[Commentary] Consciousness Makes Sense in the Light of Evolution

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Funding: No specific funding was received for this work.
Potential competing interests: No potential competing interests to declare.

Abstract

I believe consciousness is a property of advanced nervous systems, and as such a product of evolution. Thus, to understand consciousness we need to describe the trajectory leading to its evolution and the selective advantages conferred. A deeper understanding of the neurology would be a significant contribution, but other advanced functions, such as hearing and vision, are explained with a comparable lack of detailed knowledge as to the brain processes responsible. In this paper, I try to add details and credence to a previously suggested, evolution-based model of consciousness. According to this model, the feature started to evolve in early amniotes (reptiles, birds, and mammals) some 320 million years ago. The reason was the introduction of feelings as a strategy for making behavioral decisions.

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Keywords: Consciousness, Evolution, Amniotes, Feelings, Neurology, Nonconscious processing, Cognition.

1. Introduction

Consciousness is arguably the most important feature of any brain. The genes may be better off in an animal with a nonconscious brain, but for a human, it means everything. It is responsible for what we experience and thus our lives. A deeper understanding is important to make the most of this feature.

Our attempts to comprehend are confounded by the fact that consciousness is the tool we use for the purpose. It is difficult to avoid being affected by personal experiences and ideas. The problem is particularly relevant when considering consciousness in other species or in individuals with restricted capacity to communicate such as babies. The quest to understand is also confused by the diversity of scientific, and non-scientific, approaches that have been published. A literature search from 2007 to 2017 found 29 different theories [1]. Even the more widely cited approaches create a bewildering picture [2][3]. As a feature of biology, consciousness must conform to the principles of evolution. I therefore believe the effort to understand should heed Dobzhansky's advice: "Nothing in biology makes sense except in the light of evolution" [4]. Evolution offers a framework that helps us place the pieces of the puzzle in the right spot.

The first nervous systems started to evolve some 650 Mya (million years ago)[5]. The human brain is the result of the addition (and subsequent modification) of a long list of neurological features or functions since that time. The various functions can be referred to as modules and are somewhat akin to apps in a smartphone [6]. They all have an evolutionary history fueled by adaptation-based selection of the fittest. Consciousness can be regarded as one such module. The nonconscious brain turns it on when deemed useful, typically in the morning, and off again when no longer required. If we can describe its evolutionary history, including the selective advantage, we have a reasonable explanation for what it is. One should keep in mind that the primary role of all these modules is to help the animal make behavioral decisions that serve to enhance survival and procreation [7].

Attempts to describe the evolution of human traits are often troubled by terminology. The terms we use typically refer to the human version; the homologous versions in other species are necessarily different, implying that whether the trait is present in these species, depends on how broadly the term is defined. For example, answering the question of whether dogs have a nose, some will say "yes", others "no, it has a snout". The problem of finding a proper definition is particularly difficult in the case of non-visible traits. Consequently, a strict definition of consciousness (or noses) may be unwarranted; each species has a version suitable for the requirements of that species [8]. Evolution does not design to please the human desire to categorize.

Consciousness can be loosely described as the capacity to experience aspects of life, such as sensory information and feelings, and to base behavioral decisions on an evaluation of these experiences. I use the term *awareness* as roughly equivalent to consciousness and the term *cognition* for conscious deliberation on an issue. *Sentience* implies a basic form of consciousness that includes feelings and sensory perception.

Feelings presumably played a key role in the evolution of consciousness[7]. They help the individual to make decisions by acting as a 'common currency' for weighing various options [9], and they serve as motivators needed to execute the decision. It is theoretically possible for conscious processing to evolve in the absence of feelings, but an evolutionary advantage, such as weighing alternatives and translating decisions into actions, is required. As will be discussed below, it is difficult to envisage why evolution would instigate a capacity to experience unless there is an element that cannot be catered to without that capacity – such as feelings.

I have previously outlined a model for the evolution of consciousness[6][7][10]. In this model, the feature started to evolve in early amniotes. Amniotes split into one group forming reptiles and birds and another group leading to mammals some 320 Mya [11]. In the present text, I expand on this model. I do so by addressing five questions: 1) Why did consciousness evolve? 2) What are the disadvantages? 3) What can we learn from neurology? 4) Is convergent evolution of consciousness likely? 5) What happened in the amniote lineage? The questions are followed by a discussion of alternative models as to the evolution of consciousness.

2. Why did consciousness evolve?

If we can tell which species are conscious, we have a good starting point for outlining the evolution of the trait. The attempts to assess consciousness in animals are often based on behavioral observations [12]. I shall argue that this is a troublesome approach as the interpretation of observations is easily bewildered by introspection, which may lead to a tendency to misjudge. For example, the social and empathetic nature of humans may lead to a tendency to assume consciousness in organisms that may not possess it. This includes both distant species but also fetal and newborn humans. Although most forms of behavior typically engage consciousness in humans, they do not necessarily require awareness.

Nervous systems are involved in three types of tasks: 1) recording sensory information, 2) using the information to make decisions, and 3) translating the decisions into action. The second task is the core part, it includes functions such as learning, memory, selective attention, and the deciphering of a variety of sensory information. These functions are available even to very simple animals such as nematodes [5][13][14]. The nervous system of the most studied nematode, *Caenorhabditis elegans*, contains 302 neurons and is characterized in detail [15]; there is no sign of conscious processing, neither is there any reason why nematodes should be aware.

It is difficult to identify conscious processing in other species, while somewhat easier to probe for nonconscious processing in humans. The point being that many functions associated with consciousness can be catered to without. We can, for example, perform reasonably advanced forms of behavior while asleep in the form of ‘sleepwalking’. Experiments with subliminal (nonconscious) processing demonstrate that we can respond appropriately to complex sensory information that we are not aware of. For example, we are able to both identify a face and to interpret and react to nuances of expression subliminally [16]. The brain recognizes several facial characteristics – including familiarity, gender, race, emotion, threats, trustworthiness, and direction of gaze – unconsciously [17][18]. The power of nonconscious processing is substantiated by experiments with blindsight and with people troubled by diseases such as amnesia, aphasia, and agnosia [19]. Reactions such as the startle response when seeing something resembling a snake, or pulling the hand away from a hot stove, are based on nonconscious reflexes, implying that the nonconscious brain both deciphers the sensory information and launches a response before sending information to the conscious. Similarly, the nonconscious brain wakes you up to loud sounds suggesting danger but also when someone whispers your name. In short, the main part of sensory deciphering appears to be undertaken nonconsciously, information is sent to you on a ‘need to know basis’.

When we want to perform highly advanced tasks, whether physical such as hitting a golf ball, or mental as in elite chess, we train the brain to perform a major part of the processing unconsciously. The golf player knows that the strike is best without direct intervention [20], and the chess player relies on intuition. Generating awareness is a demanding activity that can be detrimental to the task at hand. As pointed out by others [21], the nonconscious brain can do (and does do) most tasks. You just tend not to give it credit, because it is not *you*.

We feel we are in charge even when the nonconscious takes care of the bulk of the task. We consequently look for advanced performance when considering whether other species are conscious. For example, cephalopods have highly sophisticated behavior [22], but does it require consciousness? I believe it is no more sophisticated than what our nonconscious brains handle.

So why did consciousness evolve?

Nonconscious neuronal processing is perhaps as versatile as a computer when it comes to solving problems. If so, tasks we can program, evolution can add to a brain. Computers can easily match some of our most demanding cognitive tasks, such as playing chess. There is, however, one thing we cannot program: true feelings. Computers can be designed to simulate feelings but to actually *feel* something requires a form of awareness. The introduction of feelings could therefore be the factor that initiated the evolution of consciousness [7]. The evolutionary advantage of feelings presumably is that they introduce a ‘common currency’, in the form of affective value (good or bad) for weighing behavioral options [9]. In short, they offer a versatile strategy for making fine-tuned decisions.

Our capacity for advanced cognition, as exemplified by our scientific advances, does require consciousness. I expect that other mammals, particularly apes, also have a reasonable level of cognitive capacity. This is likely a late elaboration, not what caused evolution to install consciousness in the first place. Even in humans, cognition did not offer much of an advantage until the evolution of language led to sophisticated, cumulative culture. Awareness was more likely initiated by the less glamorous, and perhaps minor, advantage of using feelings to find a superior response in certain types of situations.

Once initiated, evolution probably made more and more information available for conscious processing, particularly in the form of sensory input. The strategy should allow for better decisions in difficult situations, situations that are likely to occur when living in a complex and variable environment – as is the case for land-based vertebrates such as amniotes. Still, even in humans, most sensory input and most of the brain processing are probably not transmitted to consciousness.

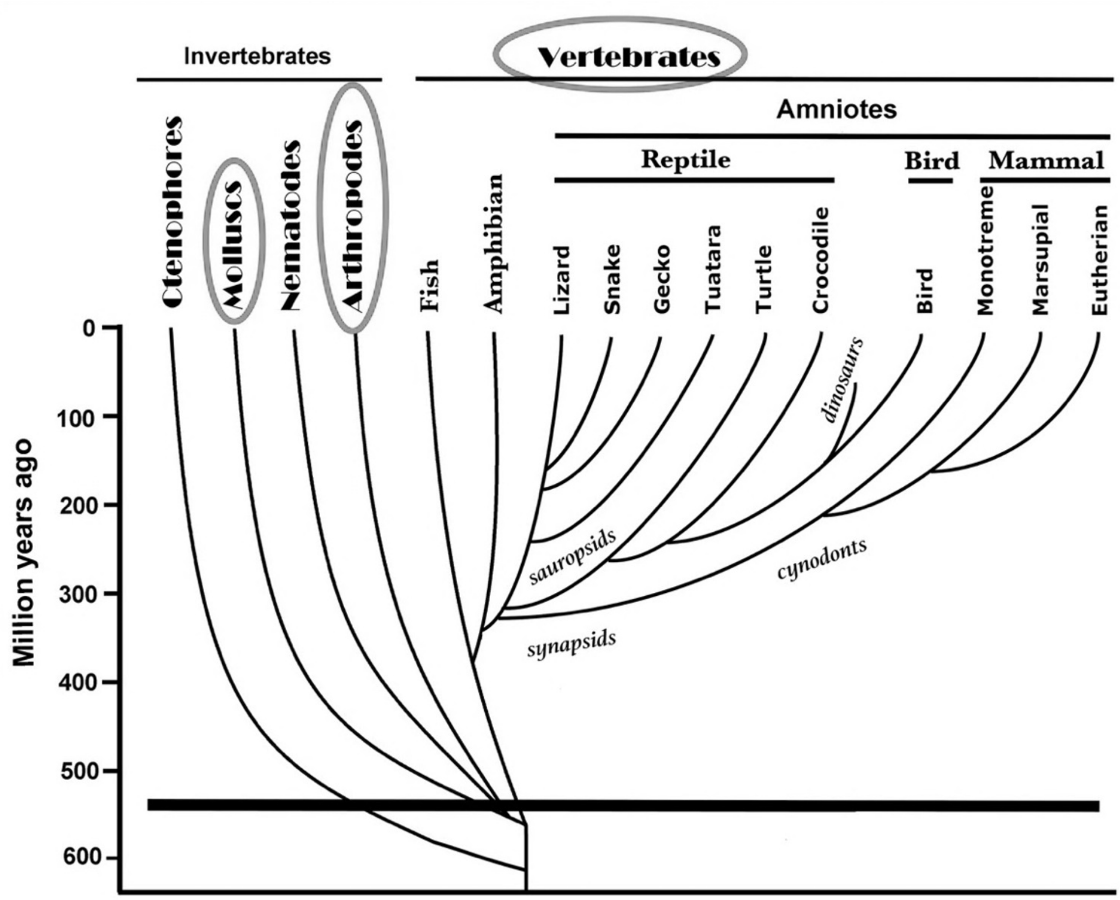

Fig. 1. Phylogenetic tree for animals discussed in the text. The overall shape of the tree is reasonably accepted, the time suggested for branching points is more controversial. The grey circles indicate the three phyla with the most advanced nervous systems. The thick, horizontal line represents the 'Cambrian explosion', a key period of animal evolutionary diversification.

3. What are the disadvantages?

In Section 2, I concluded that consciousness offers increased flexibility and versatility of behavior in complex situations. I also concluded that only a minor part of brain processes involves consciousness. Leaving so much to the nonconscious suggests that there are drawbacks.

We may think of consciousness as a brilliant invention. True, for a human being it is all that matters in life, but the biological track record for animals with a presumed advanced form is not that fantastic.

Success in biology is typically measured as the biomass of a species and the biomass or variety of life forms of a phylogenetic group. Advanced nervous systems seem to be an advantage, as the three phyla with the most complex neurology are the most successful: arthropods (*Arthropoda*), mollusks (*Mollusca*), and vertebrates (*Chordata*) (Fig. 1). However, of these three, arthropods are the definite winner, both as a phylogenetic group and by harboring the presumed most successful species, the Antarctic krill. The biomass of the krill is estimated to be twice that of humans [23]. It seems unlikely that (all) arthropods are equipped with consciousness, while our branch of the phylogenetic tree, the great apes

(*Hominidae*), are expected to have the most sophisticated form. The history of this branch suggests that advanced consciousness is not a particularly brilliant strategy. In our lineage alone, the hominins, more than 30 species or subspecies have been proposed over the last five million years [24], and all but one are extinct. The other great apes are threatened by extinction. Even the one species with recent success, *Homo sapiens*, was probably close to vanishing at one point [25]. I shall discuss four types of disadvantages that may help explain the poor track record.

1. *Response time*

The response is slow. A reflex can be executed in 20 ms, while the creation of conscious experiences, the 'broadcasting' of information, takes 300 ms or more [26]. Broadcasting is necessary to consider alternatives, but the actual decision typically takes a lot longer.

The broadcasting can be referred to as setting up a 'film of life'. The brain filters and interprets the incoming information to serve a plausible film. For example, light travels a lot faster than sound, so the sound accompanying an event will reach the brain after the visual component. If the difference is less than 100 ms, the brain adjusts the film to give a synchronous experience. Multisensory integration relies on a highly advanced form of nonconscious processing that may last for 400 ms or more [27].

The response time is often not an issue, but in certain situations, even 300 ms is too long. Consequently, sensory signals are screened nonconsciously, and those that suggest danger are acted upon before making you aware. Avoiding harmful situations is a basic function of all nervous systems. In humans, it is associated with pain and fear; but these feelings may appear after the initial response, as in the case of withdrawing the hand from a hot stove. Similarly, as pointed out in Section 2, facial expressions can be recognized subliminally, but if considered important, the nonconscious will direct attention to the face for the conscious brain to initiate further assessment [28].

Selective attention has been proposed to be an important element of consciousness[29], but the direction of attention is also decided on by the nonconscious, as exemplified by the stove and the face. On the other hand, you can direct attention in advance when expecting a stimulus – as when being particularly alert in times of danger. In this way, you can initiate a reaction that is faster than the time needed for a consciously controlled response. A sprinter can leave the start block 100 ms after the shot, presumably without being aware of the start until a bit later. It is also possible to 'post-direct' attention; that is, to access stimuli (e.g., spoken words or visual content) that were originally subliminally processed [30].

2. *Energy use*

Broadcasting presumably requires the activation of vast neurological circuits in what is referred to as the global neuronal workspace (which includes the cortex, thalamus, and basal ganglia) [26]. Neuronal signaling is assumed to be the most costly process of the brain, primarily due to the need to maintain the membrane potential [31]. Both the time required, and the size of the circuits involved suggest that broadcasting is energy intensive. The human brain consumes some 20% of the oxygen while comprising only 2% of the body mass, consciousness contributes to that cost. Moreover, the neuronal circuitry required for consciousness implies an additional expense in terms of construction and maintenance.

Somewhat surprisingly, whether the brain is currently engaged in conscious processing does not make that much difference to the overall energy use. It is about the same whether you are awake or in REM (rapid eye movement) sleep, a state somewhat equivalent to consciousness, and only down to ~80% during deep sleep [32]. The use of energy can drop to 60-70% in anesthesia [33], suggesting that even in deep sleep, the brain is more active than what is required to sustain life. The observation may reflect that neurons need to be continuously active; prolonged absence of activity tends to cause degeneration [34][35]. Exactly what the neurons are up to, may not matter that much. There is a parallel in building a home. If you choose a large house, the construction and maintenance are costly, but the expenses depend less on what you do there. We pay a price for having a brain capable of advanced conscious processing. The observation that there appears to be a recent evolutionary trend in the direction of a smaller brain [36] may be related to that expense.

As expected, conscious attention, for instance when focusing on visual information, does burn more energy in the brain region involved, but the extra energy is primarily obtained by reducing activity elsewhere [31]. Thus, the overall consumption is relatively stable throughout the day. Yet, we tend to feel exhausted after prolonged focus. Perhaps the circuits involved need a break to recuperate.

3. *Capacity, accuracy, and fluency*

The most basic form of awareness is probably not that demanding, the difficult and costly part is creating a 'high resolution' film of life and at the same time using the information for cognition. The latter requires access to ample working memory, a feature that expanded in the human lineage after we split with the chimpanzees [37]. Working memory – along with accompanying functions such as attention, task initiation, and metacognition – is primarily associated with the prefrontal cortex [38]. As expected, this part of the brain is substantially enlarged in humans.

The situation is somewhat equivalent to the limits imposed by the size of RAM (random access memory) in a computer. Humans probably have the brain with the highest capacity to handle conscious information, yet the capacity of nonconscious processing appears to be far superior, presumably because it is easier and 'cheaper' to operate. The limit of capacity determines when and for what consciousness can, or should, be employed. For example, the conscious brain is unable to execute its decisions, muscle coordination is handled by the nonconscious.

The neurological resources required for consciousness may limit other brain functions such as long-term memory. In humans, the problem can be compensated for by the size of the brain, while it may constitute a restraint in smaller-brained mammals.

Based on the size of dedicated brain resources, muscle coordination may be the most demanding assignment for the brain. The task is primarily associated with the cerebellum, which contains 80 % of the neurons in a human brain, but also engages a large part of the cortex. Speech requires a fine-tuned orchestration of some 200 muscle movements every second [39]. You may find it easy to talk, but that is because the nonconscious takes care of the job, all you do is decide on what to say.

The limit of capacity also implies that conscious perception is less accurate. For one, there needs to be a filtering of what sensory information is to be broadcasted; and two, the human film of life is reported to have only 30-60 (visual) 'frames' per second [40]. The broadcasting also includes an interpretation that easily leads to an incorrect or skewed presentation. One example is the optical illusion where two identical objects are made to appear different in size (Fig. 2). Your perception is duped, but the nonconsciously controlled fingers open to the right size when asked to grip either object [41].

Splitting behavioral management between conscious decisions and nonconscious execution implies another likely disadvantage, as reflected in the previous comment on playing golf. If you try to intervene while performing the swing, the ball most likely heads in a wrong direction. In nonconscious animals, the whole process is presumably cared for by a unified system, suggesting not only less delay but more fluency and accuracy of action. Even in other mammals, where the balance of conscious and nonconscious processing probably leans more to the latter, fluency of movement may be better. You rarely see a mountain goat stumble, while the average golf player often fails.

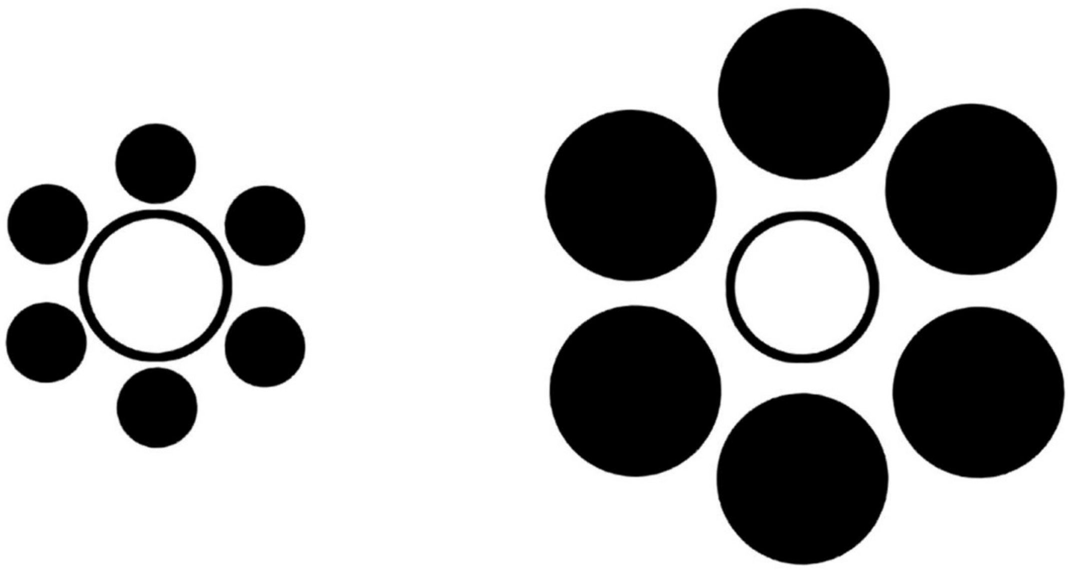

Fig. 2. The conscious brain is easily fooled. People tend to assume that the left white chip is larger than the right. However, the nonconscious brain gets it right, when asked to pick up either chip, the fingers open to the correct size [41].

4. *Multitasking*

A related issue is that conscious processing can only deal with one thing at a time (but can shift rapidly back and forth between tasks) [42]. The brain needs to take care of multiple assignments simultaneously, for example regulating heartbeat and bowel movements. *You* are simply unable to perform the required level of multitasking.

When evolution expanded the capacity for conscious processing (the RAM of the brain), there probably was a concomitant reduction in the capacity for nonconscious processing. There are limits both to the size of the brain and to how much energy should be directed there. Other species of mammals have been more successful than the great apes, perhaps because their form of consciousness is less demanding. In short, the idea that consciousness was the greatest innovation evolution ever made, is dubious – at least if one does not count the human progress in science and technology.

The disadvantages should be kept in mind when considering the evolution of consciousness. That said, one should also keep in mind the advantages such as more accurate and weighted decisions. The point is that I believe we tend to overemphasize the advantages.

4. What can we learn from neurology?

Calmers [43] claims that even if the neurological correlate of consciousness was known, the 'hard problem', how neuronal activity can give rise to subjective experience, would remain. I take a more optimistic stance. My optimism is fueled by the realization that the feature necessarily is a product of nerve circuitry, and by the observation that we have not progressed much further in our attempts to understand other complex processes. For example, we know roughly how minor differences in air pressure hitting the ear are translated to neurological signals but do not know how these signals are deciphered into words. (As pointed out in Section 2, this does not require consciousness.) The brain remains the one corner of the universe we understand the least, but it is not at all obvious that broadcasting information is either the most complex task it performs or the most difficult task to elucidate.

In the case of hearing, we have a reasonable outline of where the processing takes place[44], and some ideas about how [45], but we have roughly equivalent knowledge of conscious processing. We know that there are several ways to activate or turn off consciousness [38]. The 'switch' that typically turns it on in the morning is in the ascending reticular system of the brain stem [46]. The broadcasting most likely requires the triggering of thalamocortical circuits, or loops, in what has been referred to as the global neuronal workspace [26] or global playground [47] and entails simultaneous, itinerant (back and forth) signaling in a vast number of neurons [48]. The hub for this activity is likely in the posterior-central cortical region [38]. There is a basal, oscillating firing in these loops, observed as slow waves in an EEG, but conscious processing presumably implies an additional, more complex activity that can be observed as less ordered, high-frequency patterns in EEG [49]. Broadcasting of distinct sensory stimuli correlates with a change in activity starting some 300 ms after the stimulus [47].

Imagine an alien from Mars picking up a computer. He would, of course, like to know how the machine performs wonders like showing films and solving puzzles. Characterizing the components inside is easy, so he will soon realize that the device is driven by electrical currents in a vast network of connections. But if he knows nothing about programming, will he progress any further? Perhaps he will conclude that the wonders are beyond Martian comprehension. Or he does not give up, because he realizes that the answer must be in there, and one day he learns that it is all down to a 'peculiar form of encoding'.

I can understand that there appears to be a fundamental difference between the creation of a conscious experience and the interpretation of sounds. The latter has a physical substrate. However, I am uncertain as to whether the difference is that fundamental. Both are outcomes of neurologic activity and in neither case do we know much about the 'peculiar encoding' responsible. I believe that in the absence of contrary evidence, the various advanced functions of nervous systems should be assumed to rely on related forms of neurological activity.

The switch in the brain stem probably predates consciousness. Most if not all animals have diurnal rhythms in activity – the less active phase is typically referred to as sleep. The ancient role of the switch was likely to change from inactive to active phase. The active state is easily confused with consciousness; thus the presence of neurology in fish closely related to the mammalian wake-up switch [50] does not imply that fish are conscious. We wake up to awareness, but other animals may simply 'wake up' to a more energetic state.

When looking for signs of consciousness in distantly related species, it is important to remember that all nervous systems, except for comb jellies (*Ctenophora*) [51], are based on related genes, neurons with similar properties, and a shared collection of neurotransmitters [52]. Moreover, animals have similar requirements as to what functions their nervous systems need to provide, such as finding food and avoiding danger. Related behavior may therefore depend on comparable neurology simply because the function dates to a shared ancestor. For example, the similarities of fear response in crayfish and humans have been taken as a sign of consciousness in the arthropod [53]. In both cases, the reaction uses the neurotransmitters GABA and serotonin and can be inhibited by anxiolytic drugs. Harm avoidance was likely one of the first neurological assignments, but while the human reaction is broadcasted to the conscious, there is no need to postulate the same in the case of the crayfish. As pointed out in Section 2, even in humans the initial reaction can be nonconscious.

Three signatures of consciousness are likely to be present regardless of phylogenetic distance. One is the difference between subliminal processing and broadcasting. In mammals, the latter is characterized by the ignition of divergent brain activity in the thalamocortical loops and has been referred to as a delayed event-related potential [26][47]. The exact signature may look different in distant species, but a delayed, aberrant form of activity would be expected. Consciousness requires a procedure for broadcasting, and this is likely both time-consuming and different from other tasks performed by the brain. The delayed response has been used to assess consciousness in birds [54] and babies [55].

The second signature is large-scale, simultaneous, itinerant activity. This is assumed to signify consciousness in other mammals [56] and can be observed in the pallium/thalamus of birds[54]. Although the anatomical structures are completely different in invertebrates, a related form of itinerant activity might be expected. The third signature is related to the second, regardless of whether the signaling is long-distance and itinerant, one would at least expect it to have a complexity that stands out above other tasks [49]. The complexity should be present in both neuronal architecture and neuronal firing patterns. In mammals, and possibly distant species, it can be probed by measuring the response to perturbations such as transcranial magnetic stimulation.

To my knowledge, there are no obvious signs of these neurological signatures outside amniotes. Admittedly, it is difficult. Besides the technical problems of probing distantly related animals, the signatures would likely look different. Even in humans, the nature of the event-related potential depends on several factors such as the type of sensory signal, the part of the brain probed, and the age of the subject [57].

In section 3, I suggested that muscle coordination, not consciousness, is the most demanding assignment for the brain.

The firing pattern of the cerebellum is different. Instead of itinerant activity, it is dominated by feedforward signaling [58]. The observation strengthens the idea that itinerant activity can be taken as a signature of consciousness.

Both the cerebrum (including the neocortex) and the cerebellum expanded considerably in amniotes, and particularly in the human lineage [59]. The expansion over the last 2-3 million years in the hominins presumably signifies a selection for improved cognitive and motor skills, respectively. The advantage of cognition seems more obvious than the need for improved control of muscles. The fine-tuned use of muscles when talking or handling tools may offer an explanation. Language (as a mediator of social life and cumulative culture) and tools were likely the main evolutionary 'innovations' that led to what humans are today.

Dreaming has been considered an indication of consciousness[60]. If the animal dreams, it should be able to experience life when awake – the problem lies in deciding whether an animal has true dreams.

In mammals, vivid dreaming is associated with REM sleep. In that state, the pattern of EEG resembles the pattern when awake. REM-like neurological signatures are observed in sleeping birds [61] and somewhat less pronounced in reptiles [62]. I consider adult REM sleep to suggest a capacity for consciousness, although REM does not necessarily imply either dreaming or consciousness. During their first years of life, children seem unable to truly dream but display REM sleep [63]. In the months before birth, the fetal brain spends more time in a REM-like state than at any other point in life, yet neither the fetus nor the newborn may have the capacity for consciousness. The event-related potential assumed to signify awareness starts to appear after birth during the first year of life [55].

A lack of consciousness in non-amniotes is unlikely to be due to the size or complexity of their nervous systems. Given that all mammals are conscious, the 60 mg brain of the dwarf shrew [64] is sufficient. Laboratory mice, with clear signs of conscious processing, have a brain of roughly 500 mg, much smaller than the brain of a typical octopus. The shrew probably has a minimal form of consciousness, while the octopuses have a range of advanced functions that shrews and mice can only dream of.

A brain as large as ours (1.3-1.4 kg) is not required but most likely allows for a richer film of life and more advanced cognition. The point is illustrated by a man with only a very thin cortical mantle [65]. He appears to have a normal capacity for awareness although his IQ is reduced. Even hydroencephalic children without any sign of a cortex [66] and mammals where the cortex is removed soon after birth [67] seem to be conscious.

The various strategies for making decisions can be referred to as algorithms. Reflexes is the simplest form, while evaluations based on feelings or cognition are highly complex. A reflex caters to the complete process from sensation to execution, but as evolution went from simple to complex algorithms, the process likely separated into stages catered for my different circuits. That is, the afferent signals from sensory organs are first processed and brought to circuits that look for and evaluate options as to a behavioral response, that output is sent to circuits promoting the execution, and the execution is then coordinated by circuits directly coupled to efferent neurons. I postulate that circuits 'promoting execution' evolved into what can be referred to as (nonconscious) 'motivators'. These motivators eventually evolved into feelings.

In psychological studies of humans, motivators are closely associated with feelings (or emotions). The two concepts seem to overlap and use shared neurology [68]. Feelings presumably require a capacity to feel, yet they can be acted upon without being aware of having a particular feeling [69]. That is, both sensory and affective functions can rely on either conscious or subliminal processing. Consequently, I expect a continuum from nonconscious motivators to the feelings we are aware of. The concept of a 'mood set point' [70] suggests we are always somewhere on a scale from positive to negative feelings, whether we recognize the activity of the mood-generating modules or not.

The subcortical periaqueductal grey region of the midbrain seems vital for the generation of feelings[71][72]. Its position close to the brain stem suggests an ancient role, a notion that fits with the region being associated with core functions like harm avoidance (often referred to as pain or fear) and procreation. The neurological conversion of motivators to feelings may have started here. An interesting observation is that if the region is destroyed, it leads to a vegetative state [72]. The observation supports the idea that the region, and our affective system, served a key role in the evolution of consciousness.

5. Is convergent evolution likely?

Mammalian consciousness seems reasonably substantiated [73], there are strong arguments for including birds[54], and relevant but less distinct evidence for reptiles [74]. The present model of the evolution of consciousness therefore assumes it started in the early amniotes [7].

The less advanced form in reptiles could either reflect an early, primitive form of consciousness or be due to degeneration. The degeneration option seems less likely for two reasons. First, based on the phylogeny (Fig. 1), it requires degeneration in more than one reptilian lineage (crocodiles share a branch with birds). Second, the mammalian cortex and the pallium of birds, which are both assumed to be responsible for advanced conscious processing, stem from different parts of the forebrain and have different architectures [54][75]. This means we need to assume convergent evolution in birds and mammals.

The two other phyla with advanced nervous systems, arthropods and mollusks, split with our lineage more than 520 Mya [76]. At that time nervous systems were presumably still relatively simple and incapable of advanced functions such as consciousness. Thus, any form of awareness in for example bees and octopuses would imply convergent evolution. However, in the case of amniotes, both birds and mammals had a 'template' in the brain that could be expanded, while the presence of a similar template seems less likely in the shared ancestors of *Bilateria*. The *Bilateria* includes both protostomes (such as nematodes, annelids, arthropods, and mollusks) and deuterostomes (such as echinoderms and chordates). The point is further discussed in Section 7.

The classic examples of convergent evolution, such as wings and eyes, reflect functions with an obvious survival value and an equally obvious need for similarities in design. Based on my remarks in Section 3, consciousness is unlikely to offer a comparable advantage. Even in the case of humans with highly advanced consciousness, the bulk of sensory processing and behavioral control seem best catered to by the nonconscious. Thus, for evolution to initiate broadcasting there should be a specific reason. In the amniotes, the reason was presumably feelings, but feelings stand out as a peculiar quirk of evolution. There may be other features that require awareness, but it is difficult to envisage what that should be. Conversely, I can easily imagine nonconscious algorithms for advanced behavior that are faster, cheaper to operate, and can utilize more information than our conscious processing. In short, I favor the idea that consciousness only evolved once but expanded in different directions.

6. What happened in the amniote lineage?

One line of argument, as to the hypothesis that the evolution of consciousness started with amniotes, concerns the ecological setting. The adaptation to land-based living seems a reasonable incentive for novel behavioral strategies. The environment became more variable, for example, regarding temperature and availability of water, with a need to adapt to ever-changing challenges. The relatively large size and long generation time of amniotes, as compared to arthropods, suggest that adaptation based on evolution would be slow. The alternative was evolving a brain with a more flexible algorithm for behavior. Furthermore, the setting, a novel habitat with many options, suggests evolutionary radiation [77]. These animals already had a reasonably large and advanced nervous system, again compared to arthropods, which could be elaborated in the direction of consciousness.

Another argument is that brain expansion can only be undertaken in species with ample access to food and oxygen – due to the energetic requirements. Lungs offer a better supply of oxygen compared to gills.

The increase in brain size did not start immediately upon vertebrate colonization of land. Amphibians have a relatively low encephalization quotient (brain size divided by body size) [78], and the same seems to be the case for the first members of both sauropsids and synapsids, the two branches of amniotes that gave rise to reptiles/birds and mammals, respectively (Fig. 1) [78][79]. A possible scenario is that feelings (and eventually sentience) started to evolve before the split between sauropsides and synapsids, but it took millions of years before the strategy became sufficiently advanced to require an increase in neurological resources. This increase then appeared in both lineages due to the need to boost sentience. The expansion of the brain is evident in later sauropsids and synapsids [5][80]. The delay could also be due to the need to first establish an energy basis in the form of efficient lungs and adaptation to the food sources available in the novel niche. Amphibians have only primitive lungs; they also rely on gills and adsorption of oxygen through the skin.

Behavioral observations offer another line of argument for the amniote first hypothesis. The extra ‘layer’ of brain activity, combined with the many factors that can have an impact, suggests that conscious behavior is less predictable. Thus, variability of response, both between individuals and when the same individual confronts similar situations, is expected to correlate with consciousness. For example, bees perform elaborate ‘dances’ to communicate the direction and distance to a food source. Each dance is necessarily different in order to depict a particular location, but distinct ‘dialects’ are only found when moving from one species to another [81]; thus, the behavior can still be described as stereotypical. Octopuses can learn to navigate mazes and use tools [82], but again the behavior seems more predictable than that of mammals and birds.

According to the hypothesis, feelings were the initiator of consciousness; it is therefore relevant to look for signs of feelings. There are two main pitfalls. One, it is easy to imagine feelings in all sorts of organisms. The wriggling of an earthworm put on a hook is an example. Based on personal experience, the hook causes pain, but for the earthworm, it is more likely an escape response executed without feeling anything. Similarly, play behavior has been associated with positive feelings, but play is for exercising muscles and brains, as such it is an adaptation that also serves nonconscious animals. Two, feelings are generally displayed only when the display is to the advantage of the individual, which may lead us to underestimate their presence. It is, for example, difficult to read emotions in birds, although I expect they have something resembling feelings. One line of investigation that may indicate the presence of feelings is to look for similarities in physiological responses. Reptiles (and birds) respond to danger with rapid heartbeat and increased temperature, which is similar to what we find in mammals [83]. The response is not observed in fish and amphibians, which suggests that it depends on the introduction of feelings.

Given that the early amniotes had a rudimentary form of consciousness, an interesting question is what happened later in the sauropsid and synapsid lineages. They gave rise to ten branches of extant animals that split with neighboring branches more than 150 Mya: sauropsids to birds and six lineages of reptiles, synapsids to the three present lineages of mammals (Fig. 1).

There is limited information on the single remaining species of tuatara. The other five lineages all have various behavioral and neurological signs of consciousness such as complex forms of learning (including social and associative learning), problem-solving, and personality traits [7][74][83][84]. No lineage seems to be distinctly more advanced than the others.

As expected based on their shared ancestry with birds, crocodiles have more prominent encephalization compared to other reptiles (but smaller than that of birds) [85]. In experiments with electrical stunning of mammals, differences in EEG patterns are used to ascertain unconsciousness as opposed to immobilization. A similar difference was observed in crocodiles [86], an observation I consider to be one of the stronger signs of consciousness in reptiles. Yet, it seems likely that a major part of the evolution in the direction of higher consciousness appeared after the birds split with the crocodiles. The dinosaurs were even more closely related to birds, perhaps their form of consciousness evolved further than that of present reptiles.

Mammals have larger brains than birds. It seems likely that the main reason for brain expansion was to enhance the film of life and the concomitant cognitive capacity. Within mammals, primates and cetaceans have larger brains or encephalization quotients. Excluding them, monotremes, marsupials, and eutherians (placental mammals) all have comparably sized brains, roughly similar brain architecture, and appear to have the same level of behavioral complexity [87][88][89][90]. Cynodonts, the putative shared ancestor of the three mammalian lineages, had considerably smaller brains [89], suggesting that the main push as to the evolution of advanced consciousness occurred either shortly before the split with monotremes and/or by convergent evolution after the split. The latter alternative seems likely due to the relatively short period between cynodonts and the split [87][88][89]. If so, it suggests that advanced consciousness had an adaptive value for all three lineages. A similar argument can be made for birds, while the lack of expansion in the various reptile lineages suggests that their situation was different. That is, the disadvantages and advantages of consciousness weighed more in favor of the former.

7. Alternative models

Some people assume that consciousness is a quality of the Universe and therefore is omnipresent. I shall limit the discussion to models that consider consciousness to be a feature of nervous system. The intention is not to offer a comprehensive review, but to discuss key notions as to which animals possess the feature – moving from the selective to the inclusive.

Before the process of evolution was understood, people tended to assume that consciousness was restricted to humans. As our close resemblance to primates and other mammals became obvious, and we started to discern the neurological correlates of conscious processing, these animals were included. The questions of which other groups should be listed, and whether the feature is present in all mammals, are more contentious. The answer to both questions depends largely on two issues; one, has consciousness evolved more than once; and two, can consciousness degenerate and disappear? As to the latter, evolution can lead to the degeneration of other bodily and brain features, there are no obvious reasons why the same could not happen to consciousness. For example, has the dwarf shrew with its 60 mg brain lost the capacity? To my knowledge, no one has looked for neurological correlates of consciousness in this species.

The answer also depends on the choice of definition. As pointed out in Section 1, our terminology caters primarily to human features, whether the same feature is present in other species is a question of how much variation we wish the term to embrace. There is necessarily variation as to forms of consciousness [8], but there should also be universally present attributes to have a meaningful term [60].

There is considerable evidence for including birds in the list of conscious animals[54]. As discussed in Section 5, for consciousness to be present in birds, one would expect an element of convergent evolution. The behavioral and neurological data that favor the inclusion of birds are also partly present in reptiles.

Moving further away from humans, some people assume that all vertebrates are conscious[91]. The next step is to include select invertebrates. For example, the *Cambridge Declaration on Consciousness*[92], a consensus report from a number of key scientists, embrace the cephalopod lineage of mollusks. Others prioritize arthropods such as insects (bees in particular) [93] or crustaceans [53]. The choice of animals to be included depends on how advanced their nervous systems are and the complexity of their behavior.

The first members of the *Chordata* were lancelets and tunicates. Although the brains of even the present members are considerably less advanced than those of vertebrates [94], they may not be inferior to those of insects. If consciousness originated in the first chordates, the feature dates back to the time of the early Cambrian [95].

Several scientists consider the Cambrian explosion (Fig. 1) as a likely starting point for the evolution of consciousness [93][96]. This was a period with extraordinary evolutionary radiation and consequently a complex and changing environment [97]. As such, there would be considerable impetus for improving nervous systems. In line with this notion, the fossil record indicates that the brains of arthropods [98] and chordates [99] had started to evolve at the time.

The drastic differences in brain anatomy of these two phyla suggest that their brains evolved independently from precursors with primitive neurology. Still, it is conceivable that the seeds of consciousness appeared in their shared ancestors, which would mean the early bilaterians. This scenario would be the choice if one believes that consciousness is present in invertebrates and does not want to embrace convergent evolution. The bilaterians split into protostomes and deuterostomes before the Cambrian explosion, perhaps as far back as 600 Mya [100]. The scenario might suggest that some form of consciousness is available to all bilaterians, a notion that few scientists seem to promote. The group includes the previously mentioned nematode *C. elegans*. An alternative scenario is that convergent evolution of consciousness in arthropods, chordates, and mollusks started around the time of the Cambrian explosion. In both scenarios, the trait could have evolved to advanced forms in some lineages while degenerating in others.

An ideal model depends on gathering all relevant evidence and weighing how well their ‘combined impact’ fits various scenarios. Both the gathering and the weighing have an unavoidable subjective component, which helps explain why scientists tend to form different models. My evaluation is reflected in the present text.

8. Conclusion

Table 1. Stages in the evolution of consciousness according to the present model.

Stage	Approx time (Mya)	Lineage	Primary function
First nervous system	650	Multicellular animals[1]	Facilitate movement
Advanced nervous systems	530 – present[2]	Arthropods, mollusks, vertebrates	Improve behavioral decisions
Motivators	400-300	Vertebrates (and others?)	Execute/coordinate decisions
First feelings and rudimentary sentience	320	Amniotes	Decisions in novel and variable environments
Cognition/free will	50 – present[3]	Primates	Better decisions
Language/advanced cognition	3 – present	Hominins	Social life/tools

[1] *Comb jellies split with other lineages very early and evolved their nervous system largely independently.*

[2] *Convergent evolution in several lineages.*

[3] *Both the suggested time and the restriction to primates are somewhat arbitrary and contentious.*

The present model for the evolutionary trajectory of consciousness can be divided into various stages (Table 1). The key stage was the formation of a primitive, nascent form in early amniotes due to the introduction of feelings. According to the model, this was the only time consciousness arose.

I realize that the model I present is controversial. For one, I argue that some of the observations that have been proposed to signify consciousness are best explained without. Two, I suggest that consciousness as an evolutionary ‘invention’ is not that magnificent. It has a reasonable adaptive value, but the simpler nervous systems of arthropods seem more successful. The biological value of advanced forms of consciousness, as in the great apes, is dubious (apart from one species).

Other scientists have invested a lot in more laudatory models – both as to the species included and as to the relative value of conscious versus nonconscious processing. My model may be considered an oversimplification and perhaps a threat to their investment. To make it worse, I argue that the difference between these models and mine could be partly due to a bias brought on by the tool used to investigate; that is, the human brain. For one, our brains are tuned to gregariousness and empathy. Humans certainly have feelings, including compassion for other species and fetal members of our own species. I suggest that these feelings can bend judgment in the direction of assuming consciousness where it is unlikely to be present. Two, the only thing on your mind is what the nonconscious brain decides to serve you. You have a say as to what you want to be served, but the content is largely beyond your control. There is likely to be a bias imposed by being unable to distance oneself from the topic studied.

I should add that I appreciate being proven wrong. I aim to enhance personal insight, not to gain followers. The one thing I strongly believe is that an evolutionary perspective has merit, and that ignoring it leads to an inferior model of the brain.

The human brain, with its capacity for cognition, is arguably the pinnacle of evolution. We have evolved to a point where our brains are capable of a 'hostile takeover' – akin to what artificial intelligence did in the Matrix films. In other words, evolution has equipped us with a level of free will sufficient to make decisions that are not conducive to procreation or survival [101]. We can choose not to have children and even to commit suicide. And we can dedicate our lives to understanding what it is all about.

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