Invertebrate sentience: a review of the behavioral evidence

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INTRODUCTION

Invertebrates are animals that do not possess or develop a spinal column, including insects, mollusks, and corals. Although the exact number of invertebrate species that exist on Earth is not known, estimates repeatedly find them to comprise 95% of all animal species[1] and greater than 99.9% of all individual animals.[2] Because of the enormous number of invertebrates, if invertebrates matter morally, they are also of enormous moral importance.

Invertebrates matter morally if they are sentient. Sentience is the ability to have subjective experience. It is sometimes described using the related words *consciousness* or *phenomenal consciousness*. If invertebrates are sentient, this would mean they have the ability to experience pain and pleasure, features that would warrant them inclusion in our moral circle. Since what happens to them matters to them, sentient animals have states of welfare, and so can be helped or harmed by events that increase or decrease that welfare.

Unfortunately, the situation of invertebrates is grave. Invertebrates are harmed in human activities across many varied sectors and industries: crustaceans, insects, and mollusks are killed and eaten; cuttlefish are killed and their ink is extracted for use in cooking; cochineals are killed for dye production; and silkworms are boiled alive for silk production.[3] Many are also killed by insecticides. Beyond this, invertebrates in the wild face constant threat of disease, starvation, changes in their environments, and other sources of harm. Were an invertebrate in any of these situations replaced with an animal we attribute sentience to, such as other humans or large mammals, it would appear self-evident that these experiences would cause a great deal of suffering.

Therefore, whether invertebrate animals possess sentience is a key question. If invertebrates are sentient, this would mean they have the ability to experience pain and pleasure, features which would warrant them consideration in our moral circle.
Currently our ability to answer this question is limited because there is still little research into this topic, despite its evident importance. The difficulty of this task may be a key reason for this. Given that we have

not yet solved the hard problem of consciousness we do not have an understanding of how and why sentient beings have phenomenal experiences. However, further investigation into the anatomical and behavioral features of a range of invertebrates would aid our estimates of which of them are conscious.

Relevance of behavioral evidence in estimating sentience

Because consciousness is subjective,[4] one cannot access the mind of anyone else in this manner to verify their consciousness.[5] This is known as "the problem of other minds," and provides an obstacle to evaluating sentience. Observing behavior cannot directly give access to the discrete and personal nature of the conscious experience.

There's another reason why behavior alone can't be used to differentiate between unconscious and conscious actors. This is because a wide range of sophisticated behaviors can be coordinated as a result of unconscious mechanisms, as programmed responses. These span from reflexes in humans to robots programmed to respond to particular stimuli with behaviors that mimic pain to artificial intelligence able to play chess. Currently, neither robots nor plants are considered to have the anatomical or behavioral features required for consciousness,[6] showing the danger of relying too heavily upon behavior.

This does not mean, however, that conscious experience in others cannot be assessed from the outside, or that the observation of behavior is useless. Sentience can be assessed through arguments from analogy or by inferring sentience as the best explanation for observed behaviors. An argument by analogy is an argument that because two things share certain known similarities, they may also be similar in other respects as well. For example, if the behavior of invertebrates resembles the behaviour of larger animals, since those larger animals are sentient, invertebrates may be sentient as well.[7] We can use this type of argument to investigate the presence of consciousness in invertebrates by looking for similarities between the anatomical and behavioral characteristics that are seen in both invertebrates and in other animals we already believe to be sentient. The problem of other minds does not mean that one cannot be confident that any organism other than oneself has a conscious experience. It just shows why the methods available to estimate the sentience of nonhuman animals does not allow for a definitive answer.

This review does not seek conclusive evidence, but rather to (1) identify the behavioral features that provide probabilistic evidence of sentience and (2) evaluate the extent to which these are seen in invertebrates. Considered in conjunction with neuroscientific and evolutionary perspectives, a better understanding of behavioral indicators can contribute to more informed estimates of the likelihoods that different types of invertebrates are sentient. This knowledge will help us understand how human activities impact the wellbeing of invertebrates so that we can avoid harming them and help them when we can.

BEHAVIORS MOST LIKELY TO REFLECT SENTIENCE

This review focuses on three main categories of behavioral features that appear likely to reflect conscious experience. They are behavioral flexibility, emotion-based behaviors, and social behaviors. These do not cover every type of behavior which may be relevant.

Behavioral flexibility

Behavioral flexibility is presented here as a category of behavioral traits displaying the ability to adapt to changing environments. These include learning, adaptive behavior, and cognitive generalization. These behaviors involve the integration of different types of information and the storage of this information to be applied to future scenarios.

One of the possible roles of consciousness is to facilitate flexible behavior, which may play a role in allowing us to assess different options and decide on an overall best option.[8] Our well-practiced action routines such as riding a bicycle also often have minimal conscious involvement, whereas novel situations and the flexible responses they demand typically require more conscious involvement. We can therefore gain insights into which entities are conscious by examining the extent to which their behavior is rigid or flexible.

One illuminating example of flexible behavior in invertebrates is by funnel ants in a study by Lőrinczi et al (2017).[9] These ants were found to use available absorbent objects to transport water or sugar water back to their hive. When given different materials to perform this task, the ants quickly learned that sponges were the most absorbent and began to preferentially use them. They even cut the sponges into smaller segments that they could more easily carry. If they were only acting in a predetermined way, we would not expect them to learn that novel materials like sponges worked best for their goal of transporting liquids, as they did. This shows some ability to understand different levels of absorbency and to flexibly choose the substance that is most effective in meeting their goal.

Flexible tool use is also seen in veined octopuses. These animals have been found to carry around split coconut shell halves to use as a kind of protective shell against predators. Because the shells are a burden to carry around, the octopuses must use a novel form of locomotion called "stilt walking."[10] Carrying around shells that are a burden in most situations, but very useful in others probably represents foresight. In addition, because humans are the source of the split coconut shells, veined octopuses probably have not had time to specifically evolve this behavior. Instead it represents flexible behavior.[11] The amount of evidence available makes it hard to maintain that octopuses are not sentient.

Conditioned place preference is another kind of behavioral flexibility. Conditioned place preference works through the "wanting" reward system which increases the perceived attractiveness of a stimulus rather than inducing the affective state of liking it, meaning an affective conscious state is not necessary for a reward system to operate.[12] However, the ability to develop an association and a new learned response to form a conditioned place preference suggests an integrated system. This decreases the likelihood of an unconscious, rigid, programmed organism. It is a form of learning based on the reward system, so it may reflect sentience.

It appears that the most flexible behaviors occur in conscious organisms because they can apply themselves cognitively to choose between a range of dynamic options with a degree of unpredictability. Behavioral flexibility can also be seen in cases where animals are able to respond appropriately to new contexts with complex behavior despite this context not being part of their ancestral environment. This means they would not already have an appropriate evolved response; rather they are able to apply behaviors across contexts.

It seems the more flexible and complex the behavior of an organism is, the less likely that the full range of behaviors can be explained merely by stimulus-response mechanisms. They could, however, be explained by conscious experience and cognitive ability. The behaviors reviewed here appear to be sufficiently complex to require consciousness. They are present in conscious animals like humans and other mammals, and they may be indicators of consciousness.

EMOTION-BASED BEHAVIORS

Emotions can be considered as having primitive states which are common across species that share similar traits.[13] However, these states may manifest themselves through different behaviors across different species. These basal emotional states have three fundamental characteristics: valence (positive or negative), scalability (intensity) and persistence (emotional behaviors that outlast the stimuli that triggered them and generalize to other contexts). Looking for evidence of these three characteristics in invertebrate behaviors offers a way to assess whether invertebrates experience emotional states.

However, there might also be emotional behaviors that appear to reflect conscious basal emotional states but which are simply behaviors from an unconscious state. Therefore it would be wrong to assume that the presence of these fundamental features of emotional behaviors ensures a conscious emotional state. It can nonetheless be acknowledged that all three features of valence, scalability, and persistence are present in conscious human emotional states and so evidence of all three in an invertebrate increases the likelihood that a conscious emotional state is being experienced.

Evidence of emotional state indicators

Valence can be identified through interpretations of the behavior of more mentally complex invertebrates like honeybees. Honeybees have displayed a pessimistic cognitive bias after a predatory threat.[14] After such a threat, the bees were more likely to interpret ambiguous stimuli as negative, withdrawing their proboscis as an indication of this, as well as increasing their withdrawal from a similar threat. This shows generalization in behavioral response, which is a characteristic of emotional states.

Bumblebees have exhibited a positive emotion-like state following exposure to unexpected rewards.[15] After having a positive experience, bumblebees who subsequently face a threat took less time than usual to return to normal foraging behaviors after the situation passed. These behaviors suggest that the bees can interpret experiences on a scale of positive and negative. Persistence in the form of contextual generalization, the maintenance and application of a cognitive state to other contexts, is an indicator of emotional experience due to the presence of a cognitive state. Bumblebees have demonstrated this through the reduced time taken to continue normal foraging behavior, applying their positive emotion-like state as a result of a positive stimulus to their decision-making, and reducing their innate response of increased caution to a threatening situation. These behaviors suggest that the bees can interpret experiences on a scale of positive and negative.

Differentiating true emotional states and behaviors that have occurred as a result of the experience of emotion from programmed, unconscious behaviors such as reflexes presents a significant challenge. There are multiple parallel responses to conscious emotional states (behavioral, endocrine, autonomic, cognitive), whereas unconscious states cannot produce the cognitive aspects.[16] This aspect can be seen through the lasting cognitive biases observed in bees.

However, there is a case to be made that these behaviors, which could indicate an emotional experience, could also be complex pre-programmed responses. Indeed, some robots have been made that arguably have the capacity for complex cognition, including the use of artificial emotions producing context-dependent behavior as a result of varying degrees of responsiveness of particular circuits to inputs.[17] Other interpretations have been provided for the observations in these experiments that do not involve subjective experience, but rather refer to the fact that the bees may be adapted to respond with pre-programmed caution to a dangerous environment.[18]

Evolutionarily, emotions have an adaptive function, coordinating the response of an individual to a fitness related priority after integrating information from the environment and body. Although behaviors observed from a conscious and unconscious entity may not be distinguishable, considering the type of entity can allow for a more accurate assessment of the likelihood of sentience. Evolutionarily, emotions have an adaptive function, coordinating the response of an individual to a fitness related priority after integrating information from the environment and body.

Consciousness emerged at some point in evolutionary history, resulting in particular behaviors such as the ability to experience emotional states and respond to them. However, it is not known *when* consciousness first evolved. Therefore, when nonhuman animals display the behaviors we have described as indicating consciousness it seems plausible that there is a common conscious experience. In the case of artificial intelligence systems it appears much less likely that the mechanism for these behaviors is rooted in consciousness given that the evolutionary history is not shared. Rather, their behaviors may only superficially resemble indicators of consciousness. This means that though we cannot be certain of the presence of emotional states in invertebrates, it is likely that the behaviors discussed indicate an emotional experience of some kind.

SOCIAL BEHAVIORS

Social behaviors and communication provide a fair indicator of likely sentience.

Complex social behaviors which have emerged through the evolution of animal societies require efficient interactions between organisms who must understand each other to survive or succeed in reproducing. This requires an awareness of external events and potentially a nuanced understanding of their effects. Communication may also require some degree of self-awareness in order to modulate the message being sent. This degree of self-awareness might indicate that an animal is conscious according to, for example, higher order theories of consciousness. This case is strengthened when it can be shown that social and communicative behaviors which may be innate to an organism can be adapted and applied across different contexts, showing a level of integration and reducing the likelihood that it is the result of a purely unconscious chain reaction.

Drosophila species have demonstrated an ability to learn dialects through communal living.[19] Indeed, isolated naïve *Drosophila* females, when paired with experienced females, were able to show partial communication similar to when normal flies are paired. In this way, cohabitation allows for communication to be enhanced, through visual and olfactory signals. The ability for communication between animals of this species of fruit fly is innate. However, the extent to which it can convey information is developed through socialization. Neural plasticity allows for the hard-wired ability of communication to be developed, requiring active learning through the integration of multiple sensory inputs, showing a level of flexibility to this behavior.

Honeybees further demonstrate social behavior and communication. The observation of Asiatic and European honeybees[20] suggests that each species has their own dialect of the honeybee waggle dance, a remarkably complex method of symbolic communication which allows for foragers to convey the location of a food source to their hive mates. It has also been observed that different species (Asiatic and European honeybees) in the same colony are able to communicate with each other through their waggle dances. The Asiatic honeybee species demonstrated the ability to decode the waggle dances of the European honeybee species, and as a result, locate the food source being advertised. Thus it appears that social learning between honeybee species is possible, and that the seemingly innate honeybee waggle dance may have a more malleable learning aspect to it. These honeybees show flexibility to their behavior, which indicates increased likelihood of sentience.[21]

Most species of ants and termites have a complex communication system mediated through chemicals, but even more surprising social behavior has been found in a species of ants who do not use chemical trails to communicate. The “tandem running” in the species *Temnothorax albipennis* may be a case of teaching behavior.[22] After discovering a new food source, ants of this species will choose another ant to guide towards it. The teacher ant will move much more slowly during this instruction process, allowing the pupil ant to look around and memorize the route. When the pupil ant is ready to proceed, she will tap the teacher ant with her antennae to indicate this. This shows that, in order to facilitate learning, the teacher ant acts differently in the presence of the pupil ant and that there is bidirectional feedback between the two.[23] This shows some level of understanding of the mind of the other ant, as well as a level of self-understanding, in order to communicate in this way.

Cuttlefishes show some of the most sophisticated social behaviors. They are cephalopods, a group of invertebrates that have the most advanced brains and behavior among invertebrates. One example of this is the social behavior demonstrated in the mating behavior of cuttlefishes. Male cuttlefishes will alter their behavior depending on if they are interacting with a male or female. Some small male cuttlefishes will deceive other males who are guarding females by mimicking the appearance and behavior of females. They do this to avoid detection while they attempt to mate with females.[24] Deceptive behavior is an advanced social behavior. The significance of society in some insect species, such as cockroaches, can be understood from the behavioral consequences of social isolation.

Socially isolated cockroaches exhibit a behavioral syndrome, with behaviors integral to their survival being inhibited or reduced. This includes a decreased rate of foraging and an increased exploration avoidance. These responses mirror behavioral effects seen in socially isolated vertebrate animals, with a decrease in displayed interest in exploration and new environments. Notably, this alone does not increase the likelihood of sentience in invertebrates as plant species have also been found to interact and exchange information between organisms that allows them to thrive, with isolation showing detrimental effects to growth and development. However, a substantial difference between these two examples when considering the likelihood of sentience is the much closer evolutionary relation between invertebrate animals and the vertebrate animals who we deem sentient than between plants and invertebrate animals.

CONCLUSION

Several points have become apparent from this literature review. One is that invertebrates from different groups demonstrate a range of complex behaviors showing continual interaction between the organism and their environment in all three of the categories of behavior explored (behavioral flexibility, emotion-based behaviors, and social behaviors).

Another is that behavior is inadequate as a sole determinant of the presence of sentience in invertebrates. It should be used in conjunction with other forms of evidence, especially neuroscientific evidence.

The examples of invertebrate behavior we have discussed here are what would be expected from a conscious being, with many similarities to the capabilities of birds and mammals. This provides a guide to showing how it is possible that invertebrates have a conscious internal state. However, the fact that these behavioral indicators can be replicated to some extent in robots shows that their presence does not mean sentience can be assumed without further investigation. The difference between robots and invertebrates is key in considering these opposing principles. Invertebrate animals are biological organisms with an evolutionary relation to other animals like humans who we already attribute sentience to. Knowing sentience to be present in these animals, such as humans, and knowing conscious experience to be the basis for human behaviors which are mirrored to some extent in invertebrates, provides a reason to consider that at least some invertebrates have the capacity for conscious experience even though this cannot yet be definitively verified.

State of the behavioral literature and scope for future research

Although there have been several iconic studies observing the behaviors of invertebrates that have set a precedent in this field, the depth of these studies is lacking, with most such experiments being recent.

Most studies in the literature cover only a select handful of organisms; however, the range of invertebrates is so large that a greater variety of taxa observed and tested would allow for a better understanding of the trends in the complexity of behavior across different taxa. Furthermore, observing the behavior of invertebrates alone cannot provide a definitive answer as to whether they are sentient or not, with even the indicators of conscious experience used in this essay shown to still be insufficient to prove sentience. A larger base of invertebrate behaviors will allow for a more accurate comparison between them and assumed sentient animals. The closer their behaviors are to what is expected from sentient animals, the more plausible it will be that they too are conscious.

The moral position on what kind of moral consideration to give to invertebrate animals depends on the answer to the question of whether they are sentient. However, if this cannot be definitively answered then different approaches may be applied. One of them, Morgan's canon,[25] states that the presence of psychological states, the ability to have a conscious, emotional experience, should not be assumed if a simpler explanation or mechanism can be put forth. Indeed, the above paragraph outlines how this is possible, how behaviors that potentially indicate emotional states can be mimicked in the programming of robots. Another approach, the precautionary principle,[26] suggests we should err on the side of providing protection and moral consideration of a group of animals if there is some reason to consider them sentient. Yet another one is a Bayesian approach that considers the expected consequences of assuming and rejecting invertebrate sentience in relation to the probability that they are sentient. If such probabilities were non-negligible, then the huge amount of harm invertebrates could suffer by not being given moral consideration would render the case for giving them consideration very strong. If, as we have seen here, such probabilities are very high, then the case for giving moral consideration to invertebrates becomes even stronger. The latter two views are increasingly supported by some who are skeptical of invertebrate sentience on neurological grounds.[27] This might be due to the spread of respect for the idea of nonhuman animal sentience in general.

Further readings

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