

# Psychology of Consciousness: Theory, Research, and Practice

## Did Consciousness First Evolve in the Amniotes?

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# Did Consciousness First Evolve in the Amniotes?

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The term *consciousness* is here used to represent a feature of neural systems. This constraint allows for an attempt to model its evolutionary trajectory. Various lines of evidence point to the initiating events occurring in connection with the adaptation of vertebrates to a life on land, which started more than 300 million years ago in the early amniotes. Presumably, the main evolutionary advantage of consciousness was a more sophisticated strategy for making decisions. I suggest that this strategy depended on the use of positive and negative feelings as a common currency to evaluate behavioral options. Feelings require the ability to feel, and thus a form of awareness, which may have spurred the instigation of consciousness. According to the present model, consciousness is not required for a nervous system to display advanced computational capacity.

*Keywords:* evolution, feelings, emotions, amniotes, mood modules

The term *consciousness* here implies an ability of the organism to be aware of sensory input and thus be in a position to monitor aspects of both the external and internal environment. The attribute provides what may be referred to as a *film of life*. Besides sensory information, feelings appear to be an important, and likely universal, component of what conscious animals experience. In these animals, select types of behavior are driven by motivation based on feelings—rather than on more hard-wired responses such as fixed or acquired action patterns. A key feature of consciousness is the ability to use past experiences to evaluate the outcome of various behavioral options.

Some scientists favor the notion of *panpsychism*—that consciousness is a universal feature of all things (Brüntrup & Jaskolla, 2017). I do not take a stance as to whether there is an entity in the universe deserving of that description, but choose to restrict the concept of consciousness to a feature of neural systems. The scientific study of consciousness as a biological phenomenon is now widely accepted (Low, 2007).

Sentience comes in a variety of forms and degrees of sophistication. A common distinc-

tion is between *primary consciousness*, which can be defined as the ability to integrate observed events with memory to create awareness of the present and immediate past, and *secondary consciousness*, which includes additional features such as advanced cognition, self-awareness, and reflective thoughts (Edelman, 2004). Primary consciousness is sufficient to turn key parts of brain activity into a cohesive film of life.

Each species has a particular version of anatomical and behavioral traits, which implies an unresolvable problem when it comes to defining terms such as *consciousness*. Words are typically coined to describe human features, but when employed to portray other species, the question of appropriate use depends on a somewhat arbitrary cut-off as to degree of resemblance with the relevant human feature. For instance, some people will claim that dogs have a nose, whereas others may refute that and insist on using the term *snout*. The snout and the nose are evolutionary homologous entities, but they have evolved along different trajectories for a considerable amount of time. Similarly, the sentience experienced by a dog is most likely different from that experienced by a human, but the two versions are (presumably) derived from a common precursor, which makes it reasonable to refer to them by the same term. Whether an animal attribute has the required similarity to the homologous or analogous (that is, due to

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convergent evolution) human attribute to warrant the use of shared terminology is a subjective choice.

The above statement implies that a stringent definition of consciousness is not necessarily practical—for the same reason that it is not always useful to insist on a strict definition of the term *nose*. Thus, the answer to the question of who (or what) is conscious will necessarily turn on semantics.

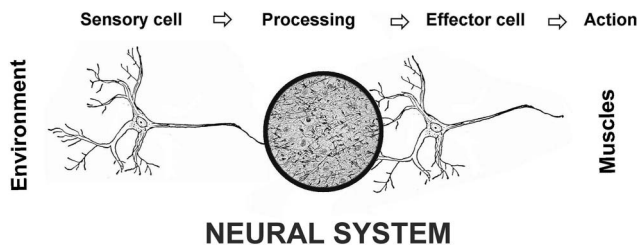
### Evolution of Neural Systems

The primary purpose of neural systems is to orchestrate *movement* (what we tend to refer to as behavior), a notion that has been referred to as “motor primacy” (Llinas, 2001). As a rule of thumb, the challenges facing an animal concern either approach or avoidance; that is, to pursue what is advantageous for the genes (survival and procreation), and to avoid what is detrimental (such as poison and predators). In the more primitive neural systems (e.g., in jellyfish), these two options are hard-wired as reflexes. Sensory cells connect more or less directly to motor cells, implying that a particular environmental stimulus will give rise to a stereotypic form of behavior. The first neural systems were presumably of a similar nature. Plants, in general, do not require a capacity to move, as they rely on sunlight for energy.

Neurons and neural systems first appeared some 600 million years ago, at about the time when *Ctenophores* split off from other phyla of multicellular animals. Whereas the neural systems of these other phyla are based on the same blueprint, the nerve cells of *Ctenophores* employ nonhomologous genes and operate in a distinct fashion (Moroz et al., 2014).

Neural systems were an obvious asset for animals; thus, evolution expanded on and refined the original design. As indicated in Figure 1, neural systems can be divided into three parts: sensory cells, processing unit(s), and effector cells. In the more advanced animals, nerve cells aggregate in ganglia or other centralized structures such as the vertebrate brain. These structures evolved to perform processing and evaluation of sensory information prior to a response. Since the time of the first neurons, evolution has facilitated considerable improvements in the capacity to sense the environment, for example in the form of complex eyes, but arguably even more substantial progress in the processing capacity of the centralized neurological structures. Although the most primitive neural systems operate entirely on reflexes, or fixed action patterns, the expansion of processing implied a gradual shift toward more sophisticated control mechanisms. The advantages for the organism were presumably: (a) a capacity to evaluate more information before executing a response (that is, information from a larger variety and more advanced, sensory organs, as well as the memory of previous experiences) and (b) to compute this information in a way that optimizes behavior. Consciousness reflects a particular strategy related to the improvement of processing. Nevertheless, even in humans several types of external stimuli and internal needs are cared for by reflexive (unconscious) processing, exemplified, respectively, by the adjustment of pupils in response to light and the heartbeat.

Three phyla of animals evolved particularly advanced neural systems, and consequently advanced forms of behavior. The three—arthropods, mollusks, and vertebrates—are today the



*Figure 1.* Layout of neural systems. Most systems can be split into three components: *Sensory cells* detect environmental information, this is transferred to *processing units* (ganglia or brains), which decide on actions and subsequently send signals to muscles via *effector neurons*.

most successful (measured as biomass or variety of lifeforms) of the 35 phyla presently inhabiting this planet. It seems likely that the key to their success came with the expansion of the neural systems. The processing or computational aspect, what I shall refer to as the *algorithm* used, allowed for gradually more flexible and adaptable behavior. It is important to note that although the systems went from simple reflexes to learning, instinctual behavior, and cognitive control, the core dichotomy of behavioral options (to pursue or avoid) remained the same. We know that in at least one of the above-mentioned phyla (the vertebrates), consciousness evolved as part of the strategy to ensure optimal behavior. The question is at what point this happened. If the event predates the split between the three phyla, invertebrate animals are also likely to harbor consciousness.

I shall argue that the more parsimonious model for the evolutionary trajectory leading to sentient animals is that consciousness evolved only once—starting with the early amniotes. A similar view has been proposed previously (Cabanac, Cabanac, & Parent, 2009; Grinde, 2013); however, alternative models flourish, ranging from humans only, to all mammals, all vertebrates, vertebrates/mollusks/arthropods, all animals, and all living things (Feinberg & Mallatt, 2013; Liljenström & Århem, 2008; Macphail, 1998). Here, I present novel evidence substantiating the model that consciousness first developed in amniotes.

### Indicators of Consciousness

To evaluate consciousness in animals, it is essential to identify relevant correlates. In humans, “accurate report” (e.g., in response to queries about a sensation or experience) is used to assess whether a person is conscious, but we need different defining qualities to probe consciousness in animals (Seth, Baars, & Edelman, 2005).

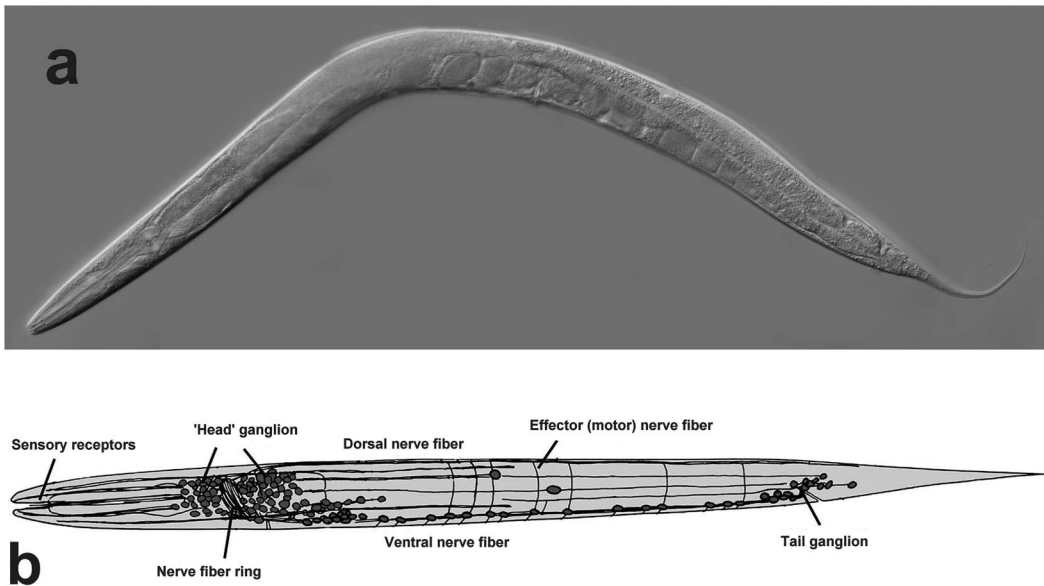
If we knew the neural correlates of consciousness, we could simply look for similar structures and neurological processes in other species. Unfortunately, we only have vague models; moreover, the divergence of neural systems implies that a reasonable comparison is restricted to vertebrates (Koch, Massimini, Boly, & Tononi, 2016). I shall therefore first consider putative behavioral correlates of con-

sciousness. The discussion of the neurological evidence for the proposed model follows in a later section.

The type of algorithm used to orchestrate behavior is a characterizing feature of advanced neural systems. Note that the word algorithm here has a less stringent meaning than in computer science. It stands for a broad strategy in terms of neuronal processing, yet a particular animal may employ more than one algorithm, as exemplified by the use of both reflexes and conscious processing in the human brain. It seems reasonable to assume that observable aspects of behavior will reflect the algorithm responsible for executing the behavior. In other words, conscious decision-making should leave some sort of behavioral mark.

The ability to respond to environmental stimuli does not require consciousness; even organisms without neurons respond to light and chemicals. In animals with neural systems, the response can be preprogrammed, a faculty that does not require extensive centralized processing and therefore is unlikely to signal sentience. Although the capacity to base decisions on previous experiences, that is learning, requires more in terms of neural processing, this capacity appears to be a relatively modest challenge: The nematode *Caenorhabditis elegans*, with some 300 neurons (see Figure 2), possesses this capacity (Zhang, Lu, & Bargmann, 2005). It therefore seems unlikely that learning qualifies as an indicator of consciousness.

A less obvious but highly relevant point is that even complex and sophisticated behavior does not necessarily imply a conscious form of processing. Humans offer the best example of what neural systems can achieve without resorting to consciousness, simply because we are the only species that can adequately report what we *do*, or *do not*, experience. We have an extensive autonomic neural system throughout the body, but also parts of the brain, such as the cerebellum, are presumably not involved in sentience. Although the decision to move is (partly) under conscious control, the cerebellum orchestrates the detailed adjustment of muscle tonus. As it contains some 80% of the brain neurons (Herculano-Houzel, 2010), the fine-control of muscles is arguably the most advanced function of the brain. Another example is the nervous system associated with the human gastrointestinal tract (Hurley, 2011), which comprises some 500



*Figure 2.* The neural system of the nematode *Caenorhabditis elegans* may reflect the sophistication in the common ancestors of arthropods, mollusks, and vertebrates. (a) A photo of the 1-mm-long animal, the mouth pointing to the left. (Reprinted with permission from Zeynep Altun, [www.wormatlas.org](http://www.wormatlas.org)). (b) Drawing where the neurons (dark, round spots) and nerve fibers (black lines) are indicated. (Modified version reprinted with permission from John White, University of Wisconsin).

million nerve cells and orchestrates sophisticated bowel movements, as well as other tasks associated with digestion, without requiring any conscious effort. Moreover, a computer can make better decisions than most brains if equipped with a suitable algorithm; yet such decisions do not qualify as consciousness in the present use of the term. Instead, I suggest that the success of computers adds evidence to the stance that advanced, neural problem-solving can be achieved in the absence of sentience. There are numerous possible algorithms, regardless of whether considering computers or neural systems, which can direct highly sophisticated decision-making processes. On the other hand, a number of features have been suggested as relevant indicators of consciousness (reviewed in Butler, 2008; Cabanac et al., 2009; Crick & Koch, 2003; Edelman & Seth, 2009). The more pertinent features are mentioned below.

A core point is that consciousness implies a particularly “open” or flexible algorithm for executing control. In terms of observable behavior, the following features can consequently be

construed as indicative of conscious processing: Cultural transmission, behavior that sometimes is unexpected and nonstereotypical, advanced forms of adaptability to minor variations in circumstances, and behavior suggesting choice based on motivation rather than on (learned) programmed options.

All the above features are expected to correlate with sentience. The problems are (a) that they theoretically might reflect other neural algorithms as well and (b) that they may not be equally well developed in all lineages of conscious animals. The position taken here is that they are suggestive of consciousness because other, independently evolved algorithms are less likely to incorporate the same qualities. However, two further lines of evidence are relevant to improve confidence in a theory that aims at singling out conscious animals: (a) a model that describes the evolutionary trajectory leading to sentience and (b) the question of whether putative neural correlates of consciousness are present. Evidence related to these two lines of inquiry will be presented in later sections.

## Conscious or Unconscious

The capacity for consciousness is one of many functions (also referred to as modules or apps) that have been added to the brain by the process of evolution (Grinde, 2016). Activity that is not brought to conscious awareness, can be referred to as *unconscious*, whereas the term *subconscious* may be used for the indistinct boundary, or “gray-zone,” between the conscious and the unconscious. The notion of a “gray-zone” reflects that consciousness is not an either/or phenomenon. The degree of arousal can shift from almost unconscious to highly alert, and relevant information can disappear from the mind or suddenly pop up. In other words, subconscious activity implies processes that can contribute to conscious experiences, as reflected in the term *intuition*, as well as in the more scientific concept of subliminal perception (Dehaene, 2014). There are a range of brain processes, such as the contraction of pupils, which was never meant to reach awareness. In humans, conscious content may be subdivided into three types: (a) information from external and internal sense organs, (b) feelings/emotions, and (c) internally generated content such as cognition, imagination, and memories.

It has been debated whether sleep implies a form of consciousness (for discussions, see Koch et al., 2016; Windt, Nielsen, & Thompson, 2016). Sleep can be either of the REM-type, which closely resembles the awake state in neurological terms, and non-REM sleep. Although dreams are more common in REM sleep, they also occur in the non-REM form. Some scientists suggest that dreaming, particularly during REM-sleep, is a state of consciousness, whereas others find attributes of consciousness even in dreamless sleep. I find it more appropriate to restrict the term *consciousness* to a select fraction of the activity that takes place in the awake brain, but this delineation is not important for the present discourse.

Conscious life rests in the hands of unconscious processes in the brain. That is, the life experienced by a human can be compared to an app that is (typically) turned on in the morning and off again at night. The neural system adds content to conscious experiences on a “need-to-know basis.” Thus, input stemming from sense organs is processed, filtered, and likely distorted, before forming a percept (Dehaene,

2014). Conveying too much information to conscious processing could cause dangerous distractions. In short, consciousness is a feature set up by evolution to help direct behavior in certain types of situations. It presumably serves complex situations where many factors ought to be included in the equation. For us, this select part of brain activity is our lives; consequently, we tend to think of consciousness as all there is, or all that matters in life. Furthermore, we easily extrapolate from that position and assume that other life forms possess the same feature.

Although consciousness necessarily must have conferred some benefits, there are several disadvantages with this algorithm, which explain why evolution designed the brain to engage sentience for particular purposes: (a) Conscious processing is presumably energy intensive; a more automated response conserves nutrients and oxygen in cases, such as the regulation of heartbeat, where awareness is unlikely to add any meaningful input. (b) Consciousness is a relatively slow process. Perception of a stimulus requires some 300 ms (Dehaene, 2014), which is considerably slower than a reflex. (c) Although unconscious processes typically work in parallel, permitting the regulation of several bodily functions simultaneously (e.g., heartbeat and temperature regulation), the conscious brain can only engage in one task at a time; if additional tasks require input, it is necessary to shift back and forth between them (Baars, 1997). (d) The capacity for consciousness presumably evolved for decision making, not for execution; thus, the conscious brain lacks the power to deal with assignments such as orchestrating the optimal performance of legs and arms (Morsella & Poehlman, 2013). (e) Feelings and awareness are limited to cases where they made evolutionary sense. For example, we do not feel a tumor unless it happens to press on nerve cells installed for other purposes, because during our evolutionary history, being aware of a tumor would not have helped. (f) Cognition is vulnerable to the whims of the individual, which means that for the genes, this form of flexible processing is risky. A sentient being may choose not to reproduce or, equally detrimental, to commit suicide.

Due to the above constraints, sentience is not the sole, and not necessarily even the prime, “mover” of behavior (Baumeister, Masicampo,

& Vohs, 2011; Cabanac & Bonniot-Cabanac, 2007). The constraints on consciousness help explain why following intuition, which presumably involve subconscious processes, is occasionally a better strategy than exercising deliberate control, such as in the case of solving certain problems and in the fine-tuning of muscles required to hit a golf ball.

### One or More Phyla?

*Homo sapiens* is the only species we can say for sure possess a conscious brain, but there is ample evidence (as will be discussed in the next section) that we can extrapolate to other mammals. As a group, the mammals have had a reasonable success, which may reflect, at least in part, a capacity for making conscious behavioral decisions. When a feature brings success, it can be construed as an argument suggesting that the feature is also likely to appear elsewhere. Before considering consciousness in the various classes of vertebrates, I shall discuss whether the trait is likely to be present in other phyla.

Among the invertebrates, the coleoid cephalopods (octopuses, squid, and cuttlefish) are considered prime candidates for consciousness (for reviews, see Edelman & Seth, 2009; Mather, 2008). These animals display advanced behavior, such as learning based on “reward-like” stimuli (Borrelli & Fiorito, 2008), navigating mazes (Moriyama & Gunji, 1997), and possibly learning by observing other members of the species (Fiorito & Scotto, 1992), a trait associated with culture. They can learn to recognize a variety of objects, and they have considerable capacity for memory (Borrelli & Fiorito, 2008). Their behavior does not appear to be as flexible, or as individualized, as what is typically seen in mammals; yet it arguably goes beyond what one would expect from a collection of mere innate or learned behavioral patterns.

Sophisticated behavior is observed in arthropods as well. Social insects, in particular, have features suggestive of consciousness (Barron & Klein, 2016). They are capable of conceptual learning (Avargues-Weber & Giurfa, 2013) and decision-making behavior reminiscent of optimism (Perry, Baciadonna, & Chittka, 2016). Yet, compared to cephalopods, insect behavior seems less adaptable and more in line with what

one might expect from advanced, preprogrammed learning.

In my evaluation, the above behavioral observations do not exclude some form of consciousness, but are neither strong, supportive evidence. There is, however, one major obstacle when arguing for consciousness in arthropods and mollusks: As shown in Figure 3, these phyla split up from the vertebrate lineage prior to, or in the beginning of, the *Cambrian explosion* some 540 million years ago (Budd, 2003). At that time, the common ancestors were relatively small and unsophisticated aquatic life forms. It seems unlikely that these ancestor had a neural system sufficiently advanced to incorporate consciousness. If this conjecture is correct, consciousness in mollusks or arthropods would need to reflect convergent evolution.

Convergent evolution of advanced features is possible. Eyes, for instance, evolved independently in several lineages, presumably from the shared starting point of light-sensitive patches of skin. The wings of insects and birds are another example. However, consciousness, as an algorithm for behavioral decisions, seems to be a less obvious candidate. For one, although wings and eyes have distinct evolutionary benefits, it is less clear that consciousness confers a similar advantage. Arguably, the most successful phylum is arthropods (in terms of species variety and having the species with the highest biomass), and in these animals behavior is more likely controlled by other types of algorithms. Moreover, the majority of present species with particularly sophisticated forms of consciousness—the apes—are close to extinction; as are all but one of the hominin species that appear in the fossil record. Although consciousness allows for flexible and adaptable behavior, as discussed in the previous section it has also several less compelling aspects. In short, sentience does not seem to be sufficiently attractive as a feature to suggest its independent occurrence in otherwise diverse lineages.

It should also be pointed out that wings and eyes are only superficially similar in these phyla. The shared features define them as respectively wings and eyes, but the actual structural solutions opted for are quite different. The resemblance reflects requirements for respectively flying and accurate vision, which explains the convergent evolution. Similarly, we do observe advanced behavior in all three phyla, and

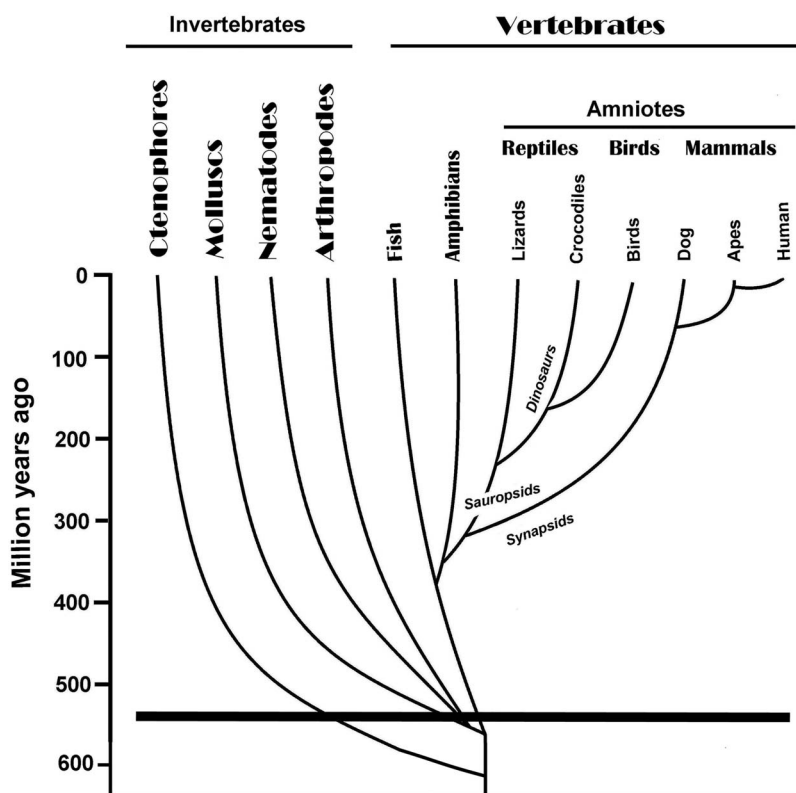


Figure 3. A phylogenetic tree depicting the lineages discussed. The type of letters used in the names suggests phylogenetic level; that is, vertebrates are a *phylum*, mammals constitute a *class*, whereas invertebrates and amniotes are trivial names. The thick, horizontal line indicates the time of the Cambrian explosion.

for that they need advanced brains with sophisticated algorithms. This can be construed as convergent evolution, even if the types of algorithm differ between the phyla. As pointed out above, other algorithms can orchestrate complex behavioral control without resorting to consciousness.

Based on the above discussion, it seems more parsimonious to assume that consciousness is restricted to vertebrates. If something reminiscent of conscious control, and a “film of life,” should exist in other phyla, one would expect it to be so divergent from the mammalian version that the term *consciousness* would not be warranted.

Although it is difficult to imagine consciousness without a certain size and complexity of the neural system, it seems pertinent to point out that at least mollusks are not excluded due to

this restriction. Their neural systems may be sufficiently advanced, but they are simply more likely to have evolved alternative algorithms. True, mammalian brains tend to be bigger and more complex than the similar structures of invertebrates, at least when comparing brain size in relation to body size. Nevertheless, the smallest mammalian brains, such as the Etruscan shrew whose brain weighs in at 60 mg, with perhaps some 50 million neurons (Anjum, Turni, Mulder, van der Burg, & Brecht, 2006), is about one 10th the size of the nervous system of typical octopi. The much-studied common octopus, which is considered medium sized with a body weight of 1–10 kg, has approximately 500 million neurons (Young, 1963). Then again, octopi have a more decentralized neurology compared with mammals, with about two thirds of the neurons situated in ganglia



within the arms. Still, based on the assumption that all mammals, including shrews, are conscious, the octopi brains should be more than sufficient in size to include this attribute.

It seems reasonable to argue that synaptic complexity is more important than the size of the brain when looking for correlates of advanced behavior (Bumbarger, Riebesell, Rödel-sperger, & Sommer, 2013; Sakai et al., 2012). Yet, I consider the above comparisons of sufficient relevance to contend that consciousness evolved in a particular lineage and for a particular purpose, rather than simply being a consequence of brain intricacy or size.

To conclude this section, consciousness seems to be restricted to vertebrates. The next questions are then: If so, at what point, and why, did consciousness first appear?

### Vertebrates

Various lines of evidence, which I expand on below and in later sections, suggest the existence of at least primary forms of consciousness in mammals and birds (Butler & Cotterill, 2006; Edelman & Seth, 2009), and likely, in a more rudimentary form, in reptiles (Cabanac et al., 2009). Obviously, the closer an animal is to our lineage in evolutionary terms, the more likely it is to share human features, and the easier it is to recognize the existence of these features. Consequently, the case for consciousness is strongest in the apes. Chimpanzees are 98–99% genetically similar to humans (Prüfer et al., 2012); thus, one would expect that many attributes are shared in some form between chimps and humans. For example, chimpanzees display diverse cultural inheritance (Whiten, 2011), and they can learn to communicate with humans (Segerdahl, Fields, & Savage-Rumbaugh, 2005).

An even more intriguing indication of sentience is offered by experiments suggesting that chimpanzees distinguish between a conscious response and a response based on subliminal signals (Dehaene, 2014): If a picture of a banana is flashed for about 20 ms, the chimp is unaware of the image, but it can still influence behavior; if the animal is subsequently asked to choose among different types of fruit, the more likely choice is a banana. This type of experiments works for both humans and chimpanzees, in that both can be asked whether they actually

did see the banana. Moreover, the brain processes involved in subliminal versus conscious processing of visual stimuli are similar; there is a broader activation of neural circuits when the stimuli are shown for a sufficient time to yield a conscious percept.

Emotions are by many considered a key feature of consciousness, and they appear to be present in most, if not all, mammals (Panksepp, 2005). Social species, in particular, show clear signs of sentiments. We recognize various types of emotions in other humans by reading facial expressions and body language, but we can also learn to recognize related signals in animals. The similarity of human and animal emotions is supported by the observation that comparable muscles tend to be activated when a human, or for example a dog, display sentiments such as sadness, joy, fear, or anger (Hallcrest, 1992). It seems unlikely that evolution would have added a way to communicate emotions without also providing the basis for initiating the underlying emotional experience.

It is possible to activate feelings by stimulating particular areas of the brain with electrodes. The resemblance between man and other mammals become evident in these experiments: Related sites cause a similar display across species; for example, by placing the electrodes at a particular subcortical location, it is possible to stimulate pleasure in humans and apparently the same response in other species such as mice and rats (Kringelbach & Berridge, 2009).

Present (placental) mammals diverged less than 100 million years ago, whereas our shared ancestors with birds and reptiles dates back more than 300 million years (see Figure 3). Consequently, to the extent that birds and reptiles possess emotions, or other aspects of consciousness, they are likely to be displayed in a different manner. All amniotes have a reasonably complex behavioral repertoire, and at least birds appear to exhibit cultural transmission (Laland & Galef, 2009). Compared with lower vertebrates, amniotes tend to have larger brains (when adjusting for body size) and are thus presumably prepared for more complex responses to the challenges of life (Butler, 2008).

As pointed out above, even bees and octopi display complex behavior. A noteworthy difference between them and amniotes is expressed in the degree of flexibility of response. In the invertebrate animals, behavior seems to be more

a question of “pushing a button,” whereas birds and mammals show hints of deliberation and individual response, in line with the expected hallmarks of decisions based on consciousness and feelings. In mammals, we recognize the feeling of pleasure by facial expression; birds may have a related reaction as suggested by the sounds they make (Riters, 2011). Moreover, a parrot that learned to use the term *good*, expanded the use to novel situations, implying that it did indeed recognize the experience of pleasure (Cabanac, 2009). Evidence also indicates that birds are able to attribute subjective mental events to other conspecifics; that is, they form some sort of theory of mind (Emery & Clayton, 2001). Another trait that separates birds, and to some extent reptiles, from amphibians is that they develop lasting partner relationships and practice extensive parental care (Reichard & Boesche, 2003). More importantly, birds appear to care about both their offspring and their mates, and the care seems to be based on feelings rather than on preprogrammed behavior. For instance, scientists claim to observe signs of grief when an infant or a partner dies (Archer, 1999). Certain species of birds, such as magpies, may even have the capacity for self-awareness in that they apparently pass the classical test of mirror recognition (Prior, Schwarz, & Gunturkun, 2008).

Some relevant features are present in all amniotes, but are not present in amphibians or fish (Cabanac et al., 2009). For example, if a reptile, bird, or mammal unaccustomed to human handling is picked up, they all display tachycardia (increased heart rate). Furthermore, amniotes, but not amphibians respond to stress with a rise in body temperature. The increase in heart rate and temperature presumably reflects an emotion-based strategy for coordinating the response to fear. If this is correct, it suggests that amphibians and fish lack the ability to *feel* fear as something unpleasant; instead, they react instinctively. Fish seem to lack certain anatomical structures associated with pain in mammals (Key, 2016), whereas reptile brains have features suggesting that these animals actually feel the pain (Cabanac et al., 2009; Mosley, 2011). It should be noted that nociceptors (neurological receptors associated with pain) most likely are present in all vertebrates as well as many invertebrates (Smith & Lewin, 2009). However, the associated response to noxious stimuli, which is

easily observed in a wide range of species, does not require feelings or consciousness.

Taken together, the above observations indicate that signs of sentience first appeared in the amniotes. As pointed out in Figure 3, the initial split in this lineage, between the *sauropsids* and the *synapsids*, occurred some 315 million years ago (Warren et al., 2008). The synapsids eventually gave rise to mammals, whereas the sauropsids split into present birds and reptiles. Birds have considerably more advanced brains and behavior than reptiles, which means the case for consciousness is stronger in this lineage. Yet, excluding the reptiles would mean that consciousness evolved independently in birds and mammals. A model that does not require recurrent invention of consciousness is, arguably, more parsimonious. A reasonable compromise is to suggest that the seed of consciousness appeared before the split of sauropsids and synapsids. Once essential prerequisites had been introduced, a certain degree of convergent evolution seems liable.

Depending on how divergent the animal versions of a trait may be before choosing a different term, one might choose to restrict consciousness to mammals alone or mammals and birds. The stance taken here is to include all amniotes in the category of conscious animals.

### Why Amniotes?

To corroborate the hypothesis that consciousness first appeared in the early amniotes, a theory as to why evolution “chose this path” would be helpful. The theory should explain why the feature served the animals in question and describe the setting that promoted this development.

It is not necessary to postulate that consciousness was an optimal solution, or even marked a substantial advantage. The evolutionary process rarely constructs optimal organisms, because mere survival is sufficient. One might imagine a robotic, or “zombie” type, brain that would be superior to even the human version, but that possibility does not negate the notion that incipient consciousness was of sufficient value to be selected for. Although the feature has proven its value by being expanded on, and by being present in several successful lineages, it is not obvious that sentience was a particularly brilliant evolutionary scheme.

Amniotes were the first vertebrates to adapt completely to life on land. It seems likely that this situation might have pointed evolution in the direction of a novel and more advanced behavioral algorithm. Nonvertebrate animals, including arthropods and mollusks, colonized land prior to, or shortly after, vertebrates—without any obvious expansion of the neural system or increased sophistication of behavior—but as discussed below, these phyla may not have had the prerequisites required for a transition to sentience. I see five arguments that can help explain why consciousness evolved in amniotes. The first three concern their particular needs:

1. Although the early, terrestrial ecosystems probably were less complex than contemporary marine environments—in terms of harboring a lower diversity of life forms—the conditions may have *changed* more rapidly on land. Aquatic life forms had gone through some three billion years of coevolution, which suggests that the relationships among the various species were reasonably stable, whereas terrestrial ecosystems were probably more fluid. This and the following point both imply that an increase in evolutionary fitness could be obtained by improving the adaptability of behavioral responses. Moreover, as discussed elsewhere, terrestrial adaptation tends to spur evolutionary innovations (Vermeij, 2017).
2. Key environmental features, such as temperature and access to water, are more or less constant in the sea, whereas they fluctuate drastically on land.
3. Amniotes are relatively large animals with long generation times and modest litters, which imply that these organisms could not evolve as fast as, for example, insects. Consequently, adaptation to novel environments relied to a greater extent on individual adaptability, rather than on genetic modification. That is, they would be more in need of advanced behavioral control.

The next two points concern their prerequisites:

4. The early amniotes most likely possessed a more sophisticated and more centralized

neural system compared with the other phyla mentioned above, and thus enjoyed a better starting point for the elaboration of behavioral algorithms.

5. Amniotes evolved lungs as an adaptation to terrestrial life. The brain is an expensive organ to operate, requiring a substantial portion of the energy (and oxygen) an organism can procure (Mink, Blumenschine, & Adams, 1981). Introducing a system of feelings and concomitant awareness, as a strategy for complex decision-making, presumably provided a push in the direction of larger and even more demanding brains. The concentration of oxygen is much higher in air compared to water, but of the terrestrial animals, only amniotes developed an efficient breathing organ.

I believe these five points contributed to the emergence of consciousness, but one should also take into account the stochastic nature of the evolutionary process. As mentioned earlier, elaborate *nonconscious* behavior is certainly feasible; the decision-making strategy employing consciousness and feelings was presumably due, in part, to chance (some may argue providence).

### The Role of Feelings

In the former section, I described why a more sophisticated behavioral algorithm would be of particular benefit for the amniotes, but not why that algorithm should entail sentience. In this section, I suggest an explanation regarding what actually triggered the evolution of consciousness.

An interesting clue is that we tend to consider the capacity for feelings to be closely associated with the capacity for consciousness. Feelings, or emotions, are typically listed among the defining features of consciousness; and they have been suggested to play a role in the evolution of consciousness (Cabanac et al., 2009; Denton, McKinley, Farrell, & Egan, 2009; Mosley, 2011). Not surprisingly, consciousness and feelings tend to follow each other in the way we reflect on animals. That is, we are worried that if a species is conscious, then the way we treat members may involve pain, and our innate tendency for empathy is repelled by that thought. It

might be argued that conscious monitoring of the environment could be a useful attribute in regard to making decisions, even in the absence of pleasant or unpleasant stimuli. In fact, it is possible to lack the capacity for physical pain (Peddareddygari, Oberoi, & Grewal, 2014), or fear of external events (Feinstein, Adolphs, Damasio, & Tranel, 2011) without diminishing the capacity for consciousness. Yet, feelings and consciousness are, nevertheless, intrinsically tied together.

Before moving on, I shall clarify how I use key terms in relation to feelings. It should be noted that the present use differs somewhat from what is common in psychology (Miskovic, Kuntzelman, & Fletcher, 2015), but is reasonably in line with a neurological approach (Kringelbach & Berridge, 2009). Feelings, emotions, and sensations are overlapping concepts. All three usually imply something good or bad (pleasure or pain) in combination with what may be referred to as a “flavor.” The flavor can, for example, be fear, love, hunger, or the taste of coffee.

*Hedonic value* refers to the positive or negative aspect of feelings, rather than the particular flavor or type. *Feeling* is used as a broader term and includes any type of experience that tend to be accompanied by hedonic value; *emotion* typically describes feelings associated with social relations, whereas *sensation* describes feelings related to external or internal senses.

The parts of the brain involved in generating any sort of pleasure or displeasure may be referred to as *mood modules* (Grinde, 2012). In the present article, the term *feelings* is used to describe the conscious output of these modules. Interestingly, the hedonic value appears to be generated by three sets of nerve circuitry regardless of the “flavor” involved; that is, there are two reward modules (*seeking* and *liking*) whereas there is only one module for displeasure (Kringelbach & Berridge, 2009; Panksepp, 1998). For example, the experience of envy activates pain-related circuitry, whereas *schadenfreude* (delight in other’s misfortune) activates reward circuitry also associated with other pleasant experiences (Lieberman & Eisenberger, 2009; Takahashi et al., 2009).

The response to the challenges of life evolved gradually from a reflexive “approach or escape” to a multifaceted decision-making process weighing a variety of pros and cons. To effec-

tively assess options, the animal requires a routine for comparing alternatives. The purpose of behavior is to benefit the genes, but the neural system needs a more proximate and tangible aim. In short, the organism benefits from some sort of “common currency” for weighing what is “good” for the propagation of the genes against what is “bad” (McFarland & Sibly, 1975). The chosen currency of the early amniotes was presumably the hedonic value. The net value is positive (pleasant) in the case where approach is appropriate, and negative (unpleasant) if avoidance is called for. The amniote brain considers the outcome of various actions (in terms of positive and negative expectations, or net hedonic value), and hence the presumed optimal option. In other words, the key principle is to motivate behavior based on *pleasure maximization*. For example, for an antelope approaching a rare source of water guarded by a lion, the question is whether the pleasure of quenching the thirst outweighs the fear of being attacked.

To summarize, feelings evolved as one, out of numerous possible algorithms that improved the neurobiological processing taking place between the sensory organs and the executive branch of the neural system. The hedonic score given to various options depends on previous experiences and future forecasting. It also depends on innate tendencies; for instance, humans may have a genetically programmed propensity to fear snakes (Silva, Gross, & Gräff, 2016). Although the primary function of the nervous system is to initiate and control movement, the primary function of the centralized unit(s) of this system, such as the human brain, is to decide the direction of movement. The present description is related to the notion of *prospect* as described by Gilbert and Wilson (2007); that is, a main function of the (mammalian) brain is to predict (by preexperiencing the future) hedonic consequences of various actions. The simpler versions of conscious brains will build their predictions primarily on innate predispositions and previous experiences from similar situations, whereas the more advanced brains, such as the human version, can extrapolate and thus simulate future events in the absence of any obvious reference points. Moreover, the advanced brains can consider not only immediate actions, but plan for the distant future. *Prospection* offers a useful tool for arriving

at behavioral decisions, but as pointed out by Gilbert & Wilson, the decisions may easily be skewed. Seligman, Railton, Baumeister, and Sripada (2016) offered a related view when describing the brain as an “engine of prediction.” However, although feelings and consciousness mark a particular flexible and powerful strategy for making predictions, even the primitive nervous system of a nematode can be said to predict the future when the reflex is changed so that the animal makes a turn upon registering the smell (chemical signature) of a bacteria that previously caused harm (Zhang et al., 2005). Furthermore, even the human brain embraces strategies that do not rely on prediction, as exemplified by reflexes.

The crucial point is that a system based on feelings requires a capacity to actually *experience* the hedonic value. It is difficult to envision how the strategy could evolve without a concurrent ability to perceive the good and the bad—feelings need to be felt. This ability would seem to require some form of awareness. In other words, the use of feelings may have been the cue pointing evolution in the direction of sentient beings.

### Alternative Explanations

Although it seems difficult to imagine feelings in the absence of some form of sentience, other advantages can have caused consciousness to evolve prior to the emergence of feelings. For example, researchers have argued that consciousness evolved as a strategy aimed at facilitating computational brainpower; or, simply, as a byproduct of a sophisticated brain (see, e.g., Harnad, 2003; Rosenthal, 2008). Given the previous discussion on the disadvantages of conscious processing, I believe the former suggestion is unlikely. The latter alternative suggests that consciousness is an epiphenomenon; that is, an incidental side effect of selection in the direction of more advanced brains. In the case of consciousness, the selection might be for advancements in sensory processing and problem solving; then, at some level of complexity, consciousness just emerged. The epiphenomenon model seems less attractive for the following two reasons: (a) Conscious processing is a complex, conspicuous, and presumably energetically expensive feature that one would expect to emerge only when providing a distinct

advantage, and (b) it is possible to outline a scenario (the use of feelings) that depicts why evolution opted for consciousness.

The capacity to learn from previous experiences is a vital component when it comes to improving decision-making, but learning does not require consciousness. I mentioned that *C. elegans* can learn, and even in humans learning can be facilitated by unconscious processing. If you experienced that an oven plate burns you, withdrawing your hand a second time can be a reflex. The point here is that an additional value is required for there to be any reason to engage a slow and often clumsy conscious response; for example, in the form of a common currency that allows for a more sophisticated algorithm. In the case of mammalian brains, that currency is the hedonic value of feelings. Other currencies are conceivable—some may require consciousness, some not—but if an alternative, conscious-requiring algorithm had evolved prior to the use of feelings, one would have expected evolution to expand on this option rather than to introduce feelings.

Part of the learning, and thus the decision-making process is to “compare predictions with reality.” The behavioral algorithm based on feelings implies that the person anticipates future rewards and punishment (by prospection), and the rewards/punishment harvested at that later point are taken into account the next time the individual encounters a similar situation. However, the trial and error process in itself does not require feelings or consciousness; in fact, trial and error is one of the foundations of machine learning. The mammalian version of trial and error learning tends to engage conscious processes, but that does not mean that the use of “trial-and-error” type reasoning fueled the evolution of sentience.

Another question is whether the expansion of sensual information could have driven the evolution of sentience? Even humans often respond without being aware of either the stimuli or the response (or both), such as when the pupils contract as a reaction to increasing light. Advancement in the capacity to sense the environment should only point toward sentience if it is combined with a consciousness-demanding algorithm for employing the information.

The *attention schema theory* (Graziano & Webb, 2015) suggests that awareness grew out of a need to limit and select the information

flow stemming from the sense organs. The main problems with this theory are, I believe, (a) that the selection of information to a large extent is handled by unconscious processes and (b) that as unconscious processing works faster than conscious processing, consciousness is likely to reduce the amount of information that can be compiled to evaluate behavioral options (Dehaene, 2014). Even humans rely on the unconscious to handle complex information; otherwise, we would, for example, not be able to perform the muscle coordination required to run across a difficult terrain.

### Neurological Evidence

It is difficult to define a neurological correlate of consciousness that applies to a wide range of animals. Consciousness engages a large, and vaguely defined, portion of the mammalian brain. Moreover, primary forms of consciousness may require different neural structures compared with the advanced human form of consciousness; and in lineages that split a long time ago, one would expect that the underlying neurology has diverged. Yet, there are neurological features that appear to be relevant to

describe consciousness in several species. Although states of consciousness are difficult to compare across species, the neurological and behavioral effects of agents known to impact on consciousness in humans can be examined in animals.

Although it is relatively easy to outline homologous brain structures within mammals, the task is more challenging when it comes to other vertebrates. Figure 4 depicts gross anatomical variations within the amniote clade. Although homologs of the main structures are easily discerned, the comparison becomes problematic in the case of various subcomponents.

As alluded to previously, consciousness does not necessarily require exceedingly advanced neurological structures. If basic forms of consciousness can fit within the 60 mg brain of a shrew, it can hardly be the most complex feature that evolution has created. Indeed, consciousness appears to be present in the absence of a cortex, as evidenced by mammals where the cortex is removed (Alkire, Hudetz, & Tononi, 2008; Panksepp, Normansell, Cox, & Sivi, 1994), and by hydranencephalic children, that is, humans born without cortex or with minimal remnants thereof (Beshkar, 2008). In

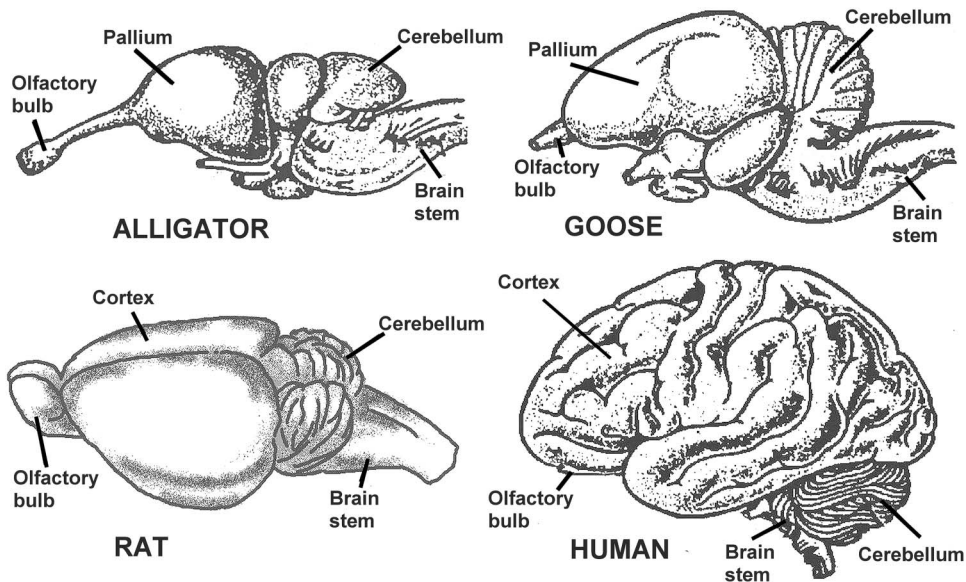


Figure 4. Drawings of reptile (alligator), bird (goose), and mammalian (rat and human) brains (not to scale). Only the main structures are indicated. (Adapted with permission from original by Richard Granger, Dartmouth College).

these individuals, it is conceivable that remaining structures of the forebrain—particularly components of the basal ganglia such as the nucleus accumbens, striatum, and ventral pallidum—are sufficient to generate a state resembling primary consciousness. The cortex is presumably required to produce a wider variety of experiences, as well as for higher cognitive functions. The above observations underline the problem of finding universal structures or activities that define consciousness.

One theoretical stance that has gained broad acceptance is that (normal) mammalian consciousness reflects a continuous and complex back-and-forth signaling in wide-ranging neural circuits within the *thalamocortical complex* (Alkire et al., 2008; Crick & Koch, 2003; Edelman & Seth, 2009). This complex, which includes the basal ganglia and possibly other parts of the forebrain in addition to the thalamus and the cortices, can be described as a *global neuronal workspace* that sets the stage for conscious processes (Dehaene, 2014). There is continuous activity in these circuits even in the absence of awareness. A sentient experience implies distinct perturbations in this basic (more orderly) signaling. The change of activity can be observed as electroencephalography (EEG) patterns in mammals and is considered to signify consciousness (Butler, 2012; Seth et al., 2005).

The observation that consciousness is regularly turned on or off (or at least drastically modified) on a diurnal basis, suggests there must be some form of neuronal “switch.” There are indeed circuits that contribute to activating or dampening arousal and/or awareness. The primary switch appears to be situated in the *reticular activating system* of the *brain stem* (Edlow et al., 2012; Steriade, 1996). This system has the capacity to turn brain activity up or down, as typified by diurnal cycling. However, this switch is not very useful as an indicator of consciousness because most organisms display diurnal cycling; that is, a related switch is present even in primitive neural systems (Funato et al., 2016).

A secondary, perhaps more consciousness specific, switch seems to reside in the *intralaminar nuclei* of the thalamus (Saalmann, 2014; Schiff, 2009). Here, direct injections of agonists to the generally inhibitory neurotransmitter GABA cause rapid sedation in rats (Miller &

Ferrendelli, 1990). A patient, who had been in the state of minimal consciousness for six years, showed signs of “awakening” upon stimulation of these nuclei by electrodes (Schiff & Fins, 2007); and thalamic damage in humans can result in a vegetative state (Alkire et al., 2008). The presence of this switch supports the notion that at least all mammals are conscious.

Birds, but to a lesser extent reptiles, have brain activity and structures associated with consciousness, whereas these features are not well developed in amphibians and fish (reviewed in Butler, 2008; Edelman & Seth, 2009). The avian pallium (which corresponds to the cortex) and thalamus support itinerant activity comparable to that found in the corticothalamic complex of mammals. In fact, an assessment of the neurobiology of reptiles, birds, and mammals reveals several aspects that suggest convergent evolution in the latter two lineages (Butler & Cotterill, 2006; Mashour & Alkire, 2013). That is, both birds and mammals apparently evolved brains better equipped to cater to advanced forms of consciousness compared with what we find in reptiles.

Dopamine may serve a key role in both the reward module referred to as “seeking” (Barbano & Cador, 2007) and in consciousness (Palmiter, 2011). Researchers have suggested that the considerable increase in telencephalic dopamine receptors in reptiles, as compared with amphibians, constitutes evidence for the notion that both consciousness and feelings first evolved in the amniotes (Cabanac et al., 2009).

Although diurnal cycling is present in most organisms, REM sleep evolved more recently. REM sleep is associated with dreaming; and based on EEG patterns, it is a state that resembles the normal awake situation. The distinct changes in EEG, between slow oscillations associated with deep sleep and the conscious-like oscillations of REM sleep, are considered to indicate a capacity for consciousness (Edelman & Seth, 2009). Previously, REM sleep was presumed to be restricted to birds and mammals (Rattenborg, 2006), but a related state has recently been observed in reptiles (Shein-Idelson, Ondracek, Liaw, Reiter, & Laurent, 2016), adding evidence to the inclusion of this lineage as sentient beings.

### The Human Version

One factor hampering our efforts to understand consciousness may simply be that the human version of the feature has progressed far beyond the original state. The human lineage obtained advanced attributes such as self-awareness, language, cognitive power, and a capacity for long-term planning; which suggests that human decisions are based largely on cognition and objectives not directly associated with hedonic value.

There are additional reasons why our experiences differ somewhat from the suggested evolutionary focus on feelings. For one, even though the primary mission of consciousness is to assist in making decisions, this task requires that the conscious brain is served information about the environment. The information stemming from sense organs does not necessarily carry a positive or negative charge; feelings are primarily activated when there are reasons for taking action or focusing attention. Once consciousness has been installed, it seems reasonable to add as much information as there is capacity to handle, to obtain the best platform for behavioral decisions.

A second point is that although much of what we experience, or think, does actually move the hedonic value slightly up or down, we do not always recognize these changes. Looking at a flower, or talking with a friend, adds small “drops of pleasure.” These “drops” are more than enough to motivate action, even if they are not recognized as pleasure.

A third point is that the algorithm based on feelings presumably evolved on top of previous (unconscious) algorithms, which are still present in our brains (as exemplified by the contraction of pupils). Habits are typically formed based on hedonic value, but can be repeated in the absence of further rewards (Pauls, Abramovitch, Rauch, & Geller, 2014; Robinson, Sandstrom, Denenberg, & Palmiter, 2005). Most likely, the mood modules still play an important role in behavioral decisions, by motivating us for actions or attention, even though we do not always recognize their presence.

### Conclusion

In the early neural systems, sensor cells activated effector neurons and thus muscles, with

little or no need for processing of the sensory information. As it seems unlikely that these animals were conscious, this attribute presumably developed at a later stage. I suggest that the evolution of conscious processes started in the early amniotes.

We humans tend to be somewhat obsessed with our conscious world, considering it to be all what life is about, when in reality it is only one of a large number of “apps” that evolution introduced to the (unconscious) brain. Other functions may actually be more advanced, or require more in terms of processing power, than a primary form of consciousness. The list of advanced functions includes how the brain translates minor variations in air pressure to yield the highly precise information present in language and music; and how the cerebellum manages to fine-tune muscle activity to create sophisticated movement. We do not understand how neural circuits create consciousness, but the gaps in our understanding of other brain functions are arguably equally large.

Below are summarized the main lines of reasoning in support of the present model for the evolution of consciousness:

1. The core function of a brain is to make behavioral decisions, and this is primarily a question of either approach or avoidance, a dichotomy that is a characteristic feature of all neural systems, including those based on consciousness. In conscious brains the decision is typically based on prospection.
2. The capacity to feel carried an evolutionary advantage as a flexible and adaptable strategy to evaluate behavioral options. That is, feelings function as a “common currency” for comparing approach-or-avoid options based on the associated positive or negative salience. The brain motivates the individual to act according to the principle of pleasure maximization.
3. For feelings to make any sense, the capacity to *experience* pleasure and displeasure seems to be required. It is difficult to conceive of distinct alternative advantages of primary forms of consciousness; for example, consciousness is not required for learning, complex behavior, or for responding to sensory information.



4. Sensory input provides an important source of information for making decisions and is therefore expected to play a dominant role in the conscious experience of life. Information relevant for conscious decisions engages the mood modules.
5. Various lines of evidence suggest that awareness and feelings evolved concurrently in early amniotes. The evidence for this contention includes physiological responses, types of behavior, and neurological features related to conscious processing.
6. Whereas convergent evolution toward more advanced forms of consciousness in birds and mammals seems likely, convergent evolution of consciousness from scratch seems unlikely, which suggests that advanced behavior in other phyla is based on different algorithms.

Evolution typically uses indirect means to promote the propagation of the genes. In mammals, for example, the pleasures of sex, rather than a desire to have children, are sufficient to ensure procreation. Pleasure maximization therefore seems to be a more likely strategy to ensure behavior catering to the survival of genes, compared with a purely cognitive notion of what is beneficial. To improve the capacity to make decisions that promote the genes, evolution would need to produce a suitable algorithm. Motivation based on feelings was the solution of choice in our lineage.

It is possible, albeit difficult, to find additional evidence favoring the present model. Perhaps the more promising line of investigation is to improve our understanding of the neurological correlates of consciousness. The technology required to examine neurological processes can be applied to any relevant species of animal. One intriguing observation is the difference in neurological signature when humans or chimpanzees experience visual information to be either subliminal or conscious (Dehaene, 2014). Present efforts tend to use pictures flashed for varying duration, but it is possible to investigate information from other sense organs. It would be interesting to compare response using representative species of fish, amphibians, reptiles, birds, and mammals. Although it is difficult to ask these animals what they experience, it should be possible to tune the conditions (e.g.,

the duration of a visual presentation) to elicit either a limited (subliminal) activation in the brain or a global activation suggestive of consciousness. Based on the present model, the latter should only occur in the amniotes.

## References

- Alkire, M. T., Hudetz, A. G., & Tononi, G. (2008). Consciousness and anesthesia. *Science*, 322, 876–880. <http://dx.doi.org/10.1126/science.1149213>
- Anjum, F., Turmi, H., Mulder, P. G., van der Burg, J., & Brecht, M. (2006). Tactile guidance of prey capture in Etruscan shrews. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 16544–16549. <http://dx.doi.org/10.1073/pnas.0605573103>
- Archer, J. (1999). *The nature of grief: The evolution and psychology of reactions to loss*. London, United Kingdom: Routledge. <http://dx.doi.org/10.4324/9780203360651>
- Avarguès-Weber, A., & Giurfa, M. (2013). Conceptual learning by miniature brains. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131907. <http://dx.doi.org/10.1098/rspb.2013.1907>
- Baars, B. (1997). *In the theater of consciousness*. Oxford, United Kingdom: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780195102659.001.1>
- Barbano, M. F., & Cador, M. (2007). Opioids for hedonic experience and dopamine to get ready for it. *Psychopharmacology*, 191, 497–506. <http://dx.doi.org/10.1007/s00213-006-0521-1>
- Barron, A. B., & Klein, C. (2016). What insects can tell us about the origins of consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 4900–4908. <http://dx.doi.org/10.1073/pnas.1520084113>
- Baumeister, R. F., Masicampo, E. J., & Vohs, K. D. (2011). Do conscious thoughts cause behavior? *Annual Review of Psychology*, 62, 331–361. <http://dx.doi.org/10.1146/annurev.psych.093008.131126>
- Beshkar, M. (2008). The presence of consciousness in the absence of the cerebral cortex. *Synapse*, 62, 553–556. <http://dx.doi.org/10.1002/syn.20524>
- Borrelli, L., & Fiorito, G. (2008). Behavioral analysis of learning and memory in cephalopods. In R. Menzel (Ed.), *Learning theory and behavior* (pp. 605–628). New York, NY: Elsevier. <http://dx.doi.org/10.1016/B978-012370509-9.00069-3>
- Brüntrup, G., & Jaskolla, L. (2017). *Panpsychism: Contemporary perspectives*. Oxford, United Kingdom: Oxford University Press.
- Budd, G. E. (2003). The Cambrian fossil record and the origin of the phyla. *Integrative and Compar-*

- tive Biology*, 43, 157–165. <http://dx.doi.org/10.1093/icb/43.1.157>
- Bumbarger, D. J., Riebesell, M., Rödelserperger, C., & Sommer, R. J. (2013). System-wide rewiring underlies behavioral differences in predatory and bacterial-feeding nematodes. *Cell*, 152, 109–119. <http://dx.doi.org/10.1016/j.cell.2012.12.013>
- Butler, A. B. (2008). Evolution of brains, cognition, and consciousness. *Brain Research Bulletin*, 75, 442–449. <http://dx.doi.org/10.1016/j.brainresbull.2007.10.017>
- Butler, A. B. (2012). Hallmarks of consciousness. In C. López-Larrea (Ed.), *Sensing in nature* (pp. 291–309). New York, NY: Springer. [http://dx.doi.org/10.1007/978-1-4614-1704-0\\_19](http://dx.doi.org/10.1007/978-1-4614-1704-0_19)
- Butler, A. B., & Cotterill, R. M. (2006). Mammalian and avian neuroanatomy and the question of consciousness in birds. *The Biological Bulletin*, 211, 106–127. <http://dx.doi.org/10.2307/4134586>
- Cabanac, M. (2009). Do birds experience sensory pleasure? *Evolutionary Psychology*, 7, 40–47. <http://dx.doi.org/10.1177/147470490900700105>
- Cabanac, M., & Bonniot-Cabanac, M. C. (2007). Decision making: Rational or hedonic? *Behavioral and Brain Functions*, 3, 45. <http://dx.doi.org/10.1186/1744-9081-3-45>
- Cabanac, M., Cabanac, A. J., & Parent, A. (2009). The emergence of consciousness in phylogeny. *Behavioural Brain Research*, 198, 267–272. <http://dx.doi.org/10.1016/j.bbr.2008.11.028>
- Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6, 119–126. <http://dx.doi.org/10.1038/nn0203-119>
- Dehaene, S. (2014). *Consciousness and the brain: Deciphering how the brain codes our thoughts*. New York, NY: Viking.
- Denton, D. A., McKinley, M. J., Farrell, M., & Egan, G. F. (2009). The role of primordial emotions in the evolutionary origin of consciousness. *Consciousness and Cognition*, 18, 500–514. <http://dx.doi.org/10.1016/j.concog.2008.06.009>
- Edelman, D. B., & Seth, A. K. (2009). Animal consciousness: A synthetic approach. *Trends in Neurosciences*, 32, 476–484. <http://dx.doi.org/10.1016/j.tins.2009.05.008>
- Edelman, G. (2004). *Wider than the sky: The phenomenal gift of consciousness*. New Haven, CT: Yale University Press.
- Edlow, B. L., Takahashi, E., Wu, O., Benner, T., Dai, G., Bu, L., . . . Folkerth, R. D. (2012). Neuroanatomic connectivity of the human ascending arousal system critical to consciousness and its disorders. *Journal of Neuropathology and Experimental Neurology*, 71, 531–546. <http://dx.doi.org/10.1097/NEN.0b013e3182588293>
- Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, 414, 443–446. <http://dx.doi.org/10.1038/35106560>
- Feinberg, T. E., & Mallatt, J. (2013). The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago. *Frontiers in Psychology*, 4, 667. <http://dx.doi.org/10.3389/fpsyg.2013.00667>
- Feinstein, J. S., Adolphs, R., Damasio, A., & Tranel, D. (2011). The human amygdala and the induction and experience of fear. *Current Biology*, 21, 34–38. <http://dx.doi.org/10.1016/j.cub.2010.11.042>
- Fiorito, G., & Scotto, P. (1992). Observational learning in *Octopus vulgaris*. *Science*, 256, 545–547. <http://dx.doi.org/10.1126/science.256.5056.545>
- Funato, H., Miyoshi, C., Fujiyama, T., Kanda, T., Sato, M., Wang, Z., . . . Yanagisawa, M. (2016). Forward-genetics analysis of sleep in randomly mutagenized mice. *Nature*, 539, 378–383. <http://dx.doi.org/10.1038/nature20142>
- Gilbert, D. T., & Wilson, T. D. (2007). Propection: Experiencing the future. *Science*, 317, 1351–1354. <http://dx.doi.org/10.1126/science.1144161>
- Graziano, M. S., & Webb, T. W. (2015). The attention schema theory: A mechanistic account of subjective awareness. *Frontiers in Psychology*, 6, 500. <http://dx.doi.org/10.3389/fpsyg.2015.00500>
- Grinde, B. (2012). *The biology of happiness*. Dordrecht, The Netherlands: Springer. <http://dx.doi.org/10.1007/978-94-007-4393-9>
- Grinde, B. (2013). The evolutionary rationale for consciousness. *Biological Theory*, 7, 227–236. <http://dx.doi.org/10.1007/s13752-012-0061-3>
- Grinde, B. (2016). *The evolution of consciousness*. Cham, Switzerland: Springer. <http://dx.doi.org/10.1007/978-3-319-43685-2>
- Hallcrest, J. (1992). *Facial expressions: Anatomy & analysis*. New York, NY: ABBE Publications.
- Harnad, S. (2003). Can a machine be conscious? How? *Journal of Consciousness Studies*, 10, 69–75.
- Herculano-Houzel, S. (2010). Coordinated scaling of cortical and cerebellar numbers of neurons. *Frontiers in Neuroanatomy*, 4, 12.
- Hurley, D. (2011, November 1). Your backup brain. *Psychology Today*. Retrieved from <https://www.psychologytoday.com/articles/201111/your-backup-brain>
- Key, B. (2016). Why fish do not feel pain. *Animal Sentience*. Retrieved from <http://animalstudiesrepository.org/cgi/viewcontent.cgi?article=1011&context=animsent>
- Koch, C., Massimini, M., Boly, M., & Tononi, G. (2016). Neural correlates of consciousness: Progress and problems. *Nature Reviews Neuroscience*, 17, 307–321. <http://dx.doi.org/10.1038/nrn.2016.22>
- Kringelbach, M. L., & Berridge, K. C. (2009). Towards a functional neuroanatomy of pleasure and

- happiness. *Trends in Cognitive Sciences*, 13, 479–487. <http://dx.doi.org/10.1016/j.tics.2009.08.006>
- Laland, K. N., & Galef, B. G. (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.
- Lieberman, M. D., & Eisenberger, N. I. (2009). Pains and pleasures of social life. *Science*, 323, 890–891. <http://dx.doi.org/10.1126/science.1170008>
- Liljenström, H., & Århem, P. (2008). *Consciousness transitions: Phylogenetic, ontogenetic, and physiological aspects*. Amsterdam, The Netherlands: Elsevier.
- Llinas, R. R. (2001). *I of the vortex*. Boston, MA: MIT.
- Low, A. (2007). What is evolution and has it evolved? *World Futures*, 61, 199–227. <http://dx.doi.org/10.1080/026040290503423>
- Macphail, E. (1998). *The evolution of consciousness*. New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780198503248.001.0001>
- Mashour, G. A., & Alkire, M. T. (2013). Evolution of consciousness: Phylogeny, ontogeny, and emergence from general anesthesia. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 10357–10364. <http://dx.doi.org/10.1073/pnas.1301188110>
- Mather, J. A. (2008). Cephalopod consciousness: Behavioural evidence. *Consciousness and Cognition*, 17, 37–48. <http://dx.doi.org/10.1016/j.concog.2006.11.006>
- McFarland, D. J., & Sibly, R. M. (1975). The behavioural final common path. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 270, 265–293. <http://dx.doi.org/10.1098/rstb.1975.0009>
- Miller, J. W., & Ferrendelli, J. A. (1990). Characterization of GABAergic seizure regulation in the midline thalamus. *Neuropharmacology*, 29, 649–655. [http://dx.doi.org/10.1016/0028-3908\(90\)90026-N](http://dx.doi.org/10.1016/0028-3908(90)90026-N)
- Mink, J. W., Blumenschine, R. J., & Adams, D. B. (1981). Ratio of central nervous system to body metabolism in vertebrates: Its constancy and functional basis. *The American Journal of Physiology*, 241, R203–R212.
- Miskovic, V., Kuntzelman, K. & Fletcher, N. (2015). Searching for affect in affective neuroscience: Challenges and opportunities. *Psychology of Consciousness: Theory, Research, and Practice*, 2, 1–18. <http://dx.doi.org/10.1037/cns0000033>
- Moriyama, T., & Gunji, Y. P. (1997). Autonomous learning in maze solution by Octopus. *Ethology*, 103, 499–513. <http://dx.doi.org/10.1111/j.1439-0310.1997.tb00163.x>
- Moroz, L. L., Kocot, K. M., Citarella, M. R., Dosung, S., Norekian, T. P., Povolotskaya, I. S., . . . Kohn, A. B. (2014). The ctenophore genome and the evolutionary origins of neural systems. *Nature*, 510, 109–114. <http://dx.doi.org/10.1038/nature13400>
- Morsella, E., & Poehلمان, T. A. (2013). The inevitable contrast: Conscious vs. unconscious processes in action control. *Frontiers in Psychology*, 4, 590. <http://dx.doi.org/10.3389/fpsyg.2013.00590>
- Mosley, C. (2011). Pain and nociception in reptiles. *The Veterinary Clinics of North America*, 14, 45–60.
- Palmiter, R. D. (2011). Dopamine signaling as a neural correlate of consciousness. *Neuroscience*, 198, 213–220. <http://dx.doi.org/10.1016/j.neuroscience.2011.06.089>
- Panksepp, J. (1998). *Affective neuroscience*. New York, NY: Oxford University Press.
- Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition*, 14, 30–80. <http://dx.doi.org/10.1016/j.concog.2004.10.004>
- Panksepp, J., Normansell, L., Cox, J. F., & Siviy, S. M. (1994). Effects of neonatal decortication on the social play of juvenile rats. *Physiology & Behavior*, 56, 429–443. [http://dx.doi.org/10.1016/0031-9384\(94\)90285-2](http://dx.doi.org/10.1016/0031-9384(94)90285-2)
- Pauls, D. L., Abramovitch, A., Rauch, S. L., & Geller, D. A. (2014). Obsessive–compulsive disorder: An integrative genetic and neurobiological perspective. *Nature Reviews Neuroscience*, 15, 410–424. <http://dx.doi.org/10.1038/nrn3746>
- Peddarreddygari, L. R., Oberoi, K., & Grewal, R. P. (2014). Congenital insensitivity to pain: A case report and review of the literature. *Case Reports in Neurological Medicine*, 2014, 141953. <http://dx.doi.org/10.1155/2014/141953>
- Perry, C. J., Baciadonna, L., & Chittka, L. (2016). Unexpected rewards induce dopamine-dependent positive emotion-like state changes in bumblebees. *Science*, 353, 1529–1531. <http://dx.doi.org/10.1126/science.aaf4454>
- Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biology*, 6, e202. <http://dx.doi.org/10.1371/journal.pbio.0060202>
- Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J. R., Walenz, B., . . . Pääbo, S. (2012). The bonobo genome compared with the chimpanzee and human genomes. *Nature*, 486, 527–531. <http://dx.doi.org/10.1038/nature11128>
- Rattenborg, N. C. (2006). Evolution of slow-wave sleep and palliopallial connectivity in mammals and birds: A hypothesis. *Brain Research Bulletin*, 69, 20–29. <http://dx.doi.org/10.1016/j.brainresbull.2005.11.002>
- Reichard, U. H., & Boesche, C. (2003). *Monogamy: Mating strategies and partnerships in birds, humans and other mammals*. Cambridge, United

- Kingdom: Cambridge University Press. <http://dx.doi.org/10.1017/CBO9781139087247>
- Riters, L. V. (2011). Pleasure seeking and birdsong. *Neuroscience and Biobehavioral Reviews*, *35*, 1837–1845. <http://dx.doi.org/10.1016/j.neubiorev.2010.12.017>
- Robinson, S., Sandstrom, S. M., Denenberg, V. H., & Palmiter, R. D. (2005). Distinguishing whether dopamine regulates liking, wanting, and/or learning about rewards. *Behavioral Neuroscience*, *119*, 5–15. <http://dx.doi.org/10.1037/0735-7044.119.1.5>
- Rosenthal, D. M. (2008). Consciousness and its function. *Neuropsychologia*, *46*, 829–840. <http://dx.doi.org/10.1016/j.neuropsychologia.2007.11.012>
- Saalmann, Y. B. (2014). Intralaminar and medial thalamic influence on cortical synchrony, information transmission and cognition. *Frontiers in Systems Neuroscience*, *8*, 83. <http://dx.doi.org/10.3389/fnsys.2014.00083>
- Sakai, T., Matsui, M., Mikami, A., Malkova, L., Hamada, Y., Tomonaga, M., . . . Matsuzawa, T. (2012). Developmental patterns of chimpanzee cerebral tissues provide important clues for understanding the remarkable enlargement of the human brain. *Proceedings. Biological Sciences*, *280*, 20122398. <http://dx.doi.org/10.1098/rspb.2012.2398>
- Schiff, N. D. (2009). Central thalamic deep-brain stimulation in the severely injured brain: Rationale and proposed mechanisms of action. *Annals of the New York Academy of Sciences*, *1157*, 101–116. <http://dx.doi.org/10.1111/j.1749-6632.2008.04123.x>
- Schiff, N. D., & Fins, J. J. (2007). Deep brain stimulation and cognition: Moving from animal to patient. *Current Opinion in Neurology*, *20*, 638–642. <http://dx.doi.org/10.1097/WCO.0b013e3282f1c6e4>
- Segerdahl, P., Fields, W., & Savage-Rumbaugh, E. S. (2005). *Kanzi's primal language: The cultural initiation of primates into language*. Basingstoke, United Kingdom: Palgrave Macmillan. <http://dx.doi.org/10.1057/9780230513389>
- Seligman, M. E. P., Railton, P., Baumeister, R. F., & Sripada, C. (2016). *Homo prospectus*. Oxford, United Kingdom: Oxford University Press.
- Seth, A. K., Baars, B. J., & Edelman, D. B. (2005). Criteria for consciousness in humans and other mammals. *Consciousness and Cognition*, *14*, 119–139. <http://dx.doi.org/10.1016/j.concog.2004.08.006>
- Shein-Idelson, M., Ondracek, J. M., Liaw, H. P., Reiter, S., & Laurent, G. (2016). Slow waves, sharp waves, ripples, and REM in sleeping dragons. *Science*, *352*, 590–595. <http://dx.doi.org/10.1126/science.aaf3621>
- Silva, B. A., Gross, C. T., & Gräff, J. (2016). The neural circuits of innate fear: Detection, integration, action, and memorization. *Learning & Memory*, *23*, 544–555. <http://dx.doi.org/10.1101/lm.042812.116>
- Smith, E. S. J., & Lewin, G. R. (2009). Nociceptors: A phylogenetic view. *Journal of Comparative Physiology*, *195*, 1089–1106. <http://dx.doi.org/10.1007/s00359-009-0482-z>
- Steriade, M. (1996). Arousal: Revisiting the reticular activating system. *Science*, *272*, 225–226. <http://dx.doi.org/10.1126/science.272.5259.225>
- Takahashi, H., Kato, M., Matsuura, M., Mobbs, D., Suhara, T., & Okubo, Y. (2009). When your gain is my pain and your pain is my gain: Neural correlates of envy and schadenfreude. *Science*, *323*, 937–939. <http://dx.doi.org/10.1126/science.1165604>
- Vermeij, G. J. (2017). How the land became the locus of major evolutionary innovations. *Current Biology*, *27*, 3178–3182. <http://dx.doi.org/10.1016/j.cub.2017.08.076>
- Warren, W. C., Hillier, L. W., Marshall Graves, J. A., Birney, E., Ponting, C. P., Grützner, F., . . . Wilson, R. K. (2008). Genome analysis of the platypus reveals unique signatures of evolution. *Nature*, *453*, 175–183. <http://dx.doi.org/10.1038/nature06936>
- Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *366*, 997–1007. <http://dx.doi.org/10.1098/rstb.2010.0334>
- Windt, J. M., Nielsen, T., & Thompson, E. (2016). Does consciousness disappear in dreamless sleep? *Trends in Cognitive Sciences*, *20*, 871–882. <http://dx.doi.org/10.1016/j.tics.2016.09.006>
- Young, J. Z. (1963). The number and sizes of nerve cells in Octopus. *Journal of Zoology*, *140*, 229–254.
- Zhang, Y., Lu, H., & Bargmann, C. I. (2005). Pathogenic bacteria induce aversive olfactory learning in *Caenorhabditis elegans*. *Nature*, *438*, 179–184. <http://dx.doi.org/10.1038/nature04216>

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