalence of these symptoms, many nonhuman animals, [including fish](#), are used as models for depression research.

Friendship, Love, Social Buffering, and Social Isolation

Different sorts of animals exhibit different types and different degrees of sociality.⁸⁷ These differences may unlock qualitatively different emotional states that extend an animal’s intensity range. Many of the putatively most positive types of human experiences involve a loving relationship (with love liberally defined to include Platonic (friendship) love, familial love, and romantic love). In humans, the number and quality of interpersonal relationships are among the greatest determinants of self-reported happiness (Bruni 2010). Thus, the ability to engage in loving relationships plausibly extends a creature’s intensity range in many circumstances.

Many mammalian species appear to have the capacity for something like maternal love and non-familial friendship. Analogues of romantic love, however, appear to be much rarer in mammals (though perhaps common in birds).⁸⁸

According to one review, “[m]other-infant bonding is a characteristic of virtually all mammals” (Numan & Young 2016: 98). Numerous behavioral, hormonal, and neural similarities have been observed between human and non-human mammalian mothers. Lactation and its associated behavioral suite is common to most mammals, including humans. Mammalian mothers protect their young from adverse weather, predators, and

and maintenance of social relationships and the organization of interindividual interactions (Darwin, 1872/1998; Keltner & Kring, 1998). Facial displays of emotion evoke and shape the responses of others by inducing specific emotional responses and reinforcing or discouraging social behaviors (Keltner & Kring, 1998). The facial expression of sadness is thought to support group social behavior by evoking sympathy and helping responses in others” (Bonanno, Goorin, & Coifman 2008: 799).

85 Learned helplessness was first described in dogs. The classic study on learned helplessness is [Overmier & Seligman 1967](#).

86 Although it may appear that learned helplessness is a relatively sophisticated cognitive condition, the basic characteristics of learned helplessness have allegedly been demonstrated in an isolated ganglion of a decapitated insect. A single cockroach leg connected to its isolated thoracic ganglion can be operantly trained to remain lifted. However, if the leg-ganglion system is subjected to uncontrollable electric shocks before the conditioning, acquisition takes much longer. Summarizing this research, as well as similar research on the severed spines of rats, Eisenstein et al. 1997 reports, “The brain is evidently not essential either in mammals or in invertebrates for demonstrating [learned helplessness]” ([Eisenstein, Carlson, & Harris 1997](#): 265).

87 See [Weiss et al. 2019](#) for a method to quantify sociality across species.

88 Most mammalian species mate in a polygamous manner and do not cultivate social relationships with their mates. Pair-bonding—perhaps a rough proxy of, or evolutionary prerequisite for, romantic love—is uncommon in mammals: only about 5% of mammalian species engage in pair-bonding between mating partners ([Numan & Young 2016](#)). In contrast, about 90% of bird species engage in pair-bonding between mating partners ([Young 2003](#)), and many species mate guard with frequent copulation.

threatening conspecifics ([Lonstein, Lévy, & Fleming 2015](#): 157).⁸⁹ The facilitation of this behavior is accomplished by similar hormonal agents and a similar neural reward mechanism ([Lonstein, Lévy, & Fleming 2015](#): 177).⁹⁰

While less common than maternal bonding, relationships akin to friendship may exist among some nonhuman animals. Group-living animals display their preference for social contact in a number of ways. Bull calves actively seek out companion animals ([Mounier et al. 2006](#)). Young chicks increase their peeping calls when isolated ([Sufka & Hughes 1991](#)). In many group-living species (especially but not exclusively primates⁹¹), individuals affiliate with some conspecifics more than others, and these affiliation preferences cannot be explained by kin relations or social hierarchies alone ([Massen, Sterck, & de Vos 2010](#)). Affiliation preferences appear to promote cooperation, health, and reproductive success ([Massen, Sterck, & de Vos 2010](#): 1386-1390).

Social buffering is the phenomenon by which animals recover better from aversive events in the presence of conspecifics. Social buffering has been documented in many mammals, as well as chickens ([Edgar et al. 2015](#)) and zebrafish ([Faustino, Tacão-Monteiro, & Oliveira 2017](#)). One review describes social buffering in rats and mice [citations omitted]: “Rodents have demonstrated surprising responsiveness to conspecifics’ needs. Mice orient to a littermate’s pain and synchronize pain behaviour [...] Female mice provide social analgesia to another in pain, choosing to spend time close to a ‘jailed’ mouse in pain at one end of the apparatus

rather than to another ‘jailed’ mouse without pain at the other end, with the effect of reducing pain behaviour in the former. [...] Rats show emotional contagion and will work to terminate

another’s distress [...] These findings are intriguing, because they occur between adults, in rodent species with different social structures and behaviours, and imply social analgesia from the unaffected individual’s voluntarily staying close to the individual in pain” ([Williams 2019](#): 4-5). Social buffering thus tends to reduce the intensity of negatively valenced experiences (perhaps by ‘diluting’ the intensity across individuals). But being a social animal raises the possibility of intense suffering due to social isolation.

In addition to the positive emotions associated with maternal love and friendship, the capacity for these relationships also raises the specter of extremely negative states when access to such relationships is denied. The adverse effects of social deprivation in group-living vertebrates is well documented. When raised in isolation, such animals are less able to appropriately process social and environmental stimuli. For example, rat pups reared in isolation exhibit a wide range of long-term behavioral and physiological abnormalities, including “neophobia [fear of new things], impaired sensorimotor gating, aggression, cognitive rigidity, reduced prefrontal cortical volume and decreased cortical and hippocampal synaptic plasticity” ([Fone & Porkess 2008](#): 1087). In humans, social isolation is about as deadly as smoking ([Pantell et al. 2013](#)). According to some researchers, social exclusion is literally painful ([MacDonald & Leary 2005](#)).⁹²

89 “Mothering of offspring is a distinctive feature of the life of many adult female mammals. Although some form of maternal caregiving behavior is displayed in many vertebrates and even invertebrate taxa (Rosenblatt & Snowdon, 1996), only in mammals is mothering so rich in its behavioral complexity and protracted in its length. For example, only in mammals do we see lactation and the behavioral systems that permit transmission of milk from mother to offspring. Furthermore, when the offspring are born in litters, these feeding behaviors necessarily involve the mothers transporting young and gathering them together in a huddle before nursing can ensue. Even if there are only a few offspring or singletons, mothers must still adjust their bodies or the position of the young to facilitate attachment to teats and suckling. In all cases, mammalian mothers must also ensure that the young are protected from the elements, kept warm, and securely away from predators or threatening conspecifics. Behaviors that accomplish these functions are seen in most mammalian mothers, including humans” ([Lonstein, Lévy, & Fleming 2015](#): 157).

90 “Numerous other features are shared between non-human and human mothers. In order to parent effectively, all mothers must develop an attraction to the young and be motivated to expend considerable resources and withstand substantial challenge to care for and protect them. This motivation is first promoted by hormone-enhanced attraction, and then more enduringly by the rewarding properties of the young that develops with physical contact and experience. Part of this process is based on maternal emotional regulation, particularly reduced anxiety or fear, which helps promote approach to young and inhibits withdrawal from them. As far as we know, postpartum depression is probably unique to human mothers, but nonetheless, features of human depression (e.g., anhedonia and low perseverance) can be modeled in laboratory rodents and affects mothering in both species. In terms of how learning impacts mothering across species, both human and non-human mothers do learn about their offspring. They learn to recognize them and they learn the ‘art’ of mothering. Parity effects are seen in both non-human and human mothers, and in both likely involve an experience-based reduction in anxiety and increase in motor competence. In humans, an enhancement of competence is also associated with a possibly uniquely human characteristic, self-esteem” ([Lonstein, Lévy, & Fleming 2015](#): 177).

91 Non-primate species that display these sorts of affiliation preferences include meerkats, horses, cows, vampire bats, ravens, rooks, jackdaws and woodhoopoes ([Massen, Sterck, & de Vos 2010](#): 1383-1384). It seems clear that domestic dogs and cats also display conspecific (and even cross-species) affiliation preferences.

92 The effects of social deprivation in eusocial insects have also been well-studied. Social isolation increases aggression in honeybees ([Breed 1983](#)) and drastically reduces lifespan in ants ([Boulay et al. 1999](#)). More recently, social isolation has been studied in group-living non-eusocial insects. In some species of cockroach, individuals reared in isolation show “stronger exploration-avoidance, reduced foraging activity, reduced willingness to interact socially, and reduced ability to assess mating partner quality compared to peers raised in groups” ([Lihoreau, Brepson, & Rivault 2009](#): 83).

Self-Conscious Emotions

Self-conscious emotions paradigmatically include shame, pride, guilt, embarrassment, jealousy, and envy (Lewis 2008). The capacity to experience self-conscious emotions may increase an animal's characteristic intensity range. Negative self-conscious emotions like shame and guilt increase one's feelings of separateness, which according to some (notably Buddhist) traditions is the root cause of suffering. Anecdotal evidence and received wisdom suggest that self-conscious affect tends to make many negatively valenced experiences more negative. Although the empirical literature on this topic appears relatively sparse, it has long been known that neurotic individuals are more likely to be self-conscious (Widiger 2009).

Self-conscious emotions are thought to require sophisticated cognitive and social skills. Nonetheless, Frans de Waal has suggested that nonhuman primates share with humans the basic building blocks for such emotions. Regarding shame, he writes, "Human shame, for example, typically stems from the violation of social norms and is characterized by a desire for invisibility. It is expressed in a shrinking body posture and downcast gaze, which brings it morphologically close to the submission displays of primates and other animals. Due to its self-conscious nature, human shame appears cognitively more complex than submission, but the associated emotions may not be so different" (de Waal 2011: 202). Regarding guilt, de Waal writes, "Similarly, guilt reflects regret at an action that may have hurt another, but that at the same time also hurt the relationship between actor and recipient. Guilt may thus help regulate reciprocity relationships. We know that nonhuman primates exhibit external signs of anxiety after aggressive acts that undermine their social relationships, and do so more often the more valuable their partner. Bonobo aggressors, for example, often approach their victim immediately after having attacked them to inspect and lick the injuries they themselves inflicted, which appears close to regret of previous behavior" (de Waal 2011: 202).⁹³ Although attributing self-conscious emotions to nonhuman animals runs the risk of anthropomorphism, de Waal has elsewhere (de Waal 1999) urged

researchers to give equal weight to avoiding the converse: anthropodenialism, the mistaken refusal to attribute human mental characteristics to nonhuman animals.⁹⁴

Measuring the Intensity of Valenced Experience

Thus far I have discussed, in broad terms, what sorts of characteristics might correlate with differences in the intensity range of valenced experience. But if these considerations are ever to amount to more than theoretical speculation, we will need to find a way to actually measure the intensity of valenced experience (at least in humans, and preferably in a variety of animals). And if we could quantify the intensity of valenced experience, we could perhaps dispense with correlative investigations altogether and instead directly assess differences in the intensity of valenced experience across species.

Regrettably, measuring the intensity of valenced experience across species is going to be difficult, for at least three reasons.

First, the neural correlates of valenced experience are poorly understood, even in humans (Walters & Williams 2019: 6).⁹⁵ In their search for the mechanisms that govern valenced experience (especially pain experience), neuroscientists have advanced a number of candidate brain regions and neural processes. Despite a huge volume of research in recent years, little consensus has emerged.⁹⁶ Significant progress appears to be perennially just on the horizon. With so much still unknown about the causal mechanisms governing valenced experience in humans, it is difficult to search for neural evidence of differences in the intensity of valenced experience across species. As an animal's phylogenetic distance from humans increases, the animal's neural architecture tends to become increasingly alien,⁹⁷ making neural evidence all the more difficult to interpret.

With neural evidence not yet helpful, we must turn to behavioral evidence. Unfortunately, behavioral evidence of valenced experience

93 He adds, "If we cannot rule out evolutionary continuity with regards to shame and guilt, there is all the more reason to expect continuity concerning emotions such as fear, anger, curiosity, and affection" (de Waal 2011: 202).

94 See Sober 2005 for extended discussion on balancing the risks of anthropomorphism and the risks of anthropodenialism.

95 "Despite impressive recent progress with human imaging and neural stimulation methods, identifying the neuronal populations critical for even transient pain experience in the human nervous system is incomplete at best. Compounding these obstacles is the fact that pain is an inferred internal state, rather than an obvious external behaviour, and thus is extremely difficult in any species to assess accurately using behavioural or neural activity measures. Consequently, there is considerable uncertainty about which behavioural features, neural circuits, cell types and molecules to compare across taxa when defining evolutionary relationships (homologous and analogous traits)" (Walters & Williams 2019: 6).

96 See Corns 2016 for exploration of the idea that pain is a gerrymandered, unnatural kind that is ill-suited to scientific investigation.

97 See [this document](#) for Tegan McCaslin's (2019) review of differences in nervous system architecture between mammals and arthropods.

rience varies considerably by species.⁹⁸ This is true even for some closely-related species.⁹⁹ For example, “urination and defecation in a new environment is a scent-marking behaviour in mice but a sign of fear in rats, and bulls show decreased corticosteroid response after tethering, while pigs show increased response” (Browning 2019: 156). Pain behavior even differs by *breed* in dogs (Dobromylskyj et al. 2000), mice (Mogil 2019),¹⁰⁰ and presumably other less well-studied species. As one review puts it, “The challenge in developing pain scales for use in animals is that it requires detailed knowledge of many different species-specific behaviors” (Stasiak et al. 2003: 14).¹⁰¹ In phylogenetically distant taxa, behavioral responses to pain may be radically different.¹⁰²

Finally, we must carefully distinguish genuine differences in the intensity of experience from mere differences in what we take to be markers of the intensity of experience.¹⁰³ We already encountered an instance of this problem in the section on the evolutionary function of valenced experience: prey animals display different behavior than predator animals in response to similar putatively painful experiences. It could be the case that evolution selected for prey animals with high pain thresholds because prey animals with lower pain thresholds were more likely to display the sort of weaknesses that got them attacked by predators. Alternatively, it might be that evolution merely selected for prey animals that were better at *hiding* their pain. Thus, in some contexts, differences in pain behavior may not be evidence for differences in pain experience.

Nonetheless, it’s a good idea to briefly survey the methods we might use to measure the intensity of valenced experience. If any of these methods proved even partially successful, that success could deliver action-relevant information. Given our large uncertainty regarding variation in the intensity of valenced experience across species and the potential importance of such variation, we ought to be willing to simultaneously pursue many different strategies for making progress in this area. In that vein, it might be worth following (and perhaps selectively supporting) the work of [Morten Kringelbach’s lab](#) (jointly housed at Oxford and Aarhus), [Kent Berridge’s lab](#) (Michigan), [Gregory Berns’ lab](#) (Emory), and [Giandomenico Iannetti’s lab](#) (jointly housed at the Italian Institute of Technology and University College London).

Below I overview three broad categories of measures: neurobiological markers of valenced experience, behavioral markers of valenced experience, and physiological markers of valenced experience.

Neurobiological Markers

Neurobiology appears to have the potential to shed light on valenced experience. If we can map the structure and function of the human brain and correlate differences in neural activity with self-reported differences in subjective experience, we may be able to identify the causal mechanisms that govern the intensity of pleasurable and painful experience. Some philosophers and neuroscientists believe that, once validated in humans, we can extend this approach to (some) nonhuman animals.¹⁰⁴

98 See [Mason 2010](#) for a nice review of closely related species with unexplained variation in welfare responses to zoo captivity, suggesting that predicting welfare differences across species is very difficult.

99 “Table 1 lists available findings of qualitative rat-versus-mouse differences relevant to pain, either in head-to-head studies or where the authors explicitly referred to a finding in the species currently under study as contrasting with the literature obtained using the other species. One would expect that many more mouse/rat species differences in pain are known to pharmaceutical company personnel, but never published in the scientific literature” (Mogil 2019: 2). Three of the differences in Mogil’s table relate to the experience of pain. If there are this many differences in pain experience between two closely related species, just imagine the differences between, say, silkworms and salmon.

100 “Differences among mouse strains in their sensitivity to various modalities of pain are ubiquitous and robust. One of the most reliable of these is the difference between the A/J and C57BL/6 J strains, which are resistant and sensitive, respectively, to inflammatory noxious stimuli causing tonic (on the order of minutes) nocifensive behaviours such as formalin (late-phase) and capsaicin licking” (Mogil 2019: 3).

101 The authors add, “Prey species, such as ruminants, often hide their pain so as not to become a target of predators. Likewise, birds often display only subtle signs, such as ruffled feathers and increased respiratory rate. There may also be variations within a species, such as pain behaviors seen with different breeds of dogs. In addition, some animals respond to pain with a fight-or-flight response, whereas others may become immobile. The lack of outward signs that we would recognize as pain does not imply that pain does not exist” (Stasiak et al. 2003: 14).

102 For example, grimacing is a common indicator of pain in mammals, but due to their hard exoskeleton, insects are incapable of grimacing.

103 See chapter 6 in [Browning 2019](#) for an excellent overview of this problem.

104 Gregory Berns, a neuroscientist: “Where structure-function relationships in an animal’s brain are similar to those in our brains, it is likely that the animal is capable of having a similar subjective experience as we do” (Berns 2017: 7). Heather Browning, a philosopher: “In terms of welfare intensity, similarities in brain structure and function would give us reason to think there is similarity in the subjective experience. The structure of the brain, and the way in which it functions, will determine the psychology of the individual, and these will vary depending on the inherited ‘instructions’ for development as well as the influence of the developmental environment. We then have good reason to think that individuals that are similar with regards to the relevant inheritance and developmental environments, will have similar types of psychology, with similar scope and boundaries. Insofar as subjective experience is a function of brain activity, and where

The neurobiological evidence suggests we should not expect big differences in the intensity of valenced experience between humans and other mammals.¹⁰⁵ In humans, a dizzying array of brain regions have been associated to some degree with valenced experience: the orbitofrontal cortex, the dorsal frontal cortex, the anterior cingulate cortex, the primary somatosensory cortex, the nucleus accumbens, the ventral pallidum, the basolateral amygdala, the mesolimbic tegmentum, and probably others.¹⁰⁶ Most of these same (or homologous) regions have been implicated in other mammals. Jaak Panksepp writes, “there is now abundant experimental evidence indicating that all mammals have negatively and positively-valenced emotional networks concentrated in homologous brain regions that mediate affective experiences when animals are emotionally aroused. That is what the neuroscientific evidence indicates” (Panksepp 2011a: 1). In a separate review, Panksepp writes, “The basic neurochemistries for emotional feelings, as far as we presently understand them, are essentially the same in all mammals” (Panksepp 2011b: 1797).¹⁰⁷ New research has demonstrated similar brain connectivity and wiring across 123 mammalian species (Assaf et al. 2020). Summarizing what we know about the neuroscience of affect, Kent Berridge and Morten Kringelbach write, “The brain’s circuitry for affective reactions spans from front to back of nearly the entire brain. Much of this circuitry is remarkably similar between humans and other mammals” (Berridge & Kringelbach 2013).¹⁰⁸

An alternative to looking at differences in the activity of different brain regions is instead to look at differences in brain-wide neural oscillations. Neural oscillations (often called ‘brainwaves’ in the popular press) are rhythmic patterns of neural activity caused by interactions between neurons. Different types of neural oscillations produce different electrophysiological signatures, and the frequency of these oscillations can be measured noninvasively

via electroencephalogram (EEG). Although EEG readings are a relatively superficial measurement of brain activity, they are nonetheless correlated with many interesting differences in cognitive state. (For example, a sleeping brain produces a characteristically different pattern of neural oscillations than an awake brain.)

Traditionally, neural oscillations are divided into five categories, based on their frequency: delta band (1-4 Hz), theta band (4-8 Hz), alpha band (8-12 Hz), beta band (12-30 Hz), and gamma band (30-150 Hz).

There are reasons to think that valenced experiences might produce measurable differences in neural oscillations. One review summarizes the case for thinking pain experience will manifest in neural oscillations: “Pain is a complex phenomenon that serves to protect the body. To this end, the brain dynamically integrates sensory and contextual information to guide behavior that aims to limit and avoid harm. Thus, pain is essentially an integrative phenomenon. In the brain, integrative functions are served by neuronal oscillations and synchrony [1]. Therefore, understanding the role of oscillations in the processing of pain can shed new light on how functionally diverse processes merge into the experience of pain” (Ploner & Gross 2019: 450).

It has recently been discovered that variation in gamma band oscillations is correlated with differences in self-reported pain intensity in human subjects (Hu & Iannetti 2019).¹⁰⁹ Importantly, gamma band activity also appears to be correlated with pain experience in mice (Tan et al. 2019) and rats (Peng et al. 2018). Gamma band oscillations thus appear to be one of the most promising biomarkers of pain across species, at least within mammals (Yue, Iannetti, & Hu 2020: 3478).¹¹⁰ Even supposing these correlations reflect a fundamental causal connection, there

there are neural correlates of experience, similarity in brain structure and function should then give us similarity in experience” (Browning 2019: 152).

¹⁰⁵ Although the number of neurons in mammalian species spans four orders of magnitude, there is little reason to think that neuron count is correlated with the intensity of valenced experience. This hypothesis has not been directly addressed in the scientific literature, and it is currently impossible to test convincingly. Thus, the hypothesis cannot be ruled out on empirical grounds. Nonetheless, I think the burden of proof falls on the defender of this hypothesis to motivate its plausibility. Nothing in the scientific literature suggests that the intensity of a pleasure or pain depends on the raw number of neurons firing at a given time.

¹⁰⁶ See, inter alia, Coghill, McHaffie, & Yen 2003; Lorenz, Minoshima, & Casey 2003; Berridge & Kringelbach 2013; Corder et al. 2019.

¹⁰⁷ Panksepp adds, “It has become increasingly clear during the past half century that primary-process affective mechanisms are concentrated in ancient subcortical midline brain regions that are anatomically and neurochemically, and hence, evolutionarily, similar in all mammalian species. However, we do not know how members of different species cognitively respond to such feelings” (Panksepp 2011b: 1801).

¹⁰⁸ They add, “Still, some real differences do exist between limbic brains of humans and other animals. The most obvious difference is the massive expansion of prefrontal cortex in humans, reflecting greater encephalization. Anatomically, encephalization also creates greater differentiation among prefrontal subregions. This may produce a few human cortex subregions that lack any clear homologue in nonprimates” (Berridge & Kringelbach 2013).

¹⁰⁹ “the magnitude of gamma oscillations within this γ -ERS [gamma-band event-related synchronization] cluster was significantly correlated with ratings of pain perception not only within-subject (mean $r = 0.16 \pm 0.23$, $P < 0.001$, one-sample t test), but also between-subjects ($r = 0.29$, $P = 0.005$). Both correlations were widespread across the scalp, but maximal over fronto-central regions (Fig. 2D). The similarity of these two correlation topographies suggests that the correlation between the γ -ERS cluster and pain sensitivity at within- and between-subject levels is subserved by similar underlying neural activities” (Hu & Iannetti 2019: 1785-1786).

¹¹⁰ There is also interesting recent work examining the relationship between pain sensitivity and alpha band oscillations. See, among others, Furman et al.

is as yet much work to be done before such data would allow us to quantify and compare the intensity of pain experiences across species. Still, this may be an area that merits more attention and perhaps carefully targeted funding in the future.

Behavioral Markers

The most obvious behavioral marker of valenced experience is a human's self-report of the experience. Psychologists and clinicians have developed and utilized a number of pain scales and pleasure scales to measure the intensity of various experiences in humans.¹¹¹ Although there are a variety of challenges concerning the reliable elicitation of subjective experience,¹¹² human self-reports nonetheless constitute crucial and invaluable data. Carefully calibrated self-reports can help us appreciate which circumstances typically engender the most intense valenced experiences in humans. Understanding the nature of the human intensity range will help us compare that range to those of nonhuman animals.¹¹³

Since self-reports are unavailable for the vast majority of animals,¹¹⁴ we must look to less obvious behaviors to infer differences in the intensity of various experiences. Unfortunately, there appear to be few, if any, good options. Behavioral pain scales have been developed for a handful of species. For instances, Lynne Sneddon reports that “grimace scales based on changes in facial

expression using Facial Action Coding Schemes have been developed for a variety of mammals including rats [7], mice [8,9], rabbits [10], horses [11] and piglets [12]” (Sneddon 2019: 2). However, these scales are at present rather coarse-grained, and it's unclear if they are able to adequately capture relevant differences in the intensity of different types of experiences. (Even with the aid of self-reports, measuring the intensity of *human* experiences is fraught with both theoretical and practical challenges.) More importantly, there is as yet no way to compare these scales across species.

Alternatively, we could look at willingness-to-pay studies, in which a nonhuman animal makes tradeoffs that reveal the strength of its preferences (Kahnau et al. 2020: 5).¹¹⁵ ‘Payment’ can be quantified in a number of ways: how long and at what magnitude an animal will endure an electric shock to access some reward,¹¹⁶ how much food an animal is willing to forgo to access some reward, or how much work (operationalized in terms of lever depressions, say) an animal will perform to access some reward. These sorts of tests have been conducted on a wide range of animals including mammals, birds, fish, insects, and crustaceans. The results of these experiments may give us insight into the relative intensity of different sorts of experiences.¹¹⁷ However, like other behavioral measures, the problem of interspecies comparisons remains (Browning 2019: 138).¹¹⁸

2018, Furman et al. 2019, and Furman et al. 2020.

111 Pain scale examples include the McGill Pain Index, the Brief Pain Inventory, the Numerical Rating Scale, the Verbal Rating Scale, and the Visual Analogue Scale. (See Hjemstad et al. 2011 and Lazaridou et al. 2018 for reviews.) Pleasure scale examples include the Temporal Experience of Pleasure Scale, the Snaith-Hamilton Pleasure Scale, the Chemosensory Pleasure Scale, and the Sexual Pleasure Scale.

112 Subjects may not be consistent in their reports (e.g., a person's mood may affect how a person reports an experience, even if the mood state doesn't affect the intensity of the experience). The same worry applies across subjects: due to differences in life history, one person's reported 4/10 may be the same intensity as another person's 6/10. These confounds can potentially be controlled for, especially when self-evaluations are paired with neurological data.

113 If our most intense experiences appear to be characteristically human (the joy of literature or the sorrow of unrequited love, say), then we can be more confident that the human intensity range is wider than the intensity range of nonhuman animals. If, on the contrary, our most intense experiences appear to be extremely common throughout the animal kingdom (the pain of starvation or the pleasure of orgasm, say), then we ought to be less confident that the human intensity range outstrips the range of nonhuman animals.

114 There may be a handful of nonhuman species that, with extensive training, are capable of communicating their inner experiences to us.

115 “Consumer demand tests can be used to determine the strength of preference for a preferred good. Vice versa, this test may also be useful to determine the strength of an aversion. The consumer demand test is based on the concept to “work” for access to a preferred good or for avoiding an aversive stimulus. In experimental consumer demand tests animals have to pay a certain price to obtain a good. This can be realized by introducing a workload or obstacles that has to be overcome. Work can be implemented, for example, by pressing a lever or a switch [50,61], or by an obstacle like water or an adjustable weight barrier [62,63] [...] By training the animals to work for the access to certain goods, the preferential strength and the grade of necessity of this good can be determined by increasing the price. Therefore, consumer demand testing is a useful method for animal welfare research and severity assessment [45,48,64]” (Kahnau et al. 2020: 5).

116 For instance, fruit flies will endure a stronger shock for access to ethanol than for access to sugar (Kaun, Devineni, & Heberlein 2012: 964).

117 Of course, preference strength is not an infallible proxy for intensity strength.

118 “We cannot escape the problem using tests for the strength of preferences, as they will hold the same problem as other indicators. We could look to see whether Paddy will work harder for her yabbies than Sneezy would, but the results we see only give us comparative information for each individual – how much they value yabbies vs. work – and can't be used to make intersubjective comparisons without assumptions such as that they both find work equally unpleasant. Sneezy may work less hard, but that won't tell us whether he values yabbies less, or dislikes work more. He may merely be lazy, and less motivated in general to try and receive his favourite things, despite enjoying them just as much” (Browning 2019: 138).

Physiological Markers

Physiological markers of valenced experience can be conceptualized as lying midway between the neural mechanisms that govern pains and pleasures and the voluntary behaviors that animals undertake in response to those experiences. Involuntary changes in an animal's heart rate, blood pressure, pupil dilation, perspiration, hormonal levels, or metabolic activity may indicate the presence of valenced states. Differences in the magnitude of such changes may indicate differences in the intensity of the associated experiences. This sort of physiological activity may be more easily studied in nonhuman animals than neural activity, and if these physiological changes are truly involuntary, they may be more reliably observed than voluntary behaviors.

Recent research has attempted to identify physiological markers of pain intensity in humans. Physiological activity, however, is affected by many factors. No single physiological variable is likely to track the intensity of pains with much precision. In response to this problem, researchers have created composite algorithms that combine and weight information from a variety of physiological sources. Using large datasets and sophisticated statistical modelling, researchers hope to identify subtle shifts in physiological activity that mirror changes in pain intensity. According to one review, "These multi-variable approaches appear to be superior predictors of pain intensity and intra-operative nociception to any individual parameter alone" (Cowen et al. 2015: 838). If this approach is validated in humans, it could plausibly be extended to closely related nonhuman animals.

Ultimately, however, even these composite algorithms have failed to deliver a measure that is reliable enough to be used in clinical settings.¹¹⁹ In the same review, Ruth Cowen and her collaborators conclude, "Although clinically needed and theoretically promising, currently there is not enough evidence to support the widespread use of any physiological markers as 'objective' measures of pain and nociception. This is despite recently increased efforts, raising the question whether this is possible in the foreseeable future" (Cowen et al. 2015: 840). Nonetheless, Cowen and her collaborators end the review on a hopeful note, observing that "there are some promising avenues on the horizon. Biomarker research as part of clinical phenotyping, and the development of composite algorithms, should be closely watched" (ibid.).

¹¹⁹ Individual physiological parameters are terrible predictors of pain intensity, so the fact that multivariable algorithms outperform this low bar doesn't suggest that the algorithms are necessarily very good.

¹²⁰ The effect of human-focused longtermist spending on animal welfare is unclear. One could reasonably believe that the best way to help animals in the long run is to ensure that humans survive long enough that they (or their descendants) use their advanced technology to eliminate (or greatly reduce) natural suffering.

Conclusion

The moral significance of a pain or pleasure varies, in part, with its intensity. A cluster headache typically demands more of our moral attention than a stubbed toe. The joy of holding one's child for the first time is typically worth more, morally, than the pleasure of a good meal. We intuitively and naturally recognize such differences in our own lives and in the lives of those close to us. Our everyday decision-making would be much worse if we did not account for differences in the intensity of experiences.

Like all our subjective experiences, valenced experiences are the product of intricate neural mechanisms that have been shaped by countless generations of natural selection. At a higher level of abstraction, the structure of our social, emotional, and intellectual nature contributes in complex ways to the intensity of our feelings. Given the enormous diversity of the (plausibly sentient portion of the) animal kingdom, it would be surprising if (sentient) animals were uniformly capable of the exact same magnitude of pleasures and pains.

Differences in intensity range could entail big and unrecognized differences in the cost-effectiveness of interventions targeting different species. We want our resources to be allocated in the way that maximizes improvements to welfare. To properly compare interventions that aid phylogenetically distant species—pigs versus carp, say, or chickens versus honey bees—we need to know, at least roughly, how the experiences of those animals are likely to differ.

Finally, thinking about differences in the intensity range of valenced experience might help us better judge the ideal split between (nearertermist¹²⁰) human-focused spending and spending on nonhuman animals. In many circles, it is taken for granted that humans have a larger capacity for welfare than nonhuman animals. This is a plausible claim, but plausibility does not entail truth: we must weigh the evidence as impartially as we can. There is at least tentative reason to believe that the intensity range of valenced experience doesn't vary dramatically among mammals, including humans (though of course capacity for welfare encompasses more than the intensity of valenced experience). In any event, *that* humans have a larger capacity for welfare than nonhuman animals is a less informative claim than the claim that humans have *x times as large* a capacity for welfare as nonhuman

animals (of type y). There is widespread disagreement about what the plausible range of x is (for a given y). Further investigation into differences in the intensity of valenced experience across species may help us narrow that range, which in turn will help us evaluate the degree to which we want to prioritize human welfare over nonhuman animal welfare.¹²¹

There is as yet much we do not know about differences in the intensity of valenced experience across species. In Appendix 1 I have compiled a partial list of open research questions. There is little reason to think that our current distribution of resources is perfect, and many reasons to think that our understanding of the nature and moral worth of nonhuman animal experiences may change dramatically over the next century.

Credits

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Works Cited

Akhtar, S. (2011). [Animal pain and welfare: Can pain sometimes be worse for them than for us?](#) in Beauchamp & Frey (eds.) *The Oxford Handbook of Animal Ethics*, 495-518.

Anderson, D. J., & Adolphs, R. (2014). [A framework for studying emotions across species](#). *Cell*, 157(1), 187-200.

Andrews, K. (2020). [Naïve normativity: The social foundation of moral cognition](#). *Journal of the American Philosophical Association*, 6(1), 36-56.

Assaf, Y., Bouznach, A., Zomet, O., Marom, A., & Yovel, Y. (2020). [Conservation of brain connectivity and wiring across the mammalian class](#). *Nature Neuroscience*, 1-4.

Bain, D. (2017). [Evaluativist Accounts of Pain's Unpleasantness](#). in J. Corns (ed) *The Routledge Handbook of Philosophy of Pain*, 40-50. Routledge.

Bateson, M., Desire, S., Gartside, S. E., & Wright, G. A. (2011). [Agitated honeybees exhibit pessimistic cognitive biases](#). *Current*

Biology, 21(12), 1070-1073.

Belzung, C., & Philippot, P. (2007). [Anxiety from a phylogenetic perspective: is there a qualitative difference between human and animal anxiety?](#) *Neural Plasticity*, 059676.

Beran, M. J., Couchman, J. J., Coutinho, M. V., Boomer, J., & Smith, J. D. (2010). [Metacognition in nonhumans: methodological and theoretical issues in uncertainty monitoring](#). in A. Efklides & P. Misailidi (eds) *Trends and Prospects in Metacognition Research*, 21-35. Springer.

Berns, G. (2017). [What It's Like to be a Dog: And Other Adventures in Animal Neuroscience](#). Basic Books.

Berridge, K. C., & Kringelbach, M. L. (2013). [Neuroscience of affect: brain mechanisms of pleasure and displeasure](#). *Current Opinion in Neurobiology*, 23(3), 294-303.

Bjekić, J., Živanović, M., Purić, D., Oosterman, J. M., & Filipović, S. R. (2018). [Pain and executive functions: a unique relationship between Stroop task and experimentally induced pain](#). *Psychological Research*, 82(3), 580-589.

Bisaz, R., Travaglia, A., & Alberini, C. M. (2014). [The neurobiological bases of memory formation: from physiological conditions to psychopathology](#). *Psychopathology*, 47(6), 347-356.

Bonanno, G. A., Goorin, L., & Coifman, K. G. (2008). [Sadness and grief](#). in J. Haviland-Jones, L. Barrett, & M. Lewis (eds) *Handbook of Emotions, Third Edition*, 797-806. Guilford Publications.

Boulay, R., Quagebeur, M., Godzinska, E. J., & Lenoir, A. (1999). [Social isolation in ants: Evidence of its impact on survivorship and behavior in *Camponotus fellah* \(Hymenoptera, Formicidae\)](#). *Sociobiology*, 33(2), 111-124.

Breed, M. D. (1983). [Correlations between aggressiveness and corpora allata volume, social isolation, age and dietary protein in worker honeybees](#). *Insectes Sociaux*, 30(4), 482-495.

Briefer, E. F. (2018). [Vocal contagion of emotions in non-human animals](#). *Proceedings of the Royal Society B: Biological Sciences*, 285(1873), 20172783.

Broom, D. M. (2007). [Cognitive ability and sentience: Which aquatic animals should be protected?](#) *Diseases of aquatic organ-*

¹²¹ Naturally, there are many reasons we might be justified in preferring to spend more money on human welfare than nonhuman welfare, even if there isn't a large difference in capacity for welfare. Helping humans may be more tractable in a variety of ways.

isms, 75(2), 99-108.

Brouwer, H., & van der Deijl, W. (2020). [All Animals are Equal, but Some More than Others?](#). *Journal of Moral Philosophy*, 17(3), 342-357.

Browning, H. (2019). [If I Could Talk to the Animals: Measuring Subjective Animal Welfare](#). PhD Dissertation.

Bruni, L. (2010). [The happiness of sociality. Economics and eudaimonia: A necessary encounter](#). *Rationality and Society*, 22(4), 383-406.

Butler, R. K., & Finn, D. P. (2009). [Stress-induced analgesia](#). *Progress in neurobiology*, 88(3), 184-202.

Casser, L. C. (2020). [The Function of Pain](#). *Australasian Journal of Philosophy*, 1-15.

Chan, S. C., Chan, C. C., Kwan, A. S., Ting, K. H., & Chui, T. Y. (2012). [Orienting attention modulates pain perception: an ERP study](#). *PLoS One*, 7(6), e40215.

Cheke, L. G., & Clayton, N. S. (2010). [Mental time travel in animals](#). *Wiley Interdisciplinary Reviews: Cognitive Science*, 1(6), 915-930.

Clement, G. (2013). [Animals and moral agency: The recent debate and its implications](#). *Journal of Animal Ethics*, 3(1), 1-14.

Coghill, R. C., McHaffie, J. G., & Yen, Y. F. (2003). [Neural correlates of interindividual differences in the subjective experience of pain](#). *Proceedings of the National Academy of Sciences*, 100(14), 8538-8542.

Corder, G., Ahanonu, B., Grewe, B. F., Wang, D., Schnitzer, M. J., & Scherrer, G. (2019). [An amygdalar neural ensemble that encodes the unpleasantness of pain](#). *Science*, 363(6424), 276-281.

Corns, J. (2016). [Pain eliminativism: scientific and traditional](#). *Synthese*, 193(9), 2949-2971.

Cowen, R., Stasiowska, M. K., Laycock, H., & Bantel, C. (2015). [Assessing pain objectively: the use of physiological markers](#). *Anaesthesia*, 70(7), 828-847.

Cutter, B. (2017). [Pain and representation](#). in J. Corns (ed) *The Routledge Handbook of Philosophy of Pain*, 29-39. Routledge.

Cutter, B., & Tye, M. (2011). [Tracking representationalism and the painfulness of pain](#). *Philosophical Issues*, 21, 90-109.

Czaczkes, T. J., & Heinze, J. (2015). [Ants adjust their pheromone deposition to a changing environment and their probability of making errors](#). *Proceedings of the Royal Society B: Biological Sciences*, 282(1810), 20150679.

Damasio, A., & Carvalho, G. B. (2013). [The nature of feelings: evolutionary and neurobiological origins](#). *Nature Reviews Neuroscience*, 14(2), 143-152.

Dawkins, R. (2009). [The Greatest Show on Earth: The Evidence for Evolution](#). Simon and Schuster.

De Waal, F. B. (1999). [Anthropomorphism and anthropodenial: consistency in our thinking about humans and other animals](#). *Philosophical Topics*, 27(1), 255-280.

De Waal, F. B. (2011). [What is an animal emotion?](#). *Annals of the New York Academy of Sciences*, 1224(1), 191-206.

Dobromylskyj, P., Flecknell, P. A., Lascelles, B. D., Livingston, A., Taylor, P., & Waterman-Pearson, A. (2000). [Pain assessment](#). in P. Flecknell & A. Waterman-Pearson (eds.) *Pain Management in Animals*, 53-79. WB Saunders.

Dolan, P., & Metcalfe, R. (2012). [Valuing health: a brief report on subjective well-being versus preferences](#). *Medical Decision Making*, 32(4), 578-582.

Dreschel, N. A. (2010). [The effects of fear and anxiety on health and lifespan in pet dogs](#). *Applied Animal Behaviour Science*, 125(3-4), 157-162.

Edgar, J., Held, S., Paul, E., Pettersson, I., Price, R. I. A., & Nicol, C. (2015). [Social buffering in a bird](#). *Animal Behaviour*, 105, 11-19.

Eisenstein, E. M., Carlson, A. D., & Harris, J. T. (1997). [A ganglionic model of "learned helplessness"](#). *Integrative Physiological and Behavioral Science*, 32(3), 265-271.

Faustino, A. I., Tacão-Monteiro, A., & Oliveira, R. F. (2017). [Mechanisms of social buffering of fear in zebrafish](#). *Scientific Reports*, 7, 44329.

Finlay, B. L. (2019). [The neuroscience of vision and pain: evolution of two disciplines](#). *Philosophical Transactions of the Royal Society B*, 374(1785), 20190292.

- Finlay, B. L., & Syal, S. (2014). [The pain of altruism](#). *Trends in cognitive sciences*, 18(12), 615-617.
- Fone, K. C., & Porkess, M. V. (2008). [Behavioural and neurochemical effects of post-weaning social isolation in rodents—relevance to developmental neuropsychiatric disorders](#). *Neuroscience & Biobehavioral Reviews*, 32(6), 1087-1102.
- Fossat, P., Bacqué-Cazenave, J., De Deurwaerdère, P., Delbecq, J. P., & Cattaert, D. (2014). [Anxiety-like behavior in crayfish is controlled by serotonin](#). *Science*, 344(6189), 1293-1297.
- Furman, A. J., Meeker, T. J., Rietschel, J. C., Yoo, S., Muthulingam, J., Prokhorenko, M., ... & Seminowicz, D. A. (2018). [Cerebral peak alpha frequency predicts individual differences in pain sensitivity](#). *Neuroimage*, 167, 203-210.
- Furman, A. J., Thapa, T., Summers, S. J., Cavaleri, R., Fogarty, J. S., Steiner, G. Z., ... & Seminowicz, D. A. (2019). [Cerebral peak alpha frequency reflects average pain severity in a human model of sustained, musculoskeletal pain](#). *Journal of Neurophysiology*, 122(4), 1784-1793.
- Furman, A. J., Prokhorenko, M., Keaser, M. L., Zhang, J., Chen, S., Mazaheri, A., & Seminowicz, D. A. (2020). [Sensorimotor Peak Alpha Frequency Is a Reliable Biomarker of Prolonged Pain Sensitivity](#). *Cerebral Cortex*.
- Gale, C. R., Deary, I. J., Cooper, C., & Batty, G. D. (2012). [Intelligence in childhood and chronic widespread pain in middle age: the National Child Development Survey](#). *PAIN*, 153(12), 2339-2344.
- Gallup Jr, G. G., Towne, J. P., & Stolz, J. A. (2018). [An evolutionary perspective on orgasm](#). *Evolutionary Behavioral Sciences*, 12(1), 52.
- Gibson, W. T., Gonzalez, C. R., Fernandez, C., Ramasamy, L., Tabachnik, T., Du, R. R., ... & Anderson, D. J. (2015). [Behavioral responses to a repetitive visual threat stimulus express a persistent state of defensive arousal in *Drosophila*](#). *Current Biology*, 25(11), 1401-1415.
- Ginsburg, S., & Jablonka, E. (2019). [The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness](#). MIT Press.
- Graham, C., Higuera, L., & Lora, E. (2011). [Which health conditions cause the most unhappiness?](#). *Health Economics*, 20(12), 1431-1447.
- Hjermstad, M. J., Fayers, P. M., Haugen, D. F., Caraceni, A., Hanks, G. W., Loge, J. H., ... & European Palliative Care Research Collaborative (EPCRC). (2011). [Studies comparing Numerical Rating Scales, Verbal Rating Scales, and Visual Analogue Scales for assessment of pain intensity in adults: a systematic literature review](#). *Journal of Pain and Symptom Management*, 41(6), 1073-1093.
- Hoedjes, K. M., Kruidhof, H. M., Huigens, M. E., Dicke, M., Vet, L. E., & Smid, H. M. (2011). [Natural variation in learning rate and memory dynamics in parasitoid wasps: opportunities for converging ecology and neuroscience](#). *Proceedings of the Royal Society B: Biological Sciences*, 278(1707), 889-897.
- Hu, L., & Iannetti, G. D. (2019). [Neural indicators of perceptual variability of pain across species](#). *Proceedings of the National Academy of Sciences*, 116(5), 1782-1791.
- Johannsen, K. (2019). [Are some animals also moral agents?](#). *Animal Sentience* 23(27)
- Kahnau, P., Habedank, A., Diederich, K., & Lewejohann, L. (2020). [Behavioral Methods for Severity Assessment](#). *Animals*, 10(7), 1136.
- Karch, D. L., Logan, J., & Patel, N. (2011). [Surveillance for violent deaths—National violent death reporting system, 16 states, 2008](#). *Morbidity and Mortality Weekly Report: Surveillance Summaries*, 60(10), 1-49.
- Kaun, K. R., Devineni, A. V., & Heberlein, U. (2012). [Drosophila melanogaster as a model to study drug addiction](#). *Human Genetics*, 131(6), 959-975.
- King, B. J. (2013). [How Animals Grieve](#). University of Chicago Press.
- Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J. Y., & Jordan, A. L. (2019). [If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals?](#). *PLoS biology*, 17(2), e3000021.
- Klein, C. (2015). [What the Body Commands: The Imperative Theory of Pain](#). MIT Press.
- Lazaridou, A., Elbaridi, N., Edwards, R. R., & Berde, C. B. (2018). [Pain assessment](#). in H.T. Benzon, S.N. Raja, S.M. Fishman, S.S. Liu, & S.P. Cohen (eds.) *Essentials of Pain Medicine*, 39-46. Elsevier.

- Lewis, M. (2008). [Self-conscious emotions: embarrassment, pride, shame, and guilt](#). in M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (eds.) *Handbook of Emotions*, 742–756. The Guilford Press.
- Lihoreau, M., Brepson, L., & Rivault, C. (2009). [The weight of the clan: even in insects, social isolation can induce a behavioural syndrome](#). *Behavioural Processes*, 82(1), 81-84.
- Lonstein, J. S., Lévy, F., & Fleming, A. S. (2015). [Common and divergent psychobiological mechanisms underlying maternal behaviors in non-human and human mammals](#). *Hormones and Behavior*, 73, 156-185.
- Lopez-Bellido, R., Himmel, N. J., Gutstein, H. B., Cox, D. N., & Galko, M. J. (2019). [An assay for chemical nociception in *Drosophila* larvae](#). *Philosophical Transactions of the Royal Society B*, 374(1785), 20190282.
- Lorenz, J., Minoshima, S., & Casey, K. L. (2003). [Keeping pain out of mind: the role of the dorsolateral prefrontal cortex in pain modulation](#). *Brain*, 126(5), 1079-1091.
- Lucas, R. & Diener, E. (2008). [Subjective Well-Being](#). in J. Haviland-Jones, L. Barrett, & M. Lewis (eds) *Handbook of Emotions, Third Edition*, 471-484. Guilford Publications.
- Lustig, C. I., Kozak, R., Sarter, M., Young, J. W., & Robbins, T. W. (2013). [CNTRICS final animal model task selection: control of attention](#). *Neuroscience & Biobehavioral Reviews*, 37(9), 2099-2110.
- MacDonald, G., & Leary, M. R. (2005). [Why does social exclusion hurt? The relationship between social and physical pain](#). *Psychological Bulletin*, 131(2), 202.
- Magee, B., & Elwood, R. W. (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](#). *Behavioural Processes*, 130, 31-35.
- Martínez, M. (2011). [Imperative content and the painfulness of pain](#). *Phenomenology and the Cognitive Sciences*, 10(1), 67-90.
- Mason, G. J. (2010). [Species differences in responses to captivity: stress, welfare and the comparative method](#). *Trends in Ecology & Evolution*, 25(12), 713-721.
- Massen, J., Sterck, E., & de Vos, H. (2010). [Close social associations in animals and humans: functions and mechanisms of friendship](#). *Behaviour*, 147(11), 1379-1412.
- Matzel, L. D., Wass, C., & Kolata, S. (2011). [Individual differences in animal intelligence: learning, reasoning, selective attention and inter-species conservation of a cognitive trait](#). *International Journal of Comparative Psychology*, 24(1), 36-59.
- McLennan, K. M. (2018). [Why pain is still a welfare issue for farm animals, and how facial expression could be the answer](#). *Agriculture*, 8(8), 127.
- McParland, J. L., & Eccleston, C. (2013). [“It’s Not Fair” social justice appraisals in the context of chronic pain](#). *Current Directions in Psychological Science*, 22(6), 484-489.
- Mogil, J. S. (2009). [Animal models of pain: progress and challenges](#). *Nature Reviews Neuroscience*, 10(4), 283-294.
- Mogil, J. S. (2019). [The translatability of pain across species](#). *Philosophical Transactions of the Royal Society B*, 374(1785), 20190286.
- Moreau, J. L. (2002). [Simulating the anhedonia symptom of depression in animals](#). *Dialogues in Clinical Neuroscience*, 4(4), 351.
- Mounier, L., Veissier, I., Andanson, S., Delval, E., & Boissy, A. (2006). [Mixing at the beginning of fattening moderates social buffering in beef bulls](#). *Applied Animal Behaviour Science*, 96(3-4), 185-200.
- Mukuria, C., & Brazier, J. (2013). [Valuing the EQ-5D and the SF-6D health states using subjective well-being: a secondary analysis of patient data](#). *Social Science & Medicine*, 77, 97-105.
- Numan, M., & Young, L. J. (2016). [Neural mechanisms of mother-infant bonding and pair bonding: similarities, differences, and broader implications](#). *Hormones and Behavior*, 77, 98-112.
- Ogden, L. E. (2016). [Fear Factor: The surprising consequences of being scared](#). *BioScience*, 66(8), 625-631.
- Öhman, A. (2008). [Fear and Anxiety: Overlaps and Dissociations](#). in J. Haviland-Jones, L. Barrett, & M. Lewis (eds) *Handbook of Emotions, Third Edition*, 709-729. Guilford Publications.
- Overmier, J. B., & Seligman, M. E. (1967). [Effects of inescapable shock upon subsequent escape and avoidance responding](#). *Journal of Comparative and Physiological Psychology*, 63(1), 28.
- Panksepp, J. (2011a). [Cross-species affective neuroscience de-](#)

- [coding of the primal affective experiences of humans and related animals](#). *PLoS one*, 6(9), e21236.
- Panksepp, J. (2011b). [The basic emotional circuits of mammalian brains: do animals have affective lives?](#) *Neuroscience & Biobehavioral Reviews*, 35(9), 1791-1804.
- Pantell, M., Rehkopf, D., Jutte, D., Syme, S. L., Balmes, J., & Adler, N. (2013). [Social isolation: a predictor of mortality comparable to traditional clinical risk factors](#). *American Journal of Public Health*, 103(11), 2056-2062.
- Peirs, C., & Seal, R. P. (2016). [Neural circuits for pain: recent advances and current views](#). *Science*, 354(6312), 578-584.
- Peng, W., Xia, X., Yi, M., Huang, G., Zhang, Z., Iannetti, G., & Hu, L. (2018). [Brain oscillations reflecting pain-related behavior in freely moving rats](#). *Pain*, 159(1), 106.
- Perry, C. J., & Barron, A. B. (2013). [Honey bees selectively avoid difficult choices](#). *Proceedings of the National Academy of Sciences*, 110(47), 19155-19159.
- Phillips, C. (2008). [Animal welfare: A construct of positive and negative affect](#). *Veterinary journal*, 175(3), 291-292.
- Ploner, M., & Gross, J. (2019). [Gamma oscillations shape pain in animals and humans](#). *Trends in Cognitive Sciences*, 23(6), 450-451.
- Reicherts, P., Wiemer, J., Gerdes, A., Schulz, S. M., Pauli, P., & Wieser, M. J. (2017). [Anxious anticipation and pain: the influence of instructed vs conditioned threat on pain](#). *Social Cognitive and Affective Neuroscience*, 12(4), 544-554.
- Rhudy, J. L., & Meagher, M. W. (2000). [Fear and anxiety: divergent effects on human pain thresholds](#). *Pain*, 84(1), 65-75.
- Ries, A. S., Hermanns, T., Poeck, B., & Strauss, R. (2017). [Serotonin modulates a depression-like state in Drosophila responsive to lithium treatment](#). *Nature Communications*, 8(1), 1-11.
- Scerif, G., Gomez, J. C., & Byrne, R. W. (2004). [What do Diana monkeys know about the focus of attention of a conspecific?](#) *Animal Behaviour*, 68(6), 1239-1247.
- Scollon, C. N., Prieto, C. K., & Diener, E. (2009). [Experience sampling: promises and pitfalls, strength and weaknesses](#). in E. Diener (ed) *Assessing Well-Being*, 157-180. Springer.
- Seligman, M. E. (1968). [Chronic fear produced by unpredictable electric shock](#). *Journal of Comparative and Physiological Psychology*, 66(2), 402.
- Singer, P. (2011). [Practical ethics, 3rd Edition](#). Cambridge University Press.
- Sneddon, L. U. (2019). [Evolution of nociception and pain: evidence from fish models](#). *Philosophical Transactions of the Royal Society B*, 374(1785), 20190290.
- Sneddon, L. U., Elwood, R. W., Adamo, S. A., & Leach, M. C. (2014). [Defining and assessing animal pain](#). *Animal Behaviour*, 97, 201-212.
- Sober, E. (2005). [Comparative Psychology Meets Evolutionary Biology: Morgan's Canon and Cladistic Parsimony](#). in Daston L. & Mitman G. (eds.), *Thinking with Animals: New Perspectives on Anthropomorphism*, 85-99. Columbia University Press.
- Stasiak, K. L., Maul, D. O. N., French, E., Hellyer, P. W., & Vandewoude, S. (2003). [Species-specific assessment of pain in laboratory animals](#). *Journal of the American Association for Laboratory Animal Science*, 42(4), 13-20.
- Stearns, S. C. (2012). [Evolutionary medicine: its scope, interest and potential](#). *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4305-4321.
- Steinkopf, L. (2016). [An evolutionary perspective on pain communication](#). *Evolutionary Psychology*, 14(2), 1474704916653964.
- Sufka, K. J., & Hughes, R. A. (1991). [Differential effects of handling on isolation-induced vocalizations, hypoalgesia, and hyperthermia in domestic fowl](#). *Physiology & Behavior*, 50(1), 129-133.
- Tan, L. L., Oswald, M. J., Heintz, C., Romero, O. A. R., Kaushalya, S. K., Monyer, H., & Kuner, R. (2019). [Gamma oscillations in somatosensory cortex recruit prefrontal and descending serotonergic pathways in aversion and nociception](#). *Nature Communications*, 10(1), 1-17.
- Tye, M. (1995). [Ten Problems of Consciousness: A Representational Theory of the Phenomenal Mind](#). MIT Press.
- Wada, M., Takano, K., Ora, H., Ide, M., & Kansaku, K. (2016). [The rubber tail illusion as evidence of body ownership in mice](#). *Journal of Neuroscience*, 36(43), 11133-11137.

Appendix I: Open Research Questions

Walters, E. T. (2018). [Nociceptive biology of molluscs and arthropods: evolutionary clues about functions and mechanisms potentially related to pain](#). *Frontiers in Physiology*, 9, 1049.

Walters, E. T., & Williams, A. C. D. C. (2019). [Evolution of mechanisms and behaviour important for pain](#). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374: 20190275.

Webb, L. E., Veenhoven, R., Harfeld, J. L., & Jensen, M. B. (2019). [What is animal happiness?](#). *Annals of the New York Academy of Sciences*, 1438(1), 62.

Weiss, M. N., Franks, D. W., Croft, D. P., & Whitehead, H. (2019). [Measuring the complexity of social associations using mixture models](#). *Behavioral Ecology and Sociobiology*, 73(1), 8.

Widiger, T. A. (2009). [Neuroticism](#). in M. R. Leary & R. H. Hoyle (eds.) *Handbook of Individual Differences in Social Behavior*, 129–146. The Guilford Press.

Williams, A. C. D. C. (2019). [Persistence of pain in humans and other mammals](#). *Philosophical Transactions of the Royal Society B*, 374(1785), 20190276.

Willner, P., Muscat, R., & Papp, M. (1992). [Chronic mild stress-induced anhedonia: a realistic animal model of depression](#). *Neuroscience & Biobehavioral Reviews*, 16(4), 525-534.

Yeates, J. W. (2012). [Brain-pain: Do animals with higher cognitive capacities feel more pain? Insights for species selection in scientific experiments](#). in K. Hagen, A. Schnieke, & F. Thiele (eds) *Large animals as biomedical models: Ethical, societal, legal and biological aspects*, 24-46.

Young, L. J. (2003). [The neural basis of pair bonding in a monogamous species: A model for understanding the biological basis of human behavior](#). in *Offspring: Human Fertility Behavior in Biodemographic Perspective*. National Academies Press (US).

Yue, L., Iannetti, G. D., & Hu, L. (2020). [The Neural Origin of Nociceptive-Induced Gamma-Band Oscillations](#). *Journal of Neuroscience*, 40(17), 3478-3490.

Zanette, L. Y., Hobbs, E. C., Witterick, L. E., MacDougall-Shackleton, S. A., & Clinchy, M. (2019). [Predator-induced fear causes PTSD-like changes in the brains and behaviour of wild animals](#). *Scientific Reports*, 9(1), 1-10.

- (1) Which animals have the capacity for valenced experience?
- (2) Is valence incomparably multidimensional or is a unidimensional analysis of valence appropriate?
- (3) Did valenced experience evolve once or multiple times?
- (4) What is the evolutionary function of valenced experience? Does valenced experience serve the same role in all animals capable of valenced experience?
- (5) Do animals with shorter lifespans have reduced pain sensitivity or increased pleasure sensitivity (compared to similar animals with longer lifespans)? Neither? Both?
- (6) Which nonhuman animals are capable of mental time travel?
- (7) Which nonhuman animals can reason normatively?
- (8) Which influences learning more: the strength of the stimulus/reward or the statistical regularity of the stimulus-reward pattern?
- (9) Are intensely pleasurable experiences as distracting as intensely painful experiences? If not, why not? Can we quantify level of distraction and use it to estimate the intensity of a valenced experience?
- (10) Is it a contingent empirical fact that intense experiences are distracting, or is intensity partly constituted by its grip on the subject's attention?
- (11) What are the neurobiological constraints (if any) that impose a limit on the maximum intensity of a valenced experience?
- (12) How large is the typical gap between an animal's characteristic intensity range of experience and an animal's possible intensity range of experience?
- (13) How do nociceptive thresholds differ across species, and what drives this variation?
- (14) Are pleasures judged to be undeserved perceived to be less intense than comparable pleasures either judged to be deserved or lacking a normative evaluation altogether?
- (15) Are pains judged to be endured for good reason perceived as less intense than pains that are not so judged?
- (16) Under what conditions (if any) does stress or anxiety increase pain sensitivity?
- (17) Does focusing on a pleasure increase the intensity of the pleasure?
- (18) How does the anticipation of a pain/pleasure influence the intensity of the pain/pleasure?

- (19) How does the pain behavior of prey animals differ in the presence vs. the absence of their predators? Is there a corresponding neurobiological difference?
- (20) How does the pain behavior of prey species compare to similar non-prey species? Is there a corresponding neurobiological difference?
- (21) Which nonhuman animals are capable of deliberately redirecting their focus and attention?
- (22) When someone 'learns to live' with chronic pain that is initially debilitating, does the person experience a reduction in pain or is the pain experience the same, the person just learns to cope with it?¹²²
- (23) How asymmetrical are intensity ranges? How does this vary across species? What drives this variation?
- (24) Are there any animals whose possible valence range is exclusively negative? Exclusively positive?
- (25) How often do combination effects affect the intensity of valenced experience? What are the most common combination effects?
- (26) What is the difference in suicide rates for people experiencing purely emotional distress (perfect health but severe depression, say) versus people experiencing purely physical distress (chronic intense pain but no depression, say)?¹²³
- (27) Is sadness more likely in social animals?
- (28) Does intensity of valenced experience change with life stage (especially in animals like insects with radically different life stages)?
- (29) What circumstances typically induce the most intense valenced experiences in humans?
- (30) Which nonhuman animals, if any, are capable of directly communicating the nature of their inner experiences to us?

¹²² A good analogy might be people habituating to spicy food. One can ask essentially the same question: I experience a characteristic phenomenal state with a negative valence when I eat spicy food. Do people who like spicy food experience a different phenomenal state, or do they experience the same phenomenal state but with a different valence? The empirical evidence suggests the former. People who have been habituated to spicy food have qualitatively different tongues, suggesting they are less sensitive to the heat (and/or maybe they pick up on different qualities of the spice).

¹²³ It's possible that these categories overlap to the extent that this question is impossible to answer. Severe depression tends to cause physical health problems, and severe physical health problems increase the risk of depression.