Varieties of Subjectivity

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In human conscious experience, many features are present in combination: objects are presented through the senses, information from different sensory modalities is integrated, events are marked with value, and we have a sense of our own location and state. Which of these might come before others in plausible evolutionary trajectories, or do they form a tight package of correlated features that cannot readily be dissociated? I take a comparative approach to these questions, focusing on a distinction between sensory and evaluative aspects of experience, and looking at the distribution of subjectivity-relevant features in a range of invertebrate animals.

1. Introduction

The main theme of this paper is the possible separability of two kinds of subjective experience.* (These might also be called forms of "phenomenal consciousness" or "sentience.") I will refer to them as *sensory* and *evaluative* aspects of experience. The sensory aspect is related to perception, point of view, and the registration of facts. The evaluative side is related to feelings, pain versus pleasure, and the imposition of values. We humans have experience featuring both, and so, most likely, do various other

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animals. But there is a distinction to consider here. What sort of relation might there be between the two sides?

This duality is one aspect of the complexity of human experience, which includes other elements as well (a sense of one's own position and state, for example). In working out plausible pathways for the evolution of subjective experience, one question that arises is which of these aspects form a tightly connected "package" and which might readily be separated. We can try to make progress on these questions by looking at the distribution of subjectivity-relevant features in various non-human animals.

If we first consider the relation between sensing and evaluation outside of questions about subjective experience or consciousness, we find the two are tied together closely. To the extent that behavior generally – almost inevitably – involves both the discrimination of conditions and expression of a preference, both sides are present. This is true even in the most minimal forms. If an organism exhibits movement towards a source or stimulus, as seen in chemotaxis or phototaxis, both are present. There is responsiveness to something in the environment – the beginning of the sensory – while the fact that one thing is done rather than another embodies an evaluation. This knitting of the two is formalized in expected utility models of action. That does not mean that the two have to be tied together in every respect; one might be present in a complex form while the other is much simpler.

A difference in complexity of this kind might have consequences for experience – for whether it is present at all, as well as what form it takes. Suppose that very simple forms of sensing and very simple forms of evaluation (as in chemotaxis) do not give rise to subjective experience. In a framework that will be questioned later but that does provide a simple way in to the issues, we might suppose there is a threshold with respect to the complexity of both sensing and evaluation, such that below-threshold cases are not associated with experience but above-threshold cases are. Then an animal might be above the threshold with respect to one side but below with respect to the other, leaving a senseonly or evaluation-only experiential profile.

2

2. Evolutionary and Philosophical Context

The Ediacaran (635-540 mya) is the first period from which animal fossils are known (Peterson et al. 2008). This period appears to include a number of branchings between animal lineages, in a context of likely behavioral simplicity. From the Cambrian (540-485 mya) onwards, complex nervous systems and behaviors evolved in several independent lines, especially in some arthropods, in vertebrates, and a small group of molluscs, the cephalopods (Trestman 2013). The evolutionary lines leading to those three groups probably diverged during (perhaps even before) the Ediacaran, so there were several independent origins of complexity in nervous systems and behavior.

This scenario puts on the table three main options for the origins of subjective experience (SE). The first is that SE evolved from its absence on two, three, or more, independent lines. This assumes that the last common ancestor of all bilaterally symmetrical animals was too simple to have experience. If so, this is likely to also apply to the last common ancestor of arthropods and molluscs. A second option is a more gradualist one, with SE of some sort present in very early animals, perhaps originating just once, and developing further down different animal lines. A third is a latecomer option – SE is present only in mammals, or some other small group. I will discount the third and begin by looking at the first option, returning to the second later.¹

Suppose there were several origins of behavioral complexity and nervous systems that enable it, and these were also origins of *something* putatively experiential that accompanies these abilities. One way of thinking about this situation sees the scenario as one with three or more origins of basically the same thing – a trait with variations but a common core. But we might also put pressure on this assumption of unity. Perhaps what evolved is not the same thing repeatedly, but something more divergent in kind. The philosophical mind-body problem is usually set up in a way that assumes there is a single target: the mind, consciousness, or SE. But that may not fit the biology. What might it be about the capacities that evolved in different animals that would entitle us to think they are all variants on the same philosophically important thing?

¹ For more detail on the second option, see Godfrey-Smith (2017), though the present paper revises parts of that one. For the third, see Godfrey-Smith (2016).

The obvious move in reply is that a single philosophical target can be indicated with the "something it's like" feature (Nagel 1974). If there is something it's like to be an octopus, a bee, and a human, then there have probably been something like three origins of *the feature* that is important from a philosophical point of view. If what originated on different lines does not have this in common, then it's not three origins of phenomenal consciousness or SE, but in some cases (not our case) the evolution of something else, something that raises fewer, or at least different, philosophical problems.

This move is reasonable as far as it goes, but it's no more than an initial gesture. The "something it's like" feature is not self-evident, such that it might, in principle, be recognized as simply present or absent across very different ways of being an animal. Something more informative is needed.

Once we push harder, we encounter several choices. One way of fleshing out Nagel's idea is to take a sensory route. Many philosophers have thought that phenomenal consciousness is inherently sensory (eg., Prinz 2012). Nagel and others sometimes flesh out the "something it's like to be..." idea with the allied idea of a *point of view*. Given the comparative orientation of this paper, we would then look for markers of sensing of a rich kind. High resolution vision (vision involving "class IV" eyes, in the sense of Nilsson 2013) is an exemplar. There have been four or more origins (along with some borderline cases) of this sort of eye from simpler visual systems. These eyes have two different designs, the simple eyes of vertebrates, cephalopods, and some spiders, and the compound eyes of other arthropods.

Alternatively, we might flesh out Nagel's "something it's like" in a different way. "Something it's like" is close to something it *feels* like, and though this can refer to sensory tracking, the paradigms of feelings are evaluative or affective, the registration of events as good or bad, welcome or unwelcome. Perhaps we should be looking for evaluative sophistication instead of, or as well as, sensory sophistication. This approach brings in different evolutionary possibilities and different lines of evidence. Now might look for evidence of pain, and related evaluative states.²

² Pain has a sensory side as well as an evaluative or affective side. It is informative of facts about the location and nature of damage, as well as being evaluative. Here we are concerned with the evaluative side.

3. Possible Separations

As seen above, in the course of probing at the "something it's like" idea we can be led in at least two directions, one highlighting perception and one exploring evaluation. Perhaps there are others as well – multimodal integration is another candidate related to the sensory side – but there needs to be *some* fleshing out of the Nagel formula; it does not suffice on its own. In the rest of this paper, I will focus on the two paths sketched above, on the idea of distinct sensory and evaluative aspects of experience. While in some animals both are present, perhaps they might be dissociated in other cases.

Invertebrates include a pair of animal groups for which there is a *prima facie* case for a dissociation of the kind being considered. These groups are insects and gastropods (slugs and snails). Insects, in many cases, have complex sensory capacities but may be simpler on the evaluative side. Gastropods are simpler on the sensory side but may have relevant evaluative complexity. These are not the invertebrates for whom a case for SE is most plausibly made: cephalopods and crustaceans; I will make comparisons to those below. Insects and gastropods are more questionable in several respects, but I will try to take some steps forward. I begin by outlining the *prima facie* case, and then look at complications.

Complexity in sensory capacities might be understood as involving complexity in discrimination or in downstream processing. Evolution might be assumed to often make these commensurate, but for discussions of SE, the processing side is more important. In the case of insects, I focus on the well-studied cases of fruit flies (*Drosophila*) and bees. Insects in many cases have high-resolution vision and acute sensory capacities, especially those that can fly. Flight is a behavior that involves dealing with complex spatial layouts and making self/other distinctions with respect to the causes of sensory events. Any inference from biological capacities of this kind to SE is uncertain, but *if* there is a sensory road to true subjectivity, insects seem plausible candidates (Barron and Klein 2016). On the other hand, their evaluative capacities have long seemed puzzling. An influential paper from some decades ago, Eisemann et al. (1984), argued that insects do not feel pain, as all known insects appear completely unconcerned about even severe body damage. Wound-tending has never been seen in an insect, and after injury these

5

animals just continue, as best they can, with the behavior appropriate to the circumstances.

In contrast, wound-tending is seen in crustaceans, and this is part of what appears a marked evaluative contrast between insects and crustaceans. Especially through the work of Elwood and his collaborators (Appel and Elwood 2009, Elwood 2012), considerable evidence for evaluative sophistication, including pain, has been found in decapod crustaceans such as crabs and shrimp. Hermit crabs show subtle evaluative trade-offs, relinquishing shells to avoid electric shock in a way affected by the quality of a shell and the apparent risk of predation. Results such as these are taken, reasonably, to be good evidence for pain-like states in these animals (Tye 2017).

Insects (bees) do avoid noxious stimulation such as heat, but immediate avoidance can be a reflex-like capacity and not indicative of SE. A tradition of work has argued that reinforcement learning is a plausible candidate for a form of evaluative cognition with inherent links to evaluative experience (Elwood 2012, Allen et al. 2015). Various insects can learn by reinforcement (though the boundaries between the right and wrong kinds of learning are unclear).³ Another assay for pain is self-administration of analgesics, in response to damage. This has been seen in a number of vertebrate animals (fish, birds) and is treated as evidence for pain in these cases. Groening et al. (2017) looked explicitly for this behavior in bees and did not find self-administration.

None of this is conclusive, but it suggests at least a patchy quality to insect evaluation, including evaluative experience, if it exists. The ecology of insects is also relevant (as emphasized by Andrew Barron, in correspondence). Insects are a mostly terrestrial offshoot of crustaceans, which in turn are mostly marine. ("Crustacean" is probably a paraphyletic group). Insects, adapting to the special context of land, have in many cases evolved short, routinized lives that are quite different from the longer and less regimented lives of their marine relatives studied by Elwood. Adult insect bodies are difficult to heal (though limbs can regrow in some cases: Maruzzo and Bortolin 2013) and there will often be no point in trying to protect an injured area; instead, one should just "soldier on." It would make sense in principle for many insects to have complex sensing and simpler evaluation.

³ See Ginsburg and Jablonka (2019) for a detailed view based on the role of learning.

I'll now turn to gastropods, the other side of the *prima facie* dissociation. This large group of molluscs includes snails, slugs, and their relatives. *Aplysia*, a large sea snail (with a small internal shell), is a model organism in neuroscience. In (nearly) all gastropods, there are no class IV eyes – unlike their cephalopod relatives – and forms of movement are generally fairly simple.⁴ But there is some evidence for evaluative richness. Relevant work in this area has been done especially by Terry Walters (reviewed in Walters 2018; see also Crook and Walters 2011).

Though pain is what people tend to look for, there are related kinds of evaluative responses, including emotion-like states – medium-term effects of aversive events, such as fear. Walters emphasizes *nociceptive sensitization*, a heightened sensitivity after damage. Electric shock is used as an aversive stimulus in this work, and as well as inducing immediate responses, it leads to a sensitization of withdrawal behaviors in response to other stimuli. Shock when paired with the smell of shrimp leads to not only a freezing response when exposed to shrimp alone, but a "state resembling conditioned fear" that affects responses to previously neutral stimuli, such as touching, when they are combined with the shrimp smell. These responses "suggest that memory of a noxious event in snails can be linked to a fear-like motivational state that can dramatically alter the animal's response to other biologically significant stimuli" (Crook and Walters 2011, p. 189).

A feature that gives this work a plausible connection to SE, a *felt* dimension, is the fact that the result of the aversive stimulus is a pervasive state of negative readiness, one that affects the animal's response to a wide range of events. Sensitization is a simple version of a mood-like state of this kind, but one that does have plausible links to SE. Walters himself, in correspondence, is cautious about making connections of this kind, but a *prima facie* connection is acknowledged; one can see an adaptive rationale for an ability to "maintain functional "awareness" of injury-induced vulnerability until the vulnerability subsides" (Walters 2018, p. 13). As Walters also emphasizes, molluscs such as *Aplysia* are longer-lived as adults than many insects (1-2 years). Their soft bodies are easily damaged but have well-developed capacities for healing and repair. The gastropod

⁴ "Sea elephants" are borderline cases of Class IV eyes. They are pelagic, swimming, predatory gastropods.

body does not permit would-*tending* (I assume), but sensitization may protect animals during recuperative periods in related ways. (Walters reports, incidentally, that while some octopuses wound-tend – Alupay et al. 2014 – squid apparently do not.)

However, if nociceptive sensitization is given this evidential role for gastropods, it is important that forms of it are also seen in insects. This is another piece of evidence bearing on the puzzling insect case (Tye 2017). Sensitization to aversive events has been seen mostly in insect (fly) larvae, a fact I will return to below. In addition to sensitization itself, other medium-term states, often described as emotion-like, have been seen in insects. Bateson et al. (2011) found that an aversive shaking could induce a kind of pessimism in honeybees – an inclination to treat ambiguous stimuli pessimistically. They interpreted this state as emotion-like. Cwyn Solvi and her collaborators have followed this up and shown that a *positive* emotion-like state, a kind of optimism, can be induced in bumblebees by means of unexpected reward (Perry et al, 2016). This has analogous effects on the interpretation of ambiguous stimuli.

Where do these findings take us? First, a number of discussions of invertebrates have used a combination of two kinds of behavioral contexts when assessing questions about pain and evaluative experience. These are responses to immediate damage (which include such things as withdrawal, tradeoffs, and wound-tending), and learning by reinforcement. This leaves out a middle scale, in temporal terms, a scale occupied by what are sometimes called emotions, and might also be seen as moods – evaluatively laden medium-term states.⁵ Processes occurring at this scale seem, in the light of the work discussed above, very informative.

Uncertainties certainly remain about experience in both gastropods and insects. Given the small nervous systems of gastropods, it can be tempting to rule them out altogether. In the case of insects, the results seem full of puzzles. But the work discussed above does seem to reveal a hidden dimension to evaluative states in insects and gastropods, one that complements the slightly clearer cases of cephalopods and crustaceans. In the case of insects, there would be two ways of developing this idea. One would be to conclude (or at least suspect) that this work shows an evaluative sophistication in these animals that is broad, despite the older observations showing an

⁵ This was neglected in my 2017 paper.

apparent unconcern with damage. Heat seems to be a stimulus that insects find more aversive than some others, and some earlier work might have looked at the wrong stimuli. A different response is to conclude that evaluative processing in insects is very patchy; perhaps they do not have pain-like immediate felt registration of damage, but do have valenced mood-like or emotion-like states. The empirical picture can be expected to evolve further; a new paper about nociceptive sensitization interprets the state of its *Drosophila* subjects as more akin to chronic pain than to an emotion (Khuong et al. 2019).

Another factor in insects not highlighted so far, one related to life on land, is the differences between larval and adult states. Many insects lead two lives, in effect, one on each side of a metamorphic divide, with extensive breakdown and reconstruction at that stage. In the kinds of insects considered here, it is the adult who has acute sensing that controls complex motion; the larva does not. Larvae in many cases do have eyes, but much simpler ones (just 12 photoreceptor neurons in the case of *Drosophila*: Sprecher et al. 2011). On the other hand, "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, p. 12). Studies like those of Eisemann et al. (1984) and Groening et al. (2017), finding obliviousness to damage, are looking at adults. Adult insects have the bodily capacity to tend and protect wounds, like crustaceans, but do not. A larva might be more sensitive, but can probably wound-tend no better than a gastropod can. The emotion-like states uncovered by Bateson et al. (2011) and Perry et al. (2016) are found at the adult stage, on the other hand, and I don't know if larval behaviors are rich enough to support optimism and pessimism. In insects, the adult body is often a "disposable reproductive machine," as Barron has put it, while the larval stage has different tasks. So within an individual insect's lifetime, there may be transition with some resonance to the distinction discussed here in comparative terms.

9

4. Questioning the Threshold Model

A sharp divergence between sensory and evaluative complexity in cognitive capacities seems possible in principle. Empirically, there also seems to be at least some "slack" in the association. The consequences of this relationship for questions about subjective experience, or minimal forms of "phenomenal consciousness," are a separate matter. As this paper has gone on, it has moved from crustaceans and bees to snails and fruit fly larvae, organisms who many will see as too neurally simple for questions of this kind to be sensibly asked. A picture that is often applied in this area can be called a "threshold model." This model supposes that there is a lower bound in the complexity of cognitive processing below which subjective experience cannot be present. Within the framework of this paper, there will then be two distinct ways of being above or below threshold. An animal can be above or below threshold on the sensory side, and also on the evaluative side, yielding a $2x^2$ table. As well as ourselves, nonhuman vertebrates and some invertebrates such as octopuses might be above threshold on both sides, while other animals might be below on both, and still others might be above on one and below on the other.

I worked within a threshold model to some extent above, but this view may be mistaken. The alternative is a gradualist model, in which perhaps within neural animals, or within cellular life, all the differences are, roughly speaking, matters of degree. A gradualist model is harder to countenance and even discuss, but may be better motivated by biology. In a gradualist approach, we aim not to give an account of which features *suffice to make you* an experiencing subject, but an account of how some organisms have internal goings-on that are *more experiential*. This talk of gradations should not be taken to suggest a single scale, or a pair of such scales as discussed here, as the situation may include additional dimensions.⁶

⁶ The "integrated information theory" (IIT) approach to these questions is gradualist (see Tononi and Koch 2015; see also Koch's contribution to this Symposium), though I do not support that particular approach (Godfrey-Smith 2015), and it also measures the basis of consciousness with a single scale.

5. Conclusions

The goal of this paper was to explore possible separations between sensory and evaluative forms of experience, both in principle and empirically. Though discrimination and evaluation are almost inevitably combined in all forms of action, this leaves open the possibility of differences in the complexity on each side, and those differences may have consequences for the presence of experience. An initial picture of insects, especially based on earlier work on pain, suggests that they may be much richer on the sensory side than the evaluative. Recent work on emotion-like states has made this verdict much less clear. Gastropods are candidates for the other separation, but they have simpler nervous systems and, it appears, simpler behavioral repertoires, though less is known about their abilities.

The framework of Feinberg and Mallatt (2016) is in some ways close to mine; they distinguish *exteroceptive*, *affective*, and *interoceptive* aspects of experience. I would collapse the interoceptive to the sensory (or perhaps treat parts of it as sensory and parts as evaluative). Feinberg and Mallatt also see exteroceptive consciousness as in a sense the basic form, and that is not a feature of my view.

Lastly, questions of evaluative experience have clear relevance to animal welfare. Investigations of this kind can and should inform policy debates in a number of areas. As Crook and Walters note (2011), it is because we think molluscs and arthropods have relevant continuities with us that time and money are spent doing experiments on their brains. But the more informative these animals are about us, the more questionable it is that we *do* the experiments, at least as they have traditionally been done. This is animal experimentation that is likely to lead relatively directly to welfare benefits for humans and other animals; it probably has a better accounting, in its costs and benefits, than much animal experimentation. But as Crook and Walters say, the cost side is becoming clearer.

- Allen C, Fuchs P, Shriver A, Wilson H (2005). Deciphering animal pain. In M Aydede (ed.), Pain: New Essays on Its Nature and the Methodology of Its Study. Cambridge MA: MIT Press, pp. 351-366.
- Alupay, JS, Hadjisolomou SP, Crook, RJ (2014). Arm injury produces long-term behavioral and neural hypersensitivity in octopus. *Neuroscience Letters* 558: 137– 142. doi: 10.1016/j.neulet.2013.11.002
- Appel M, Elwood RW (2009). Motivational trade-offs and potential pain experience in hermit crabs. *Applied Animal Behaviour Science* 119: 120-124
- Barron AB, Klein C (2016). What insects can tell us about the origins of consciousness. *Proceedings of the National Academy of Sciences, USA:* 113: 4900-08.
- Bateson M, Desire S, Gartside SE, Wright GA (2011). Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology* 21: 1070–1073.
- Crook R, Walters ET (2011). Nociceptive behavior and physiology of molluscs: Animal Welfare Implications. *ILAR Journa*l 52, 185–195. doi: 10.1093/ilar.52.2.185.
- Elwood RW (2012). Evidence for pain in decapod crustaceans. *Animal Welfare* 21: 23-27.
- Feinberg T, Mallatt J (2016). The Ancient Origins of Consciousness. Cambridge MA: MIT Press.
- Ginsburg S, Jablonka E (2019). *The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*. Cambridge: MIT Press.
- Godfrey-Smith P (2015). Integrated information. URL: http://metazoan.net/27-integratedinformation/
- Godfrey-Smith (2016). Animal Evolution and the Origins of Experience. In *How Biology* Shapes Philosophy: New Foundations for Naturalism, ed. D. Livingstone Smith.
 Cambridge: Cambridge University Press, pp. 51-71.
- Godfrey-Smith P (2017). The evolution of consciousness in phylogenetic context. *Routledge Handbook of Animal Minds*, ed. K. Andrews and J. Beck. London: Routledge.

- Groening J, Venini D, Srinivasan MV (2017). In search of evidence for the experience of pain in honeybees: A self-administration study. *Scientific Reports* 7:45825. DOI: 10.1038/srep45825
- Khuong TM, Wang QP, Manion J, Oyston LJ, Lua MT Towler H, Lin YQ, Neely GG (2019). Nerve injury drives a heightened state of vigilance and neuropathic sensitization in *Drosophila*. *Science Advances* 2019; 5: eaaw4099
- Maruzzo D, Bortolin F (2013). Arthropod regeneration. In Minelli A, Boxshall G, Fusco G eds. (2013). Arthropod Biology and Evolution: Molecules, Development, Morphology. Berlin: Springer-Verlag
- Merker B (2005). The liabilities of mobility: A selection pressure for the transition to consciousness in animal evolution. *Consciousness and Cognition* 14: 89–114.
- Nagel T (1974). What is it like to be a bat? *Philosophical Review* 83: 435-450.
- Nilsson D-E (2013). Eye evolution and its functional basis. *Visual Neuroscience* 30: 5–20.
- Perry CJ, Baciadonna L, Chittka L (2016). Unexpected rewards induce dopaminedependent positive emotion–like state changes in bumblebees. *Science* 353:1529-1531.
- Peterson K, Cotton J, Gehling J, Pisani D (2008). The Ediacaran emergence of bilaterians: Congruence between the genetic and the geological fossil records. *Philosophical Transactions of the Royal Society of London* B 363: 1435–1443.
- Prinz J (2012). *The Conscious Brain: How Attention Engenders Experience*. Oxford University Press.
- Sprecher SG, Cardona A, Hartenstein V (2011). The *Drosophila* larval visual system: high-resolution analysis of a simple visual neuropil. *Developmental Biology* 358: doi:10.1016/j.ydbio.2011.07.006.
- Tononi G, Koch C (2015). Consciousness: here, there and everywhere? *Philosophical Transactions of the Royal Society* B 370: 20140167.http://dx.doi.org/10.1098/rstb.2014.0167
- Trestman M (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory* 8: 80–92.

- Tye M (2017). *Tense Bees and Shell-Shocked Crabs: Are Animals Conscious?* Oxford: Oxford University Press.
- Walters ET (2018). Nociceptive Biology of Molluscs and Arthropods: Evolutionary Clues About Functions and Mechanisms Potentially Related to Pain. *Frontiers in Physiology*, 2018, 9: 1049