



# Inferring Consciousness in Phylogenetically Distant Organisms

Peter Godfrey-Smith 

## Abstract

■ The neural dynamics of subjectivity (NDS) approach to the biological explanation of consciousness is outlined and applied to the problem of inferring consciousness in animals phylogenetically distant from ourselves. The NDS approach holds that consciousness or felt experience is characteristic of systems whose nervous systems have been shaped to realize subjectivity through a combination of network interactions and large-scale dynamic patterns. Features of the vertebrate brain architecture that figure in other accounts of the biology of consciousness are viewed as inessential. Deep phylogenetic branchings in the

animal kingdom occurred before the evolution of complex behavior, cognition, and sensing. These capacities arose independently in brain architectures that differ widely across arthropods, vertebrates, and cephalopods, but with conservation of large-scale dynamic patterns of a kind that have an apparent link to felt experience in humans. An evolutionary perspective also motivates a strongly gradualist view of consciousness; a simple distinction between conscious and nonconscious animals will probably be replaced with a view that admits differences of degree, perhaps on many dimensions. ■

## INTRODUCTION

When we encounter octopuses and some other complex invertebrate animals, we find behavioral indicators, or at least suggestions, of various kinds of subjective experience. We might see suggestions of pain, for example, and can note an attentive engagement by the animal with events around them. First impressions based on behavior are not enough to infer that felt experience is actually present. If we want to work out whether it really feels like something to be one of these animals, how should we proceed? Further observation can give us a richer sense of their behavioral capacities, and we can also try to work out what is going on inside them. When we look inside, we find similarities to ourselves along with many differences. We find a nervous system, but one with a different architecture from ours. In some respects, these different nervous systems are evidently doing similar things: Octopuses and bees can see; they can navigate and learn. However, the neural structures that figure in recent attempts to explain consciousness are generally absent—they have no cortex or thalamus, for example. Which similarities between us and them matter, and which do not? How can inferences about consciousness in phylogenetically distant animals be more than speculation?

This Perspective article offers a position on these matters. The topic is consciousness or felt experience in a minimal sense—whether it feels like something to be one of these animals (Nagel, 1974). The problem will be approached through an evolutionary framing, looking at

the history of nervous systems and the phylogenetic relationships between different animals alive now. I will link this evolutionary perspective to a general view about the biological basis of conscious experience, and consider several invertebrate groups. The discussion will focus on animals but will suggest conclusions about other organisms as well. My positive account of the biology of consciousness is speculative in many respects, as are its rivals. I can offer defenses for some claims, but it is not possible in a short essay to establish it as the best option. The aim of the discussion is to outline the view, link it to empirical work, and consider how it relates to some alternatives.

## BIOLOGY OF CONSCIOUSNESS

My view of the biological basis of consciousness has two elements; two ideas are used to bridge the “explanatory gap” between the physical and the experiential (Levine, 1983). First, the problem of consciousness is sometimes picked out with the idea of subjectivity or point of view. This feature is not antithetical to biological explanation, and an account can be given of the evolution of systems that have points of view, systems that are subjects (Godfrey-Smith, 2019). Action or behavior is a central feature of animal life, part of the animal way of being. Effective action usually requires a responsiveness to the environment and is also furthered by the integration of processing, by learning, and by the modulation of sensory processing in the light of the fact that the animal’s own acts have sensory consequences (reafference). These features, together, generate the existence of systems that have subjective

University of Sydney

points of view, from which the action that is central to animal life proceeds.

The second part of my approach asserts the importance of some features of nervous systems themselves. Central nervous systems have a pair of properties; there are the networked, cell-to-cell interactions that enable computation, and there are what I will call *large-scale dynamic properties*—the more diffuse, often oscillatory dynamic patterns that can be picked up using an EEG and similar technologies. These involve less localized electrical activity in a brain.

The large-scale dynamic features of nervous systems have empirical connections to a number of subjectivity-relevant features. They appear to play a role in sensory integration, selective attention, sleep/wake cycles, and anesthesia (see Singer, 2018; Melloni et al., 2007; van Swinderen, 2005, and various articles in this issue of the present journal). A complementary point can be made on the phenomenological side. Ordinary human experience appears to be organized, at each moment, with what can be called an *experiential profile* (Godfrey-Smith, 2020a). An experiential profile is a total way things feel to someone at a time. These profiles are inherently multifaceted, gestalt-like. There will be something (or perhaps a few items) in attention, whereas others are in the background; there is bodily awareness, and the whole is also modulated by mood and energy level—usually far from attention, but part of “what it’s like” at that moment. I conjecture that this profile-based organization is characteristic of experience in general, not just experience in us. The combination of nervous system features mentioned above offers, in a preliminary form, a natural explanation for this aspect of phenomenology. When large-scale patterns of activity are modulated by sensory input of various kinds, along with other events, this makes sense of the combination of unity and differentiation in conscious experience.

My proposal about the biology of consciousness combines this view of nervous system activity with the more schematic, subjectivity-related properties outlined at the start of this section. Putting the two together: Conscious experience is characteristic of systems that are configured as subjects, with a relationship to their milieu of a kind that can be roughly characterized with the idea of “point of view,” and that achieve subjectivity with nervous system activity. This sketch leaves many questions unanswered; is every animal with some version of these properties conscious, or only the more complex ones? I return to that question below (in the section titled “Gradualism”). The account is preliminary in these and other ways, but it does contrast with alternatives in how it handles questions and cases. I will call this the NDS approach, for *neural dynamics of subjectivity*.

Here are some of those contrasts. First, although the NDS approach treats nervous systems as special, it does not recognize an essential role in consciousness for architectural features of the mammalian, or vertebrate, nervous system. Once an animal has a nervous system (of

reasonable complexity), there are many ways or configuring it that are compatible with consciousness. This is discussed further in the next section.

Second, the gestalt-like feature that I see as inherent to experience is sometimes denied, by views that assert that only one or a few items (or a few “contents”) can be in consciousness at a single time (Dehaene, 2014). Some “global workspace” theories of consciousness have this character; the workspace cannot hold a lot of items at once, perhaps only one item. These views accept the initial appearance of a broad and multifaceted nature to experience, but explain this in terms of rapid switching or replacement of one item by another, or say that the item in consciousness at a moment can be the general “gist” of a scene or situation (Simons & Levin, 1997). The idea of gist makes sense within a single sensory modality, but is questionable in a multimodal context. The idea that it is impossible to experience, simultaneously, the visual appearance of a band on stage (a stimulus that is quite complex in itself) and the sound of the song they are playing is extraordinary, although not out of the question given the possibility of fast switching. If broad experiential profiles are accepted as genuine, on the other hand, this motivates views of the biology of consciousness that emphasize integration along with differentiation.

Other recent work does include the multifaceted character of experience and handles it differently. LeDoux (2021) recognizes what he calls “fringe states” of consciousness, such as “a feeling of rightness.” These are seen as characteristic of a particular “anoetic” form of consciousness. Such fringe states can also be seen as subtle facets of typical experiential profiles—ease, energy level, mood, and the elusive feature referred to as *presence* in some discussions (Seth, Suzuki, & Critchley, 2012).

The NDS view gives a role to the schematic or functional set of properties that fall under the umbrella of the concepts of subjectivity and point of view. How essential is this side? All views must make sense of consciousness existing within humans who have had their sensory and behavioral interaction with their environment greatly reduced, as in severe forms of locked-in syndrome and, in some cases, the persistent vegetative state (Bayne, Seth, & Massimini, 2020; Shea & Bayne, 2010). These are not cases of total isolation, especially on the sensory side. However, they do raise the question of whether brain–environment commerce is necessary in principle to conscious experience. Tononi, working also with Larissa Albantakis, has argued for a strong separation between the functional side of the mind and the “intrinsic” character of experience (Albantakis & Tononi, 2021). For Tononi, intelligence and the other functional capacities are only contingently associated with consciousness. They are linked by evolution—the demands associated with action and cognition led to the evolution of nervous systems—but that is purely a matter of origins. What matters to whether a system is conscious is a certain kind of internal complexity

of activity (as measured with  $\Phi$ ), whether it is doing any of the kinds of things that minds were shaped by evolution to do (Tononi & Koch, 2015).

Two kinds of disconnection of a mind from its environments can be considered. First, there are cases where the usual environmental interaction is removed but the system is configured, internally, to engage in these interactions (analogously: The car is set up for driving, but the axles are removed). The other cases are those where a system is very complex in its activity but is not set up to enable perception and action even in principle (the engine is built just to run, and not to be responsive to, or have effects on, anything outside it). The NDS view can accept that systems of the first kind can be conscious. The claim that complexity of activity, of a particular kind, is all that matters is more contentious, as it untethers consciousness from what have appeared to be very basic features. Such claims cannot be ruled out, given what we currently know. The limitations of our concepts themselves may be coming into view here; if we throw away all ties to perspective, self-world relations, and the like, are we left with another form of consciousness, or something other than consciousness? I return to this topic below.

A moment ago, I raised the question of whether functional properties associated subjectivity and point of view are essential to being a conscious system, or only contingently related to consciousness. A question of the same kind can be asked about the nervous system features employed in the other part of the NDS account. Must these be present in any conscious system, or are they a contingent feature of the implementation of consciousness in animals like us? Is the combination of features employed in the NDS account strictly necessary, as well as sufficient, for consciousness?

The NDS approach and our general understanding of the phenomena are not sufficiently developed to enable a resolution of these issues. In my discussion of the role of sensing and point of view, I said that part of the problem is determining whether a case very different from our own is a different form of consciousness or something other than consciousness, but related to it. The same kind of question arises here. Some issues may, in the end, be handled stipulatively (“We will only count something as consciousness if it has feature X”), although others can be expected to have a more constrained resolution as we learn more. Perhaps, for example, the gestalt-like integration emphasized above can be achieved with different mechanisms from those in brains, while having the form, in each case, of large-scale patterns of activity with modulation. All conscious systems must then have some version of the duality of properties found in nervous systems (point-to-point influences enabling local computation, and non-epiphenomenal large-scale dynamic properties). In the case of artificial systems, this view would not suggest a barrier to artificial

consciousness per se, but a need for new architectures if such systems were to be built.

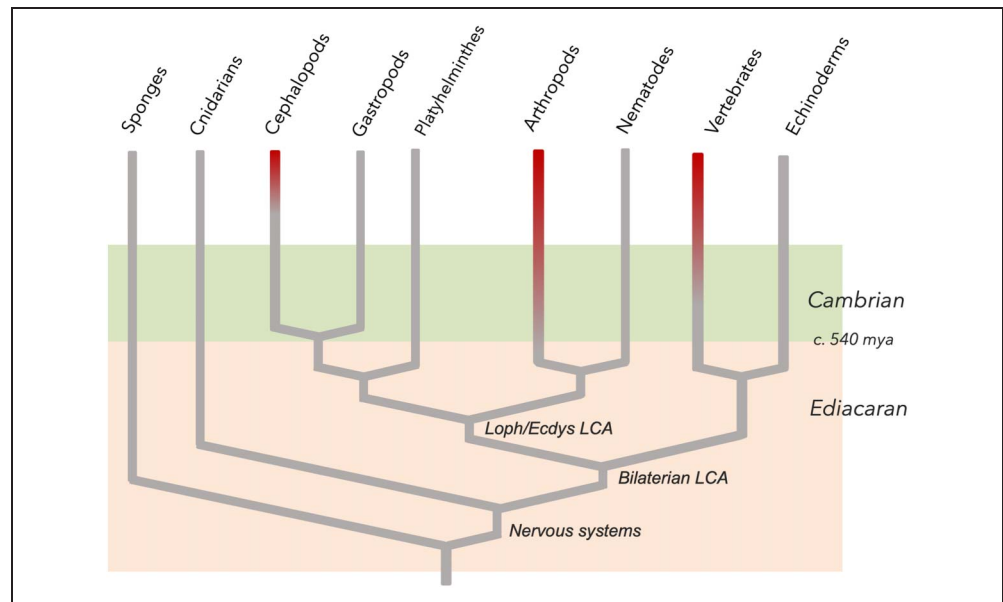
## AN EVOLUTIONARY PERSPECTIVE

More of the motivation for the NDS view can be developed by looking at the evolutionary side. Nervous systems evolved perhaps around 600 million years ago (mya), during the Ediacaran (635–540 mya), very probably before 565 mya, as several macroscopic mobile animals are seen in the fossil record at that time (Godfrey-Smith, 2020b). Molecular clocks have suggested earlier origins for neuralian animals, as they push the date of the divergence between cnidarians and bilaterian animals further back, but these methods are often now seen as less reliable in this context (Budd & Mann, 2020).

Even the more recent plausible dates for the evolution of nervous systems place their origin before the familiar regime of animal life, featuring predation and other real-time direct interaction, unless the deficiencies of the fossil record obscure from us a scene of extensive interaction in the water column as opposed to the seafloor (unresolved questions about the phylogenetic placement of ctenophores are relevant here: see Burkhardt et al., 2023). Animals with bodies suited to active motion and targeted behavior become apparent in the Cambrian, from about 540 mya. This transition took place after many of the deep branchings—all the phylum-level branchings and some others—in the animal tree (see Figure 1). Conspicuous behavioral complexity evolved separately, although almost certainly in a coevolutionary process, within several different evolutionary lines: in arthropods, vertebrates, and cephalopods, a group of mollusks (Trestman, 2013). This behavioral complexity evolved in groups with different bodily resources, and they ended up with different brain architectures. However, they also had things in common. The project of generating coherent agency, and matching actions to the state of the world, was common across them. Some parts of each clade evolved acute senses; high-resolution image-forming eyes (“Class IV” eyes: Nilsson, 2013) are found in all these groups, and only in them. All three groups contain species today with sophisticated navigation (octopuses, bees, many vertebrates). Associative learning is found more broadly and may have existed in some form in the common ancestor (Bielecki, Nielsen, Nachman, & Garm, 2023). Different groups, with different brain architectures, converged on a cluster of traits that further effective agency.

Nervous systems themselves were a common resource, including the combination of network properties and large-scale dynamic patterns described above. Pioneering work on these large-scale patterns was done by L. M. Passano and his collaborators, working on *Hydra*, a freshwater cnidarian with a very small nervous system (Passano, 1963). Some subjectivity-relevant features of this form of activity are conserved across animals with very deep evolutionary divergences.

**Figure 1.** Evolutionary relationships between some animal groups. Branches are not to scale, ranks are mixed, and many groups are omitted (including ctenophores, whose placement is uncertain). The “Bilaterian LCA” is the last common ancestor of extant bilaterian animals. This is the last common ancestor of a human and an octopus. “Loph/Ecdys LCA” is the last common ancestor of Lophotrochozoa and Ecdysozoa, hence the last common ancestor of an octopus and a bee. Red shading on branches indicates conspicuous behavioral complexity.



Bruno van Swinderen’s laboratory has studied an apparent link between oscillatory activity (especially in the beta range, 20–30 Hz) and selective attention in flies. Grabowska, Jeans, Steeves, and van Swinderen (2020) show that attentive locking onto particular objects in the visual field is associated with, perhaps enabled by, beta oscillations. In one experiment, the fly’s attention to an object can be ascertained by associating that object with a flicker rate (not beta range) that can be tracked in the brain. The fly’s attention, tracked with beta oscillations, could be redirected between different objects by optogenetically stimulating a reward circuit and associating an object that usually receives less attention with a reward. Findings bearing on active sleep and anesthesia complement this work, suggesting an experience-related role for large-scale, dynamic patterns in the fly brain.

Paleontology and the phylogenetic relationships between animals suggest the following sequence of events (Figure 1). Nervous systems evolved (either once or twice, depending on the phylogenetic placement of ctenophores). The origin of nervous systems is followed by branchings between cnidarians and bilaterians, between protostomes and deuterostomes within bilaterians, and also between lophotrochozoans and ecdysozoans within protostomes (separating mollusks from arthropods), all before the Cambrian. In the Cambrian, complex behavior and sensing evolves in several lines. A life based on mobility and targeted behavior puts a premium on sensing, informational integration, learning, and more subtle features such as selective attention. Versions of these features appeared in different bodily architectures, but with similarities in the nervous system activity that makes them possible. Structures like the cortex and thalamus that figure in recent discussions of the neural basis of consciousness are not present on evolutionary lines other than ours. Agency, and hence subjectivity, were shaped several times in

different bodies and brains, but with large-scale dynamic properties of nervous systems playing a subjectivity-related role in at least some of the different cases. This provides motivation for the combination of included and excluded features in the NDS approach.

## THE OCTOPUS

Octopuses have larger nervous systems than any other invertebrates (except perhaps their cuttlefish relatives), around 500 million neurons in some cases. Around two thirds of these are found outside the central nervous system. Their brain architecture is very different from that of vertebrates (Hochner, 2013). The brain is a collection of ganglia, expanded and fused to some extent, and organized also into lobes. The esophagus runs through the middle of the brain. Areas associated with more complex processing include the optic lobes behind each eye, which are separate enough from the rest that they are sometimes treated as distinct from the central brain, and within the central area around the esophagus, the vertical lobe. This unpaired structure is sometimes seen as analogous to the mammalian cortex and insect mushroom bodies (Shigeno, Andrews, Ponte, & Fiorito, 2018; Shomrat, Turchetti-Maia, Stern-Mentch, Basil, & Hochner, 2015). An octopus has high-resolution eyes convergently organized on a “camera” principle, as ours are. Octopus brain activity shows large-scale dynamic patterns (Gutnick et al., 2023; Bullock, 1984), although this activity has not yet been associated with subjectivity and cognition in the way seen, in the previous section, in flies.

Octopuses have a range of features suggestive of felt experience. Robyn Crook (2021) gave good evidence for the presence of something like acute pain. The stimulus was a single acetic acid injection. This showed up in a number of linked responses. An initially preferred location was

avoided when it was associated with the injection. An initially less-preferred location was preferred when paired with an analgesic drug (lidocaine) in animals that received the injection, although not otherwise. Injected octopuses also groomed the injured part, and this behavioral evidence was complemented physiologically.

In this case, we have a behavioral first impression, but recognize that this could be defeated; a closer look might reveal responses that are peripheral and reflexive. Instead, we see an integrated, multifaceted handling of the aversive stimulus, one that is quite similar to profiles of behavior seen in similar circumstances in fish and in chickens.

Recent octopus studies also show evidence for an alternation between active and quiet sleep, and skin patterning sequences during bouts of active sleep resemble those seen when the octopuses are awake. This suggests dream-like episodes (Pophale et al., 2023). In addition, octopuses in some settings show an inquisitive, exploratory engagement with novel objects. At the “Octopolis” and “Octlantis” sites in Australia, where octopuses (*Octopus tetricus*) live in higher densities than are probably normal for this and most other species, several complex behaviors are seen in interactions between individuals, including the apparent targeting of projectiles on other octopuses (Godfrey-Smith, Scheel, Chancellor, Linquist, & Lawrence, 2022; Scheel, Godfrey-Smith, & Lawrence, 2016). If an argument is made that their large, vertebrate-range nervous systems have the wrong layout to enable consciousness, this would be the claim that an exploratory, apparently attentive engagement with the world, with complex, nonroutinized interactions between individuals in some settings, and an integrated, multifaceted response to aversive experiences could be wholly unconscious. Such a claim could be true, but this is far from the usual kind of “unconscious processing.”

The case of the octopus makes the following contribution to the main argument of this article. In our own, human case, we find (i) sophisticated agency, (ii) a particular brain architecture, and (iii) a nervous system with a combination of biological properties, including network-based computation and large-scale dynamic patterns. The branchings between major animal groups predate the origin of behavioral complexity, and that complexity evolved on several lines in animals with different brain and body plans, conserving in at least some groups the subjectivity-related role of large-scale, dynamic patterns (cf. van Swinderen’s flies). Given the many uncertainties, it can still be claimed that none of the invertebrate animals has the right sort of brain for even a basic form of consciousness or felt experience. However, octopuses make that move difficult, through their display of what appear to be a range of consciousness-related behaviors despite brains very different from our own. The question here is not whether they have experience of the same kind as us, but some kind. If octopuses are regarded as conscious, this frees us up to take the marks of felt experience

seriously in other organisms with the “wrong” architecture, such as various arthropods.

## GRADUALISM

The previous section used the case of the octopus to argue that we should not take architectural differences to be strong evidence against the possibility of consciousness in animals phylogenetically distant from us. If octopuses are “in,” then this has consequences for our reasoning about other cases. The present section will introduce some further complexity to the situation, challenging the talk of “in or out,” “conscious or not” that has been used often so far.

Suppose we conclude there is pain in octopuses. Where are the new frontier cases? Insects are natural candidates to consider. There is now some evidence for acute pain in bumblebees (Gibbons et al., 2022), which have much smaller nervous systems than octopuses (around a million neurons as opposed to hundreds of millions). As data come in, we may find that many more cases probably fall within the category of conscious animals than we thought, but we should also reflect on the concepts and distinctions being used here.

An eventual view in this area will probably have a gradualist character, not only in a recognition of gradations and differences of degree within animal experience, but in the replacement of the binary distinction between conscious and nonconscious animals with a more graded treatment. This view can be motivated diachronically. Fully fledged conscious experience probably evolved from marginal and gray-area forms in neurally simpler animals, through a series of situations where the trait was neither clearly present or absent (Godfrey-Smith, 2020a). There is no reason to assume that there was a “lights on” moment. In evolution, complex adaptive characteristics tend to be constructed in gradual stages, rather than appearing in a single step. This situation is familiar from cases like flight, warm-bloodedness, and probably life itself. A *weakly gradualist* view of consciousness posits a discrete step from *no* to a minimal *yes*, and gradations from there. A *strongly gradualist* view has no discrete step to *yes*.

The likelihood of strong gradualism, in the light of evolutionary considerations, invites us to look at the faintest versions of some of the traits that figured as positive evidence for consciousness above. An example is *nociceptive sensitization* (Walters, 2018; Crook & Walters, 2011). Nociceptive sensitization is seen in gastropods such as *Aplysia*, also in fly larvae, and others. It is a heightened sensitivity after an aversive event, such as electric shock, pinching, or application of chemicals like table salt. Nociceptive sensitization can be either “peripheral” or more central and general, and can involve a state that has been described as fear-like, anxious, or hypervigilant. If the animal has a predictor of the aversive event, then it may acquire a conditioned fear-like response to that predictor, while behaving more normally the rest of the time. If it has

no available predictor, the response is a more pervasive hypervigilance (Walters, 2018).

The 2021 Crook octopus study provided evidence for felt pain because, in part, of the integrated nature of the animal's response to an aversive event—the response is not reflex-like, and pervades several behavioral contexts. In nociceptive sensitization, we have a much fainter version of something like that.

Whereas Crook's octopus study gives us evidence for pain, nociceptive sensitization gives us evidence for something harder to categorize—something akin to aversive experience, but in an animal with a nervous system that is so much simpler that new concepts may be needed to describe it. The impoverished nature of our present stock of concepts arose also at an earlier stage in this article, when we considered systems that lack the kind of orientation to their environment usually associated with subjectivity. When are we encountering another kind of conscious experience, and when is it something other than conscious experience, but related to it? At the moment, our conceptual framework can often do little with these questions that goes beyond stipulation.

Nociceptive sensitization is an example of the kind of phenomenon that pushes us to reconceptualize consciousness and experience. It is notable, also, how evolutionarily distant some animals that share this capacity are; the common ancestor of *Drosophila* and *Aplysia* probably lived in the Ediacaran. Nociceptive sensitization is a simple enough trait that a single origin is more plausible than it would be for pain itself. It is a plausible feature of an ancestral worm-like animal of that kind. However, being a simple but useful feature, nociceptive sensitization may also have arisen independently several times.

## Conclusion

The NDS approach holds that conscious experience is characteristic of systems whose nervous systems have been shaped to realize subjectivity in the service of coherent agency, and holds that the combination of network properties and large-scale dynamic patterns seen in nervous systems is important in the explanation of consciousness, whereas the vertebrate brain architecture is inessential. Wholly artificial systems may one day be conscious, but will require new architectures with greater low-level functional similarity to neural systems. The evolutionary perspective taken in this article also motivates a gradualist view; a simple distinction between animals who are “in” or “out” will probably be replaced with a view that admits differences of degree on perhaps many dimensions. Neurally simpler animals such as gastropods and annelids may be inadequately handled with a binary distinction between conscious and nonconscious. Our conceptual frameworks in this area will continue to co-evolve with the growth of our empirical knowledge.

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Corresponding author: Peter Godfrey-Smith, University of Sydney, or via e-mail: pgodfreysmith@gmail.com.

## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were  $M(\text{an})/M = .407$ ,  $W(\text{oman})/M = .32$ ,  $M/W = .115$ , and  $W/W = .159$ , the comparable proportions for the articles that these authorship teams cited were  $M/M = .549$ ,  $W/M = .257$ ,  $M/W = .109$ , and  $W/W = .085$  (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

## REFERENCES

- Albantakis, L., & Tononi, G. (2021). What we are is more than what we do. *arXiv*. <https://doi.org/10.48550/arXiv.2102.04219>
- Bayne, T., Seth, A. K., & Massimini, M. (2020). Are there islands of awareness? *Trends in Neurosciences*, 43, 6–16. <https://doi.org/10.1016/j.tins.2019.11.003>, PubMed: 31836316
- Bielecki, J., Nielsen, S. K. D., Nachman, G., & Garm, A. (2023). Associative learning in the box jellyfish *Tripedalia cystophora*. *Current Biology*, 33, 4150–4159. <https://doi.org/10.1016/j.cub.2023.08.056>, PubMed: 37741280
- Budd, G. E., & Mann, R. P. (2020). Survival and selection biases in early animal evolution and a source of systematic overestimation in molecular clocks. *Interface Focus*, 10, 20190110. <https://doi.org/10.1098/rsfs.2019.0110>, PubMed: 32637066
- Bullock, T. H. (1984). Ongoing compound field potentials from octopus brain are labile and vertebrate-like. *Electroencephalography and Clinical Neurophysiology*, 57, 473–483. [https://doi.org/10.1016/0013-4694\(84\)90077-4](https://doi.org/10.1016/0013-4694(84)90077-4), PubMed: 6201342
- Burkhardt, P., Colgren, J., Medhus, A., Digel, L., Naumann, B., Soto-Angel, J. J., et al. (2023). Syncytial nerve net in a ctenophore adds insights on the evolution of nervous systems. *Science*, 380, 293–297. <https://doi.org/10.1126/science.ade5645>, PubMed: 37079688
- Crook, R. J. (2021). Behavioral and neurophysiological evidence suggests affective pain experience in octopus. *iScience*, 24, 102229. <https://doi.org/10.1016/j.isci.2021.102229>, PubMed: 33733076
- Crook, R. J., & Walters, E. T. (2011). Nociceptive behavior and physiology of molluscs: Animal welfare implications. *ILAR Journal*, 52, 185–195. <https://doi.org/10.1093/ilar.52.2.185>, PubMed: 21709311
- Dehaene, S. (2014). *Consciousness and the brain: Deciphering how the brain codes our thoughts*. New York: Viking.

- Gibbons, M., Versace, E., Crump, A., Baran, B., & Chittka, L. (2022). Motivational trade-offs and modulation of nociception in bumblebees. *Proceedings of the National Academy of Sciences, U.S.A.*, *119*, e2205821119. <https://doi.org/10.1073/pnas.2205821119>, PubMed: 35881793
- Godfrey-Smith, P. (2019). Evolving across the explanatory gap. *Philosophy, Theory, and Practice in Biology*, *11*. <https://doi.org/10.3998/ptpbio.16039257.0011.001>
- Godfrey-Smith, P. (2020a). Gradualism and the evolution of experience. *Philosophical Topics*, *48*, 201–220. <https://doi.org/10.5840/philtopics202048110>
- Godfrey-Smith, P. (2020b). *Metazoa: Animal life and the birth of the mind*. New York: Farrar, Straus and Giroux.
- Godfrey-Smith, P., Scheel, D., Chancellor, S., Linquist, S., & Lawrence, M. (2022). In the line of fire: Debris throwing by wild octopuses. *PLoS One*, *17*, e0276482. <https://doi.org/10.1371/journal.pone.0276482>, PubMed: 36350820
- Grabowska, M. J., Jeans, R., Steeves, J., & van Swinderen, B. (2020). Oscillations in the central brain of *Drosophila* are phase locked to attended visual features. *Proceedings of the National Academy of Sciences, U.S.A.*, *117*, 29925–29936. <https://doi.org/10.1073/pnas.2010749117>, PubMed: 33177231
- Gutnick, T., Neef, A., Cherninsky, A., Ziadi-Künzli, F., Di Cosmo, A., Lipp, H.-P., et al. (2023). Recording electrical activity from the brain of behaving octopus. *Current Biology*, *33*, 1171–1178. <https://doi.org/10.1016/j.cub.2023.02.006>, PubMed: 36827988
- Hochner, B. (2013). How nervous systems evolve in relation to their embodiment: What we can learn from octopuses and other molluscs. *Brain, Behavior and Evolution*, *82*, 19–30. <https://doi.org/10.1159/000353419>, PubMed: 23979453
- LeDoux, J. E. (2022). As soon as there was life, there was danger: The deep history of survival behaviours and the shallower history of consciousness. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *377*, 20210292. <https://doi.org/10.1098/rstb.2021.0292>, PubMed: 34957848
- Levine, J. (1983). Materialism and qualia: The explanatory gap. *Pacific Philosophical Quarterly*, *64*, 354–361. <https://doi.org/10.1111/j.1468-0114.1983.tb00207.x>
- Melloni, L., Molina, C., Pena, M., Torres, D., Singer, W., & Rodriguez, E. (2007). Synchronization of neural activity across cortical areas correlates with conscious perception. *Journal of Neuroscience*, *27*, 2858–2865. <https://doi.org/10.1523/JNEUROSCI.4623-06.2007>, PubMed: 17360907
- Nagel, T. (1974). What is it like to be a bat? *Philosophical Review*, *83*, 435–450. <https://doi.org/10.2307/2183914>
- Nilsson, D.-E. (2013). Eye evolution and its functional basis. *Visual Neuroscience*, *30*, 5–20. <https://doi.org/10.1017/S0952523813000035>, PubMed: 23578808
- Passano, L. M. (1963). Primitive nervous systems. *Proceedings of the National Academy of Sciences, U.S.A.*, *50*, 306–313. <https://doi.org/10.1073/pnas.50.2.306>, PubMed: 14060649
- Pophale, A., Shimizu, K., Mano, T., Iglesias, T. L., Martin, K., Hiroi, M., et al. (2023). Wake-like skin patterning and neural activity during octopus sleep. *Nature*, *619*, 129–134. <https://doi.org/10.1038/s41586-023-06203-4>, PubMed: 37380770
- Scheel, D., Godfrey-Smith, P., & Lawrence, M. (2016). Signal use by octopuses in agonistic interactions. *Current Biology*, *26*, 377–382. <https://doi.org/10.1016/j.cub.2015.12.033>, PubMed: 26832440
- Seth, A. K., Suzuki, K., & Critchley, H. D. (2012). An interoceptive predictive coding model of conscious presence. *Frontiers in Psychology*, *2*, 395. <https://doi.org/10.3389/fpsyg.2011.00395>, PubMed: 22291673
- Shea, N., & Bayne, T. (2010). The vegetative state and the science of consciousness. *British Journal for the Philosophy of Science*, *61*, 459–484. <https://doi.org/10.1093/bjps/axp046>, PubMed: 22654125
- Shigeno, S., Andrews, P. L. R., Ponte, G., & Fiorito, G. (2018). Cephalopod brains: An overview of current knowledge to facilitate comparison with vertebrates. *Frontiers in Physiology*, *9*, 952. <https://doi.org/10.3389/fphys.2018.00952>, PubMed: 30079030
- Shomrat, T., Turchetti-Maia, A. L., Stern-Mentch, N., Basil, J. A., & Hochner, B. (2015). The vertical lobe of cephalopods: An attractive brain structure for understanding the evolution of advanced learning and memory systems. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *201*, 947–956. <https://doi.org/10.1007/s00359-015-1023-6>, PubMed: 26113381
- Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, *1*, 261–267. [https://doi.org/10.1016/S1364-6613\(97\)01080-2](https://doi.org/10.1016/S1364-6613(97)01080-2), PubMed: 21223921
- Singer, W. (2018). Neuronal oscillations: Unavoidable and useful? *European Journal of Neuroscience*, *48*, 2389–2398. <https://doi.org/10.1111/ejn.13796>, PubMed: 29247490
- Tononi, G., & Koch, C. (2015). Consciousness: Here, there and everywhere? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *370*, 20140167. <https://doi.org/10.1098/rstb.2014.0167>, PubMed: 25823865
- Trestman, M. (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory*, *8*, 80–92. <https://doi.org/10.1007/s13752-013-0102-6>
- van Swinderen, B. (2005). The remote roots of consciousness in fruit-fly selective attention? *BioEssays*, *27*, 321–330. <https://doi.org/10.1002/bies.20195>, PubMed: 15714556
- Walters, E. T. (2018). Nociceptive biology of molluscs and arthropods: Evolutionary clues about functions and mechanisms potentially related to pain. *Frontiers in Physiology*, *9*, 1049. <https://doi.org/10.3389/fphys.2018.01049>, PubMed: 30123137