

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Noxious Nomenclature: Inconsistent Language Hampers Our Assessment of Invertebrate Pain, Sentience, and Awareness

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Whether invertebrates possess the capacity for subjective experiences, particularly that of pain, is a frontier question in cognitive ethology. Central to this inquiry is the examination of pain-like behaviours elicited by noxious stimulation under leading sentience frameworks. Here we discuss our concerns on how the usage of the terms ‘noxious’ and ‘aversive’ in an interchangeable manner throughout past and emerging work may hamper current assessments of invertebrate pain-related literature. We briefly discuss the etymology of these terms, provide use cases that illustrate how conflation obscures interpretation, and propose a simple yet effective solution.

Keywords: behavior, cognitive ethology, neuroscience, non-human animal, physiology

The Shifting Perception of Invertebrate Awareness

As industries such as farming and research continue to grow and use invertebrates in a myriad of practices (Delvendahl et al., 2022; Drinkwater et al., 2019), questions regarding their capacity for subjective experience have become pressing. For instance, do farmed black soldier flies experience the full extent of the slaughtering process, which can include starvation, sun baking, and microwaving (Barrett et al., 2023)? At its core, this inquiry seeks to understand whether invertebrates possess a felt awareness of their environment, if our current interactions with them negatively impact their well-being, and how such interactions might be ethically governed, as is standard practice in vertebrate management (Brink & Lewis, 2023). Our response to this frontier of cognitive ethology over the coming years will be critical in shaping policymaking as we increasingly rely on invertebrates as solutions to global challenges, such as food shortages and sustainable agriculture (Barrett & Fischer, 2023).

A common focus for those interested in animal awareness is sentience: the capacity to have valenced, subjective feelings (Birch et al., 2021). These feelings can range from pleasure to pain, but the latter is often of particular interest because of the ramifications it has on how we treat animals (Mellor, 2019). A key issue, though, is that pain is a private, first-person experience and cannot be demonstrated with certainty in another individual, even within our own species (Wideman et al., 2019). Whereas questionnaires and conversations enable us to infer pain in humans (Mogil, 2022), animals cannot articulate the sensations they experience. This challenge has pushed researchers to use alternative lines of evidence as proxies for pain-like states.

One such proxy is the aversive behavioral response of animals to noxious stimulation, with much of this evidence drawn from vertebrates since the late 20th century. Examples include frenetic vocalization (Whitham & Miller, 2024), the active defense or grooming of an injury (Carstens & Moberg, 2000), and perturbations of social and general activity (Khosravi et al., 2021). These lines of

evidence, among others, demonstrate flexible changes in behavior and motivation consistent with pain-like states. The fact that these same behaviors are exhibited by humans experiencing pain forms much of the reason as to why they are used as proxies of pain-like states in animals (Williams, 2019).

Recent evidence suggests that invertebrates may be similarly capable of experiencing pain. Building upon frameworks laid out by Sneddon et al. (2014) and Birch et al. (2021), which propose neuroanatomical and behavioral indicators of pain, researchers have identified a growing suite of pain-like behaviors in cephalopods, crustaceans, and insects (Birch et al., 2021; Crump et al., 2022; Gibbons, Crump, et al., 2022). Except for vocalizations, facial contortions, and changes in social behavior, much of this evidence parallels what is observed in vertebrates. Invertebrates, for instance, display self-protective behaviors (Gibbons et al., 2024; Manzi et al., 2025), associative learning (Yarali et al., 2008), and reductions in aversive responses to noxious stimuli when treated with analgesics (Barr & Elwood, 2024). Despite the compelling nature of this body of work, key gaps still exist, such as whether invertebrates beyond octopuses have a preference for analgesics when injured (Crook, 2021; Groening et al., 2017) and if other groups (e.g., gastropods; Birch, 2024) satisfy the criteria for pain perception.

To further our understanding of invertebrate pain, sentience, and awareness, we must first address a growing concern: the inconsistent use of the terms *noxious* and *aversive*. These terms denote different concepts in the investigation of pain, but historical and recent literature have used them inconsistently and sometimes interchangeably. This relaxed use of the terms hinders our ability to evaluate evidence, especially under leading frameworks that rely heavily on the term *noxious* as part of their inference criteria (Birch et al., 2021). In this commentary, we explore this inconsistency and highlight how it can impede the assessment of pain-like behaviors, using invertebrates as a

case study. We argue that differentiation is needed, and we offer suggestions to standardize language in pain-related research, thereby improving our understanding of invertebrate pain, sentience, and awareness.

Why Should We Differentiate Noxious and Aversive?

The terms *noxious* and *aversive* refer to distinct concepts in the scientific study of pain: the harmfulness of an object or its properties, inferred through physiological damage, and the behavioral response of the animal, respectively. The case for maintaining this distinction stems from both their etymology and the unique role each plays in the behavioral evidence used to suggest that invertebrates, alongside other nonhuman animals, may experience pain-like states. If these terms are used interchangeably, essential parts of this evidence risk being obscured, which reduces clarity and hinders the assessment of the literature. To remedy this, we clarify the distinct meanings and use cases for each of these terms.

Stemming from the Latin adjective *noxa* ('harm'), *noxious* describes the tissue-damaging characteristics of an object or its properties to a subject (Cervero & Merskey, 1996; Raja et al., 2020). In humans, the perception of these *noxious* characteristics can be influenced by age, sex, and affective states (Edwards & Fillingim, 2001; Rhudy et al., 2008; Zimmer et al., 2003). In animals, however, we suggest that the term *noxious* be used in a strictly physiological sense to denote sufficiently intense stimuli that activate nociceptive pathways (Armstrong & Herr, 2026; Sherrington, 1911). We believe this usage offers the greatest consistency, yet we caution against its use without adequate physiological evidence or justification, as the *noxiousness* of a stimulus is determined by its type and intensity in relation to an animal's ecophysiology. For example, a probe heated to a temperature that is innocuous for a lowland-dwelling animal may very well be harmful for a species from an alpine environment (García-Robledo et al., 2016); thus, failure to account for species-level differences can lead to confusion among readers who wish to assess the degree of harm that occurred.

One caveat to our definition is the challenge of determining whether clear physiological damage has occurred in animals when nociceptive pathways are activated (nociception). In humans, nociception can occur without obvious harm (e.g., menthol or capsaicin; Andersen et al., 2014; Frias & Merighi, 2016), underscoring that these two concepts—*noxiousness* and *nociception*—should be teased apart. The question of whether this differentiation

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Acknowledgments: We thank Rachel, Fiona, and Jupiter Wong, in addition to the Invertebrate BEACON Lab, for their insightful discussions regarding this manuscript. This work was partly supported by the Australia Pacific Science Foundation (APSF24014).

	Physiological Damage	Behavioral Response
Noxious	<p>... likely to be noxious as they produced tissue indentation ... (Alupay et al., 2014)</p> <p>... a noxious, potentially painful stimulus induces grooming behaviour in cuttlefish. (Kuo et al., 2022)</p>	<p>... <i>Drosophila</i> nociceptors can be sensitized upon tissue damage, leading to heightened noxious response to both innocuous and noxious stimuli. (Jang et al., 2023)</p> <p>... undefined noxious gaits were observed ... (Reho et al., 2024)</p>
Aversive	<p>... responding to the aversive copper ... (Campbell et al., 2017)</p> <p>... opportunity for the fly to associate one of the stimuli with the aversive quinine experience. (Burns & Saltz, 2024)</p>	<p>... alters an aversive withdrawal behavior. (Babcock et al., 2009)</p> <p>... velvet ant's sting produced aversive behavior in a predatory praying mantis. (Borjon et al., 2025)</p>

Figure 1. Examples of *Noxious* and *Aversive* Use Throughout Pain-Related Literature. In practice, *noxious* has been applied to harmful stimuli and behavioral responses, despite meaning the activation of nociceptors (physiology). *Aversive*, on the other hand, describes observable avoidance (response) but can become ambiguously associated with a characteristic of a stimulus or an implication of a subjective “unpleasantness” toward a stimulus or event. The overlap of these terms blurs the line between physiological harm and behavioral responses, complicating comparison across studies and obscuring evidence relevant to pain. Green cells indicate use aligned with etymology and our suggested framework, and orange cells denote ambiguous and disfavored use that may reduce the clarity of research.

extends to invertebrates, of which we know little regarding pain, makes it a challenge to assess damage beyond obvious markers such as postinjury sensitisation (allodynia) or neural degeneration through excitotoxic processes (Crook et al., 2011; Khuong et al., 2019). To remedy this uncertainty, behavioral or biochemical proxies for damage could be used, but these would work best alongside further research into invertebrate nociceptive systems, particularly in regard to profiling damages that occur when encountering noxious stimuli. Ultimately, any operational use of the term noxious should require an empirically justified threshold, and so we expect our definition to evolve as invertebrate nociceptive systems, and their injury correlates, are better characterized.

Whereas stimuli or their properties (e.g., temperature or voltage) can be described as noxious, the term aversive appropriately depicts an animal’s behavioral response (Lovibond, 1970), reflecting its Latin root *avertere* (‘to turn away’). Such responses are often avoidance based, ranging from reflexive withdrawal to voluntary escape (Magee & Elwood, 2016; Maza et al., 2023), but may also be confrontational (Okada & Akamine, 2012; Stevenson & Rillich, 2016). A common way to study these behaviors is through learning paradigms, where animals build

associations between stimuli and display shifts in preferences or motivation, such as avoiding a once-attractive stimulus (Lyu & Mizunami, 2022; McCurdy et al., 2021) or ignoring aversion-eliciting stimuli in favor of rewards (Gibbons, Versace, et al., 2022).

A complication with the term aversive is that within psychology and associative learning, it has expanded to encompass “unpleasant” states or stimuli (Kauvar et al., 2025; Likhtik & Johansen, 2019; Wang & Delgado, 2021). This definition, by nature, implies subjective experience, which is appropriate in human research but problematic when applied to other animals, where the existence of such states remains debated. To avoid such confusion, we suggest that aversive be reserved for an animal’s expected or observed behavior toward a stimulus or event, unless explicit inferences about experiences are made. Responses to noxious stimulation that are labeled “nociceptive behaviors” also fall under this definition and are therefore better described as aversive behaviors. These responses should be kept conceptually distinct from nociception, understood here as the physiological detection and encoding of noxious stimuli.

Having laid out the definitions of these terms, we can discuss how ambiguity arises when they are used

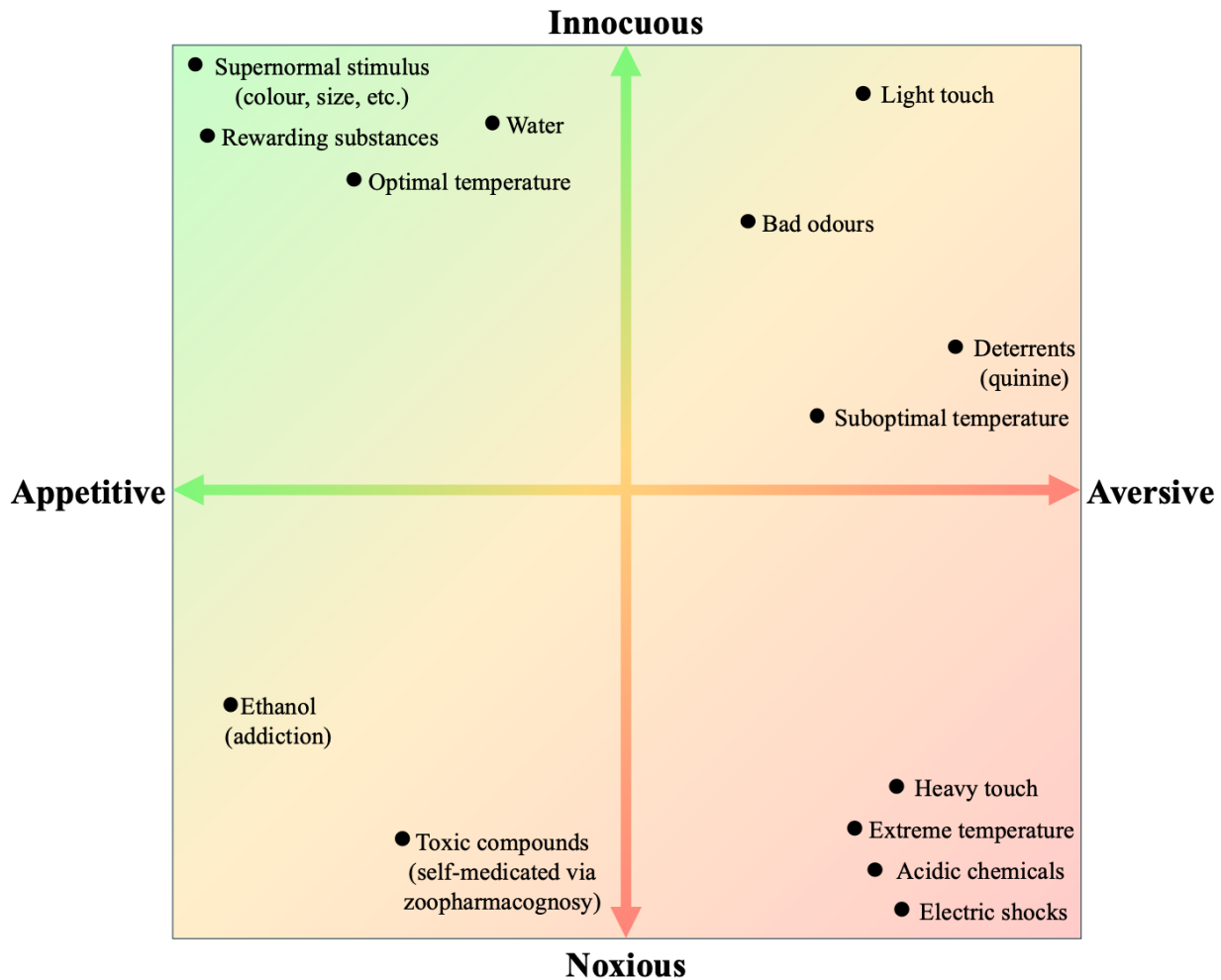


Figure 2. Integration of the terms noxious and aversive in a unified model. The model comprises two spectrums: physiological harm, which is affected by the characteristics of a stimulus that range from noxious to innocuous, and behavioral responses, which span from aversive to appetitive. Together, these axes capture both the putative physiological harm expected when an animal is exposed to a stimulus and the behavioral response the animal is expected or observed to take. Example stimuli have been provided, though their position depends on intensity relative to an animal's ecophysiology, which shapes both harmfulness and response. In this way, each stimulus is plastic and may shift across quadrants at different intensities. Motivation and preference also influence whether a stimulus is treated as aversive or appetitive. Although neither axis alone establishes the experience of pain, using both clarifies and unifies related evidence.

inconsistently or interchangeably (Figure 1). For example, how might a reader interpret the “noxious reactions” and “aversive reactions” exhibited by planarians to high temperatures (Reho et al., 2024), or the “noxious response” and “aversive response” of fruit flies to chemical stimulation (Jang et al., 2023)? In such cases, the term noxious is likely employed for rhetorical variety. Still, when used to describe behavior best captured by the term aversive, readers are left uncertain about whether these phrases denote physiological harm or behavioral responses. In a slightly more ambiguous instance, how would we determine whether the withdrawal of the nematode *Caenorhabditis elegans* in response to “aversive copper” (Campbell et al., 2017) is a description of behavioral avoidance or

the genuine inference of a subjective disinclination toward copper? Here, inconsistent terminology complicates interpretation and risks misaligning studies that might otherwise be comparable.

Beyond semantics, differentiating these terms has practical consequences for evaluating pain-like behaviors, a problem evident within the invertebrate literature. The behavioral criteria of the Birch et al. (2021) framework rely on a stimulus being noxious when judging whether a behavior suggests a pain-like state. Thus, any record of a stimulus that causes physiological damage to an animal would be relevant. Issues arise here because of the interchangeable use of noxious and aversive throughout the literature, alongside the fact that idiosyncratic behavioral

responses exist from one animal to the next, even in those that share the same genome (Smith et al., 2022). How then might researchers assess the relevance of two studies under leading frameworks if one describes a temperature as noxious and the other refers to a similar temperature as aversive (Aldrich et al., 2010; Kavaliers & Hirst, 1986)? Initially, the first study would be taken to indicate that physiological damage occurred (Aldrich et al., 2010). The second, however, could have described observed avoidance behaviors, or even implied a subjective dislike, without clarifying whether the temperature was damaging for that particular animal in a way that might elicit nociception and potential pain-like responses (Kavaliers & Hirst, 1986). Extending this hypothetical, if a third study describes the chemical quinine as aversive (Zhou et al., 2024), should the second “aversive temperature” study then be treated as comparable to quinine, despite apparent differences in stimulus type, intensity, and potential for physiological harm? This problem can become compounded if neither term is used (Nakamura & Yamashita, 2000). Such examples illustrate how the casual interchange of these terms—particularly aversive, given its long history in associative learning—may hinder our assessment of past and emerging literature on animal pain.

Integrated Use of Terminology

We propose a simple solution to this growing problem. The key distinction between noxious and aversive stimuli lies in their placement on two separate scales (Figure 2). The term noxious belongs at one end of a spectrum of physiological harm, opposite the term innocuous, and describes the degree of damage a stimulus will inflict on an animal. Aversive, on the other hand, sits at one end of a behavioral spectrum, with the terms neutral and appetitive at the other points, and denotes how an animal is expected or observed to respond to a stimulus or event. Through the distinction of these terms and subsequent integration of evidence corresponding to both concepts, we can capture both the degree of physiological harm a stimulus produces and the behavioral response it elicits in an animal. Maintaining this distinction will improve writing clarity, highlight avenues for future research, and strengthen inferences about an animal’s capacity for subjective experiences.

Consider the following complementary examples where standardized use of these terms either clarifies interpretation or identifies gaps in our understanding. In the study of animal drug addiction, unnaturally high doses of ethanol are initially aversive to fruit flies, shown through conditioned avoidance behaviors (Gelfand & McDonald,

1980; Kaun et al., 2011). Despite its harmful effects—namely, oxidative stress and inhibited motor control (Logan-Garbisch et al., 2015; Scholz et al., 2000)—sustained exposure to high ethanol concentrations often leads to a conditioned attraction from an initial avoidance; behaviors best described as addiction. In this case, the once-*aversive*, *noxious* stimulus now becomes an *appetitive*, *noxious* stimulus, which can drive motivational trade-offs (a key line of evidence for pain perception), in which other stimuli that elicit aversion, such as electric shocks and quinine, are endured to reach a valued reward (Devineni & Heberlein, 2009; Kaun et al., 2011). This phrasing clearly distinguishes between the physiological harm of ethanol (noxious) and the shifting behavioral responses it elicits (aversive to appetitive).

A second case in which distinguished terminology is helpful comes from work on the venom from the velvet ant, *Dasymutilla occidentalis*, which is composed of a peptide cocktail, with at least three (Do6a, Do10a, and Do13a) activating nociceptive acid-sensing ion channels in animals (Borjon et al., 2025). Do10a and Do13a are *noxious* to mice, demonstrated through the excitation of nociceptive pathways that trigger *aversive* behaviors such as limb licking, tapping, and shaking. The Do6a peptide, however, appears *innocuous* and *neutral* to mice, whereas being *noxious* to one species of invertebrate and eliciting *aversion* in another. In fruit fly larvae, Do6a activates nociceptive neurons for more than 200 s, consistent with noxiousness, but no behavioral responses—aversive or otherwise—were reported (Borjon et al., 2025). By contrast, the same study qualitatively described how an unspecified mantid species displayed flexible, pain-like self-protective behaviors by grooming the site of a velvet ant sting for several minutes, though no tests of physiological noxiousness were conducted. Whether fly larvae respond aversively to velvet ant stings, or whether mantids suffer physiological harm, remains unresolved. Here, maintaining the distinction between noxious and aversive highlights two promising research avenues that would otherwise be obscured.

Ultimately, the importance of using these terms in tandem is that neither physiology nor behavior alone can support inferences about pain. If an animal grooms after exposure to high temperature, we can only conclude that a shift in thermal conditions elicited grooming behavior. To reach further and suggest that the grooming behavior is indicative of a negative experience, such as pain corresponding with a site of injury on the body, we would also need to demonstrate that the increase in temperature caused physiological harm and was therefore noxious. In

cases where physiology and behavior are both observed and reported, we can make richer inferences about subjective states, such as pain. This is why the motivational trade-offs of bumblebees, enduring noxious heat to obtain a sucrose reward, are considered compelling evidence (Gibbons, Versace, et al., 2022). The same applies to animals that exhibit zoopharmacognosy, where compounds are ingested at toxic concentrations to attenuate the effects of pathogens (Bos et al., 2015) or parasites (Baracchi et al., 2015; Milan et al., 2012), but only under circumstances in which the compounds are beneficial. Finally, this integrative approach is crucial in the broader investigation of sentience, where, for example, agricultural stakeholders discuss the degree to which certain stimuli are noxious and/or “painful” under current pain assessment frameworks in reference to aversive responses (Steagall et al., 2021).

Toward The Future

As research on invertebrate pain progresses, a clear distinction between the terms noxious and aversive will become increasingly essential. Beyond semantics, differentiating these terms will help us assess bodies of work related to pain-like behaviors more objectively, uncover gaps in our understanding, and improve the clarity and interpretation of research. More broadly, standardizing this terminology will help unify the language of pain research and strengthen its application in developing areas such as invertebrate welfare, sustainable farming, research ethics, and conservation practice. Strengthening our understanding of animal pain perception will have a ripple effect on our understanding of sentience and awareness in general, as we attempt to tackle questions that have long stimulated philosophers and researchers.

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