What is it like to be an invertebrate?

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I. Introduction

We assign moral value to other people based on a variety of factors including social norms, physical and temporal proximity, and similarity to ourselves. One key factor is what sort of mental capacities we think someone has. This morally relevant mental capacity is often referred to as consciousness or subjective experience. When we consider the ethics of our treatment of nonhuman animals, consciousness becomes a paramount consideration. In the cases of primates, mammals, and birds, the behavioral evidence itself seems to clearly indicate a conscious experience. However, the number of mammals and birds on earth is vastly outweighed by the number of invertebrates. So there exists an obvious need to collect and review the evidence of invertebrate consciousness to inform this moral question.

In this paper, we address invertebrate consciousness from a purely scientific, material perspective. Consciousness will be defined by the set of physical processes we recognize as perception, thought, and emotion such as the smell of the ocean, the feeling of anger, and the look of the color green. This paper will focus primarily on emotion, or affective consciousness, since it is widely considered the most morally relevant aspect. This paper will not address the more ineffable philosophical concepts of consciousness such as dualism or purely subjective experience, which are difficult to assess for humans and nonhumans alike.

We worry about the existing literature that rejects evidence of animal consciousness based on such notions, with claims like, “Well, this animal might show such-and-such behavior and such-and-such neuroanatomy, but we can’t really *know* they are conscious since consciousness is purely subjective. For all we know, it could just be sophisticated reflexes." This sort of argument involves an implicit assumption that consciousness is some sort of indescribable, supernatural phenomenon beyond physical processes. This notion of dualism holds no basis in the scientific evidence and would likely be rejected upon further reflection by the authorities who make such claims. And even if we granted this notion, similar arguments of uncertainty would also hold up for other humans and are therefore not compelling bases for discrimination against nonhuman animals. Additionally, analogous arguments can be made in the other direction, "Well, this animal might show such-and-such behavior and such-and-such neuroanatomy, but we can't really *know* they are not conscious since consciousness is purely subjective." In this paper, we avoid such qualifications and instead address consciousness as only the physical processes.

First, we consider a simple foundation of negative experiences, nociception. Second, we will consider higher-level conscious processing like generalized emotional states and integrated input from various sensory domains. Third, we will investigate evidence for intelligence in invertebrates, taking the example of cephalopods, and discuss the interaction between intelligence and consciousness. Fourth, we consider the two cases of bivalves and crustaceans. Then, we assess the general conclusions for invertebrate consciousness.

II. Nociception

A natural and well-understood starting point for consciousness is the presence of nociception, the ability to react to and avoid harmful stimuli. For example, the larvae of *Drosophilia*, commonly known as 'fruit flies,' display a distinct rolling behavior when subjected to aversive thermal and mechanical stimulation. This is mediated by the class IV multidendritic neurons. These neurons are similar to the nociceptors of vertebrates in that they utilize naked dendrites rather than specialized receptor cells.[1]

Insects also display more complex nociception in realistic situations like violently struggling when trapped in a spider's web and could have other nociceptive processes like using certain firing patterns through non-specific sensory neurons. This has been a proposed mechanism for nociception in some mammals as well. However, nociception is also seen in unconscious humans with simple reflex processes, therefore it is not a perfect indicator of consciousness.[2]

Despite this limitation, we can still argue that because nociception is followed by conscious processes in our own central nervous systems, it is at least some evidence for conscious processes via an argument by analogy.

III. Higher-level Processing in Insects

In mammals, nociception is transmitted through 'A delta' and 'C' classes of nerve fibers, which enter the spinal cord through the dorsal root ganglia. The signals then travel through the ventro-lateral spinal cord to multiple brain systems, including the limbic system and cortex. Unfortunately, the details from that point forward are currently poorly understood. In insects, we do not know of analogous pathways, but it is certainly the case that they could exist given

[1] Tracey et al. 2003
[2] Eisemann et al. 1984

our limited understanding of the brain. In fact, endogenous opioid peptides and receptors have been found in insects, which are known to mediate responses to pain and other processes in mammals and thus could serve as imperfect evidence of analogous processes.[2]

At least one study suggests a function of opioids specifically related to nociception in insects. Crickets have been shown to escape at increasing speeds from temperatures of 49° to 56° C. In the study, crickets were placed in a box heated to 54°C and injected with either 0.32, 0.52, or 0.69 mg/g of morphine, which is an opioid agonist, or 0.9% saline solution. The crickets injected with each concentration of morphine showed a decreased escape response time from the heated box. They also exhibited symptoms of addiction – a suppression on the fifth day of morphine produced "big jumps," a hyper-response to vibration. They also exhibited drug tolerance after repeated injections of a 0.50 mg/g dose of morphine. When 0.064 mg/g of naloxone, an opioid antagonist, was added to 0.50 mg/g of morphine, the morphine effect was fully blocked. And the addition of more than 0.064 mg/g naloxone alone increased the escape response time of the crickets, similar to the effect in vertebrates. Although this could be a function of something other than pain mediation, it does seem to be a likely explanation due to the similarities with vertebrate responses in each of these aspects.[3]

One key example of higher-level conscious processing in our own minds is response to physical injury. In humans, we know that some behaviors are caused by suffering rather than simple nociception like the withdrawal of an injured limb, protection of injured body parts, or stopping

[3] Zabala and Gómez 2991

normal behavior when injured. In insects, however, these behaviors have not been observed. Examples include a locust continuing to feed while being eaten by a mantis and male mantids that continue to eat while being eaten by their partners. Although this evidence does not preclude the presence of suffering, it is evidence that the suffering, if any, of insects is fundamentally dissimilar to our own in that it does not seem to be tied to these behavioral responses. Without behavioral consequences, suffering would presumably lack an adaptive benefit, which makes it seem less likely to exist in insects. However, as is the case with neuroanatomical processes, there could be behaviors in insects that do satisfy the adaptive function of consciousness that we do not fully understand.[2]

One example of higher-level processing is the ability to integrate information from various sensory domains. An example of this is cross-domain overshadowing, which occurs when conditioning to a compound stimulus, one with two distinct components like a triangle and circle, is weaker than conditioning to each individual stimulus. Researchers found overshadowing in honeybees when both components were of the same sensory domain like smell or vision. When different domains were used, no overshadowing occurred, and the strength of the compound stimuli was equal to the sum of the strength of its components. Similarly, blocking involves (i) conditioning to a single stimulus, (ii) conditioning to a compound stimulus including that first stimulus, (iii) conditioning to the second stimulus from the compound stimulus. Blocking occurs when the conditioning to the second stimulus is weaker than it would be if the subject were conditioned to that stimulus alone. This also only occurs in honeybees when the stimuli are in the same sensory domain. This seems to indicate that honeybees lack at least one key version of consciousness, the integration of various sensory domains. But this could just indicate a different form of consciousness than we experience, one that is more domain-specific.[4]

However, one interesting behavior indicative of insect consciousness is the pessimistic cognitive bias exhibited by agitated honeybees, an effect also found in humans. Researchers conditioned honeybees to associate a 1:9 ratio of a two-component olfactory stimuli with reward and a 9:1 ratio of the same two-component olfactory stimuli with punishment. Then some bees were agitated by shaking them in a container for 60 seconds, designed to simulate a predatory attack on a bee colony by a honey badger or other similar predator. An additional set of bees was also shaken and used to measure changes in biogenic monoamine levels. These bees exhibited significantly reduced levels of octopamine, dopamine, and serotonin. The experimental bees were then shown stimuli with features between the two conditioned stimuli in two-component olfactory stimuli ratios of 3:7, 1:1, and 7:3. Shaken bees were more likely to interpret the 7:3 and 9:1 stimuli as indicative of punishment than bees who were not shaken, indicating a general pessimistic cognitive bias. Since their interpretation of the stimuli was judged by whether they extended or withheld their mouth-parts, it could be the case that the pessimistic bias was simply an aversion to extending their mouth-parts, but the agitated honeybees were not less likely to extend for the 1:9 stimuli. This confirms that these results were actually indicative of a pessimistic cognitive bias. Additionally, the effect was shown to be consistent across various concentrations of sucrose or quinine as the unconditioned stimuli.[5]

[4] Vitti 2010
[5] Bateson et al. 2011

This is a particularly important finding for two reasons. First, it shows a holistic mental response. Rather than simply having one behavioral response to one specific stimuli in a single domain, the bee is stimulated in one domain – physical agitation – and shows an altered response in a different domain – judging ambiguous stimuli. Second, the effect shows a great similarity to negative emotion in humans, as our negative conscious states also lead to a general pessimistic bias. This, to me, is the strongest single piece of evidence for insects having some meaningful sort of consciousness for these two reasons.

One behavior in spiders, a group closely related to insects, is autotomy. Orb-weaving spiders remove their own legs where they detect certain venoms used by some of their prey. This response is interesting in that it is similar to the withdrawal of an injured limb in mammals in its complexity, but is more stereotyped like simple nociceptive response behavior. This might be indicative of a mental life that is no less rich, but still different than ours in insects. It is also suggestive of degrees of consciousness, where it is beneficial to consider consciousness as a spectrum of complexity and richness rather than a switch that is turned on at some arbitrary level of complexity.[6]

The rest of this paper will consider invertebrates more generally, highlighting some particularly interesting cases. Nociception, again defined as the ability to react to and avoid harmful stimuli, is common to all invertebrates with the possible exception of *Porifera*, or sponges. For example,

[6] Eisner 1983

Cepea nemoralis, a gastropod land snail, shows a foot-lifting behavior when exposed to a surface with temperature exceeding that of its native habitat. Even protozoa show some simple forms of nociception like changes in locomotive speed and direction.[7]

This might be best thought of as some extremely primitive level of consciousness since it is not clear where the dividing line between nociception and consciousness is, despite the intuitive appeal of having such a line. But we will attempt to gauge each individual case to see where it lies on this spectrum of consciousness.

IV. Intelligence in Cephalopods

One promising candidate for further investigation into invertebrate consciousness is the cephalopods, a group with an established literature on their intelligence. It is important to distinguish intelligence from consciousness, as we can easily imagine very intelligent computers that lack any processing reminiscent of our own emotional states and therefore would not warrant moral value. Despite this limitation, intelligence could be an indicator for consciousness. A useful framework here, which we will use moving forward, is to think of consciousness as a basic mental state and the ability to reflect and more deeply process this basic state. In this way, intelligence can magnify the basic conscious experiences and make them more worthy of moral consideration. We might intuitively call this framework self-awareness, although note it is not an on/off classification as, again, might seem like an intuitively appealing approach. We illustrate this framework using evidence for cephalopods,

[7] Kavaliers 1988

which are well-studied, but note that it also applies to many social insects and other invertebrates. However, it does seem that the raw emotions represent the best and worst of the human experience, such as the pain of torture or serious illness, the utter grief of losing a loved one, or the joy of physical intimacy, all of which seem to be deeply conscious experiences despite their unreflective nature. It could also be the case that consciousness without intelligent reflection is similar to being in a dream or on certain drugs.

One example of cephalopod intelligence is tool use. Tool use was long considered a defining feature of human intelligence, but has since been discovered in other primates and even other mammals and birds. More recently, tool use has also been documented in soft-sediment dwelling octopuses. Researchers observed octopuses carrying portions of coconut shells, which are cumbersome and require the carrier to 'stilt-walk,' a form of locomotion where the octopus sits in the coconut shell while extending their arms over the edges to walk. Stilt-walking is costly, in terms of energy requirements and predator susceptibility, but they seem to make a motivational trade-off because that cost is outweighed by the benefit of using the coconut shell to set up shelter when needed. Other examples of tools used by invertebrates are the leaves and pellets used to collect and transport food in some ant species.[8]

Tool use and other reasoning capabilities could indicate a certain understanding of objects and concepts across time. In the case of tool use, this means perceiving these objects as having their potential use at a later point in time. In a similar fashion, creatures that show tool use

[8] Finn et al. 2009

could have a deeper perception or reflection of their own emotions. For example, a human going through anger management classes and working to avoid anger could respond to his own anger with further anger or sadness because he failed to achieve his goal.

Additional evidence cited for cephalopod intelligence and consciousness comes from brain physiology. The octopus brain exhibits lateralization like ours does. For example, studies have shown that octopuses can learn to discriminate stimuli with one eye and perform the discrimination with the other eye. Even birds lack this ability. The octopuses fail to make this switch if the connections between the two halves of the brain, similar to our corpus callosum, was severed. Octopuses also sleep in a similar way to our own. They narrow their pupils, withdraw into their home, and become unreactive. Because the octopuses also undergo a particular color change sometimes during sleep, some researchers suggest they exhibit a mental state similar to REM sleep in mammals.[9]

Cephalopods also exhibit play behavior, defined as “activity having no immediate benefits and structurally including repetitive or exaggerated actions that may be out of sequence or disordered.” Eight subadult octopuses, five males and three females, were each presented with four novel plastic pill bottles, weighted to just above neutral buoyancy and varying in color (white vs. black) and texture (smooth vs. rough). The objects were presented to each octopus twice daily for five days. Each session ended when the octopus made no contact with the object for 30 minutes. Two of the octopuses sprayed jets of water at the objects, moving them

[9] Mather 2008

towards the tank intake water flow, which then pushed the objects back for another jet, similar to bouncing a ball off a wall.[10] [8]

It is difficult to infer consciousness from such behavior, but we consider play to be an important consequences of our own rich mental lives. It could also indicate the possibility of boredom, an important consideration for the welfare of invertebrates in captivity.

Another example of intelligence in cephalopods is their sophisticated decision-making capability. When preying on clams, for example, they selectively deploy three different techniques to penetrate the clam's shell: pulling the shell open, drilling through the shell, and chipping at the shell's margin. When they first find a shell, they attempt the quick but energetically costly method of pulling the shell open. If that is not successful, they use one of the other two options to penetrate the shell and inject a paralyzing venom to weaken the muscles keeping it closed. They also switch to the two more time-consuming options if a *Venerupis* clam, which can normally be pulled apart, is forcibly shut by researchers with a twisted wire. Octopuses were able to adjust their drilling location based on artificial adjustments like dental cement or metal coating. They also adjust for difficulty of penetration when selecting prey, preferring the thin-shelled *Mytilus* under normal circumstances, but preferring the thick-shelled *Protothaca* if the shell was already open. This illustrates sophisticated reasoning processes.[8]

[10] Mather et al. 1999

More studies have been done on the problem-solving ability of octopuses. One study relevant to the question of consciousness presented *Enteroctopus Dofleini* with a jar containing a small crayfish and plugged with a stopper. Octopuses were previously shown to not be able to learn to open the jar more quickly with repeated trials, but this version of the task also included chemical cues from herring being smeared on the surface of the jar. With this modification, the octopuses decreased the time to open significantly within 10 trials. This study is important because it suggests an integration of visual and chemotactile information, something indicative of conscious processing. Although this conclusion would be strengthened if researchers directly compared the learning with and without the crayfish and with and without the chemical cues.[8]

Finally, a key feature of the mental lives of octopuses is their ability to think about thinking, also known as metacognition, either in their own self or for other individuals. This ability to consider the mental states of other beings is often referred to as theory of mind. In primates, these abilities can be tested by deception tasks or, controversially, by the mirror test. The mirror test does not work well for octopuses as they are solitary animals and not highly dependent on vision. However, adult male cuttlefish have been shown to treat mirror reflections as conspecifics, giving them agonistic displays. In this way, they fail the mirror test, but the mirror test is highly controversial evidence for self-awareness. One version of metacognition is the ability to interpret the location of self in space. Octopuses notably have a decentralized motor system. They actually have 3/5 of their neurons located outside of the brain. This limited central processing could be indicative of a lack of spatial self-awareness, but because we do not fully understand the functions of the brain in motor control, it is difficult to interpret. It could just mean octopuses, like honeybees, might have a different form of consciousness than our own. And evidence exists in favor of spatial self-awareness. When octopuses manipulate and open clam shells, they do so while the clam is outside their field of vision, and the decision-making is based on the orientation of the clam in space, which would involve understanding the location of their arms as well. And in natural habitats, octopuses are known to have predatory ranges based on central locations and cover different areas each day, indicating some sense of where the octopus has already covered.[8]

V. Bivalves and Crustaceans

Bivalves, such as clams and oysters, are an interesting example in that they are animals often consumed for food in Western cultures, but they lack some of the key features associated with consciousness. Bivalves lack cephalization. Instead, their nervous system consists of only two pairs of nerve cords and three pairs of ganglia. Some show rudimentary nociception like the foot withdrawal reflex in a razor clam. Clams and scallops have basic sensory organs that initiate swimming when threatened. However, researchers were unable to find record of physiological or behavioral responses to physical injury in bivalves. Additionally, the evidence for opioids and opioid receptors in bivalves is controversial.[11]

Some scientists and philosophers cite the lack of a brain as definitive evidence that bivalves do not suffer. It can also be argued that bivalves do not suffer because they lack an opioid system. Both these arguments seem lacking, however, as consciousness could exist in the nerve cords

[11] Crook and Walters 2011

and ganglia or with different transmitters just like it could exist in a sufficiently sophisticated computer. Consciousness, as defined previously in this paper, is not dependent on a specific substrate like a brain. But, even so, the largely sessile nature and lack of response to physical injury in bivalves does seem to limit the adaptive value of consciousness. And it seems unlikely that an animal would spend energy on consciousness without significant adaptive value, so it seems bivalves are the animal included in this paper with the most minimal mental lives, either by degree or likelihood of consciousness.

Crustaceans, such as lobsters and crabs, are another group of animals often consumed for food that seem to have relatively simple behavior and nervous systems. Their minds are particularly worthy of consideration due to the often gruesome way we treat them like boiling them alive. Crustaceans have a brain-like structure in their anterior region where several ganglia fuse together. Lobsters, crayfish, and shrimp have fused ganglia along the entire length of the ventral nerve cord, while in crabs the ganglia fuse into a single mass. Generally, in crustaceans, the nervous system is more distributed across these ganglia than centralized in the brain-like structure. In addition to extensive sensory organs, crustaceans have sophisticated proprioception to indicate body position.[12]

Crustaceans also show complex nociception that is consistent with the hypothesis of negative affective states. Although crustaceans have a strikingly different neuroanatomical structure than vertebrates or even some insects, that does not preclude the existence of analogous

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[12] Sømme 2005

processes just as the lack of a visual cortex does not preclude vision in crustaceans. Crustaceans do show reactions to physical injury. For example, prawns exhibit a protective motor response when their antennae are rubbed with a noxious substance. Avoidance learning, as well, has been demonstrated in crayfish. Additionally, crustaceans have opioid receptors and show a morphine response similar to vertebrates and at least some insects. The crab *Carcinus maenas* even shows a motivational trade-off with nociception, being more likely to leave a dark shelter when shocked if the ambient light is low, indicating a trade-off between the shock and the light level.[13]

Hermit crabs also show complex, integrative decision making in their selection of gastropod shells. They integrate visual and textile information on size, shape, weight and other factors, even simultaneously comparing two different shells. Some researchers have suggested hermit crabs use information about how well a given shell would fit another crab competing for ownership when deciding whether to fight them. Hermit crabs show a motivational trade-off between shell quality and electric shocks given by researchers by being reluctant to leave a high quality shell.[13]

Some of the evidence for crustacean consciousness is compelling like the synthesis of shell and opponent knowledge when competing for ownership, which could even suggest a theory of mind. It certainly seems that crustaceans are more conscious than bivalves. The evidence of

[13] Elwood and Appel 2009

proprioception is also compelling because it suggests at least some rudimentary form of self-awareness and perhaps perception of bodily injury.

VI. Concluding Remarks

Biological consciousness seems to vary greatly across invertebrates. Social insects and cephalopods show capabilities that match or exceed many vertebrates and seem to indicate complex, integrative processing and generalized emotional states. Bivalves show evidence for little beyond nociception, at a similar level to some plants. Other invertebrates like crustaceans have limited evidence and require further investigation. This is undoubtedly a difficult area of study, but once we accept consciousness as a physical process accessible by scientific investigation, we can make serious strides in better understanding the animal mind. Most importantly, given the growing evidence for nonhuman consciousness, we must seriously reconsider our current treatment of nonhuman animals and the suffering we inflict. Even if we only assign relatively small moral value to the mind of each invertebrate, they are still a prevailing moral concern given the sheer numbers of individuals, both in captivity and the wild, and the grisly treatment they endure.

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