



Review

The emergence of consciousness in phylogeny

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ABSTRACT

The brains of animals show chemical, anatomical, and functional differences, such as dopamine production and structure of sleep, between Amniota and older groups. In addition, play behavior, capacity to acquire taste aversion, sensory pleasure in decision making, and expression of emotional tachycardia and fever started also to be displayed by Amniota, suggesting that the brain may have begun to work differently in early Amniota than in Lissamphibia and earlier vertebrates. Thus we propose that emotion, and more broadly speaking consciousness, emerged in the evolutionary line among the early Amniota. We also propose that consciousness is characterized by a common mental pathway that uses pleasure, or its counterpart displeasure, as a means to optimize behavior.

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1. Introduction

What is consciousness? Bering and Borklund [1] define it as “a higher-order cognitive system enabling access to intentional state.” That new property may have emerged because of the increasing

complexity of life in a terrestrial environment [2]. In this new adaptive landscape, existence required more and more stimulus–response pathways; eventually, a point was reached where it became more efficient, in terms of speed and flexibility, to route all decision making through a single mental space. Within this space, different possible responses could be simply matched according to the criterium of maximal pleasure [3]. With Rial et al. [4] we may acknowledge that “attaining a positive proof of adaptiveness is extremely difficult”. However, it seems obvious that such a simplified process gave a survival advantage to those animals that

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acquired it, and pleasure/consciousness was maintained and transmitted to us.

Based on experimental as well as theoretical arguments Cabanac proposed previously that it was sensory pleasure/displeasure that made consciousness so useful that such emerging new property was selected and maintained through natural selection [3,5]; thus conscious animals did not have anymore to accumulate behavioral reflexes to produce useful responses but could just maximize sensory pleasure. In the following we shall define it as an abstract private model of reality, with four dimensions: quality, intensity, hedonicity, and duration.

The first dimension of sensation is qualitative and describes the nature of the stimulus or the mental object. A blue color, a sweet taste, a remembrance, etc., describe the nature of the mental experience. The second dimension of sensation is quantitative and describes the intensity of the stimulus, a bright color, a loud noise, etc. The third dimension is affective (hedonic). It may be difficult to disentangle affectivity from intensity because they most often covary together. Yet, this can be done (e.g., in the cases of sensation). All sensations are either unpleasant, indifferent or pleasant. Incidentally, this includes pain, a sensation most often unpleasant but sometimes indifferent or even, but rarely, pleasant. Sensory pleasure possesses several characteristics: pleasure is contingent, pleasure is the sign of a useful stimulus, pleasure is transient, pleasure motivates behavior. The fourth dimension of sensation is duration, which describes the extent of time a stimulus is present.

These dimensions allow the human mind for example to call up a broad range of recollected, apprehended, or even totally imagined realities. The result is increasingly complex mental activity: thoughts, feelings, and emotions assume a life of their own within a space that is relatively independent of simple stimulus–response pathways. When this space includes a representation of oneself and how this self interacts with reality, we have the beginnings of self-consciousness.

Consciousness was long considered a human privilege, all other animals being merely machine-like beings [6]. This view was challenged when Darwin [7] pointed-out that other mammals could express emotion. The question then faded into the background, largely because of the excesses of psychoanalysis and the efforts of the behaviorist school to make behavior the only object of study, to the exclusion of *underlying* thought processes [8]. Recently, there has been renewal of interest in animal consciousness [9,10] and a growing acceptance that humans are not the only thinkers. Indeed, if we accept indirect evidence for the existence of human consciousness in other people, i.e., from the verbal and behavioral signs that they provide, why should similar indirect evidence be rejected when it comes to animals? Although less direct than that provided through verbal communication, such evidence is available [9–13].

Yet, one must be prudent and always remain aware that the evidence is always indirect [14]. For example many fishes display complex behaviors such as cheating, altruism, species recognition, individual recognition, cleaning symbiosis [15] that we would be tempted to consider signs of consciousness, but can be explained on the basis of simple reflexes. Also, the complex foraging and social communication behavior of bees is often considered intelligent and ‘conscious;’ however, Gould and Grant-Gould [16] have shown that it was purely reflexive, in the same way as a computer can be artificially intelligent.

If we exclude self-consciousness – a human property¹ – from the private model of reality that consciousness is, we may ask the question of which animals are conscious? And which are not? At what point in evolution did nervous systems cease to operate

only on a reflexive basis [17,18]? Before apes? Mammals? Vertebrates? In the following we will argue that the transition occurred between Lissamphibia and Amniota, i.e., among the amniotes, common ancestors of present-day Mammalia, Chelonia, Lepidosauria, and Archosauria.

This argument has support from the two lines of evidence developed below: anatomy and behavior.

2. Anatomy

2.1. Brain volume and structure

Because consciousness places a high demand on brain capacity, it should vary with brain size. For interspecies comparisons, brain size is best measured by the ratio of brain mass to body mass, i.e., the encephalization quotient (EQ), which corrects for differences in overall body size. EQ shows a clear-cut difference between two categories of vertebrates: ectotherms on the one hand, and endotherms on the other. The latter are warm-blooded tachymetabolic animals and have brains that are about 10 times larger than those of cold-blooded bradymetabolic vertebrates with the same body mass. In ectothermic vertebrates, the brain has the same general structure with five vesicles at the cephalic end of a neural tube. In most Lissamphibia, the telencephalon retains the structure of a simple embryonic vesicle. In Lepidosauria, we see a major change with the appearance of a new structure: the cortex (Fig. 1a). Not that the cortex should necessarily be accepted as the locus of consciousness (see Ref. [19]) but this new structure shows that complexity rose qualitatively between frogs and lizards. This anatomical difference coexists with a histological one in dopamine production.

2.2. Neurotransmitters

Brain dopamine production differs so much between Amphibia and Lepidosauria that it reaches the level of a qualitative difference (Fig. 1b) [20]. Although there is some doubt about the exclusive role of dopamine in hedonic experience, the difference remains significant given its likely involvement in mammals’ hedonic experience, i.e., a conscious process [21–23].

Thus, although the coefficient of encephalization may be similar in Amphibia and lower Sauropsides, neuronal signaling has undergone a substantial qualitative change in the latter. This change is paralleled by behavioral and sensorial differences.

3. Behavioral signs of consciousness

3.1. Emotion

Handling a mammal or a bird produces tachycardia and fever [24–28], the same physiological responses of humans when they experience an emotion. Such responses are produced in Lepidosauria [27,29–31] but not in Amphibia [32] or in Teleostea [31,33] (Figs. 2 and 3).

3.2. Sensory pleasure

Rats display different facial and gestural responses when different stimuli are injected into their mouths [34–39]. These motor patterns resemble the ones that humans display when feeling pleasure or displeasure in response to the same stimuli. Similar evidence of sensory pleasure has been obtained from rats in response to temperature stimuli and temperature rewards in the absence of shivering [40]. Taste stimuli likewise induce pleasure in birds, as evidenced by a verbal response [41].

When mammals suffer nausea or diarrhea in the hours following first contact with a new food, they develop an aversion to the taste

¹ And possibly of some apes.

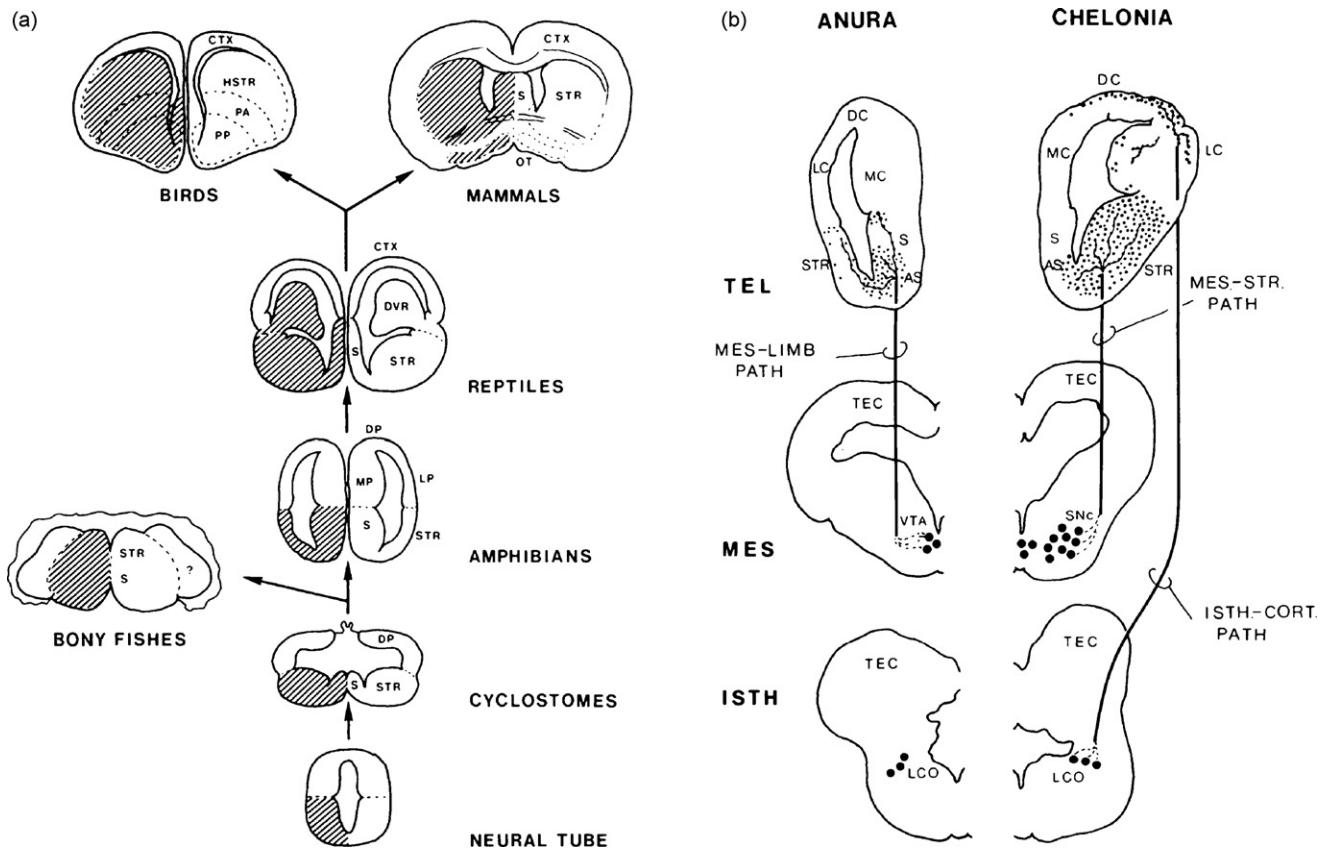


Fig. 1. From [20] anatomical evolution of the cephalic end of the neuraxis. (a) Gross anatomy: the cross-sections show that the cortex, which takes up so much of the mammalian brain, first appeared in Amniotes. Before Amniotes, the neuraxis was a relatively simple tube. (b) Shows the telencephalon and the difference in density of dopamine receptors between an amphibian (frog) on the left and a chelonian (turtle) on the right.

stimulus. Such “taste aversion learning” exists also in humans, who will describe an initially pleasant taste as now unpleasant if it has been associated with indigestion [42]. We investigated this associative learning in lizards and amphibians, both Anoura and Urodeles, by first presenting a new food and then giving intra-peritoneal injections of lithium chloride, which is known to produce nausea in mammals. When subsequently shown the same food item, the lizards avoided it if previously injected with lithium chloride, but the amphibians did not. In control sessions, intra-peritoneal saline injections produced no taste aversion learning in the lizards [43].

Because taste aversion learning in mammals is a conscious experience of what is pleasant and what is not, it is likely that Lepidosauria but not Amphibia can experience pleasure (Fig. 4).

3.3. Pleasure and decision making

In humans, conscious hedonic experience, i.e., pleasure, is the common currency that allows motivations to talk to each other. Thus, pleasure maximization provides a shortcut for making decisions without thinking them through rationally [44]. Other mammals and lizards show evidence of this mechanism: if forced to choose between avoidance of cold and hunger, lizards will maintain food intake by going out into the cold for shorter and more frequent periods [45]. But when the choice is between cold avoidance and consumption of tasty but unnecessary food (as judged from their good health and indefinite survival in the laboratory), they will go out into the cold less often and eventually give up, thus showing that the motivation is pleasure and not need (Balaskó

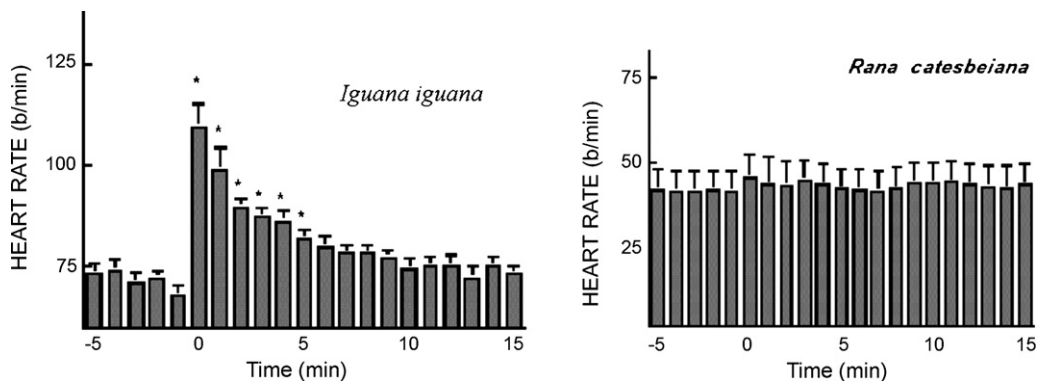


Fig. 2. Mean heart rates, over several sessions, of a lizard (left) and a frog (right) while being gently handled for 1 min at time 0. Emotional tachycardia was present in the Squamate but not in the Amphibian [31].

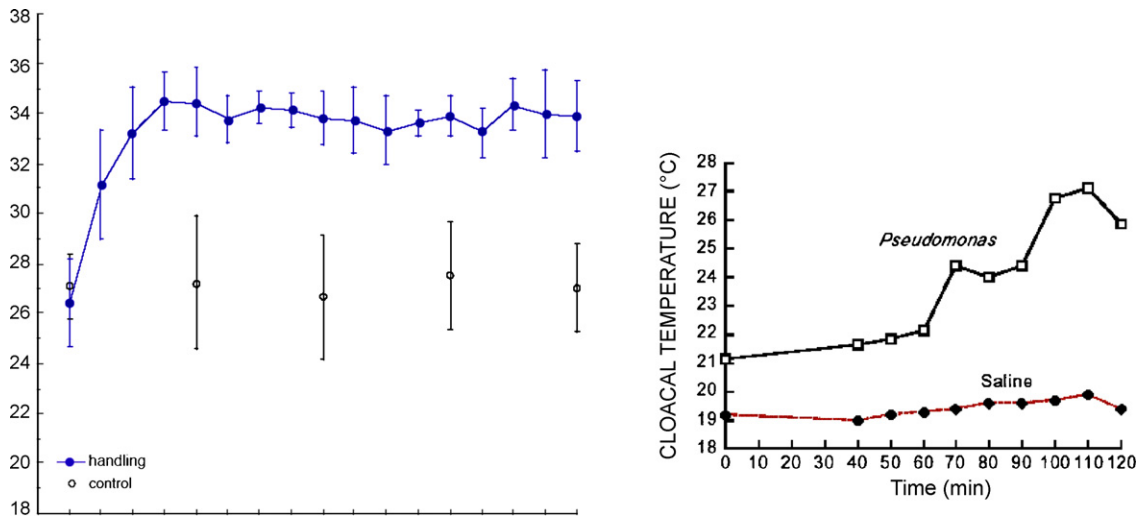


Fig. 3. Behavioral fever in a lizard (left) and a frog (right). In the lizard the fever (continuous line) was produced simply by repeated gentle handling to record cloacal temperature. The separate dots, below, give the lizard's normal temperature at the same time of day when not handled [29]. (right) No such association is present in the amphibians. Injection with pyrogens produced fever, but subsequent injection with saline caused no temperature change [32].

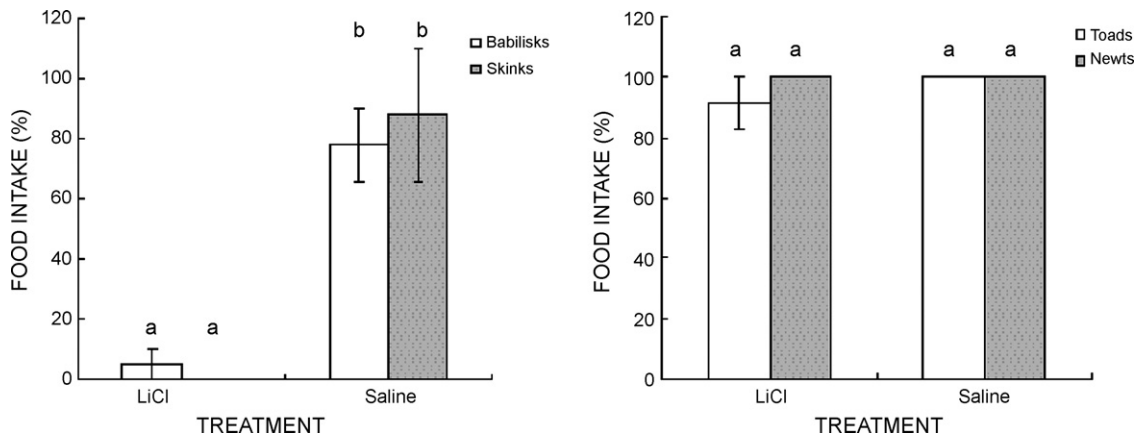


Fig. 4. Taste aversion learning in Lepidosauria (*Basiliscus vittatus*, *B. basiliscus*, *Eumeces schneideri*, *Mabuya multifasciata*) (left) but not in Amphibia (*Bufo paracnemis*, *Pachytriton breviceps*) (right). Left: pooled results from all species of lizards expressed in % of the food intake before treatment. LiCl columns: intake of novel food 1 week after first intake of it followed with i.p. injection of LiCl (0.15 M, 190 mg/kg). LiCl reduced intake of the novel food with which it was paired, but intake of normal food remained unaffected (102.5%, $P=0.92$, not shown in the figure). This difference in response points to the presence of taste aversion learning. Injection of isotonic saline had no significant effect. Right: pooled results from all amphibians expressed in % of food intake before treatment. Left-hand columns: intake of novel food after i.p. injection of LiCl (0.15 M, 190 mg/kg). LiCl had no significant effect ($P>0.10$). This similarity of response in Amphibia points to an absence of taste aversion learning. Injection of isotonic saline had no significant effect. Columns marked by the same letters are not significantly different. Those marked with different letters are significantly different ($P<0.01$) [43].

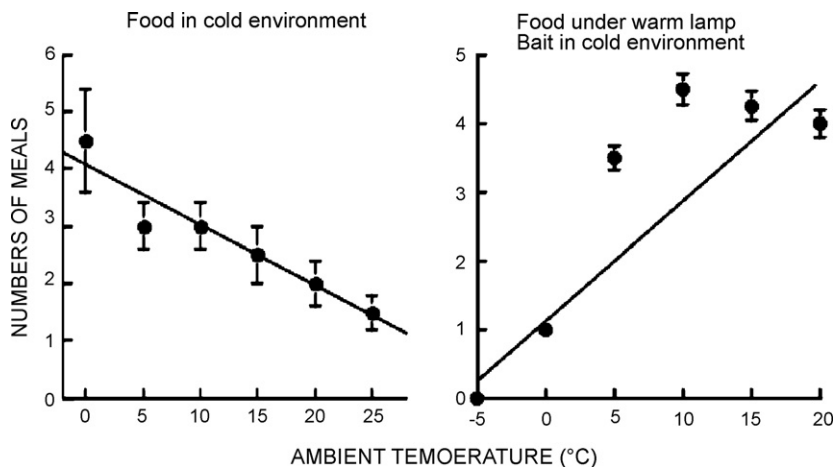


Fig. 5. Lizard food intake as a function of ambient temperature in the climatic chamber (y -axis: number of trips to food; x -axis: ambient temperature). Lizards were placed in a terrarium with an infrared lamp at one end and food at the other. Left (*Tupinambis teguixin*): when there was no food in the warm corner, they ventured into the cold to feed but did not stay long; they returned to heat themselves when their core temperature dropped. As ambient temperature fell, they made more trips to the food and back [45]. Right (*Iguana iguana*): same experiment, except that tasty food (fresh lettuce) was available at the far end while less tasty food was available under the lamp. As ambient temperature fell, the lizards made fewer trips to the far end and back. The tastiness of the food was balanced against the unpleasantness of the cold [46].

and Cabanac [48]) (Fig. 5). They behave like mammals in similar situations [46–48].

3.4. Sleep, play, and detour behavior

Mammals are awakened via the cortex whereas lepidosauria retain a simpler system controlled by brainstem neural mechanisms [49]. This older system persists in mammals but was transformed into slow wave sleep when the cortex was developed. No sleep/wake system exists in amphibians.

Burghardt [50] defined play as an “incompletely functional activity, deliberately initiated because pleasant, non-serious, repetitive, when the subject is relaxed”. Such a definition implies consciousness, especially because pleasure implies consciousness. Play can be easily recognized in mammals, birds, and lepidosaurians but has never been observed in amphibians [50], thus seems “to have been originated in amniotes” [4]. However, many fishes, especially Teleost displayed behaviors that fulfilled the criteria for play, including mental properties as established by Burghardt [50]. Bshary et al. [15] examined Fish behavior and found social strategies, social learning and tradition, and co-operative hunting that resembled those of primates including foraging skills, tool use, cognitive maps, memory, anti-predator behavior, and the manipulation of the environment.

The detour behavior, consists in being able to reach a goal with moving around an obstacle and temporary loss of the target in the process. Such a behavior, that implies a memory of the target object, can easily be observed in mammals, birds, and reptiles but not in other animals [4]. Yet, as reminded by Rial et al. [4] such a response can be produced but pure artificial machines such as GPS; detour as a sign of consciousness should, therefore, be accepted with caution.

4. Discussion and conclusion

The theoretical and anatomical arguments, and the direct experimental evidence of sensory pleasure and signs of emotion mentioned above are an updated version of a previous paper drawing similar conclusions, but based on emotion data only [51]. They suggest that consciousness, understood not as self-consciousness but simply as the presence of a mental space, emerged in the Permian Amniotes common ancestors to present-day Sauropsides and Mammalia rather than converging emergence in those various groups (Fig. 6).

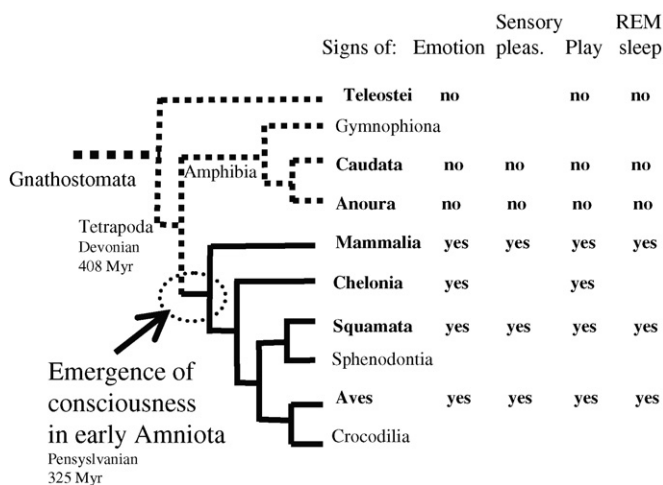


Fig. 6. Phylogenetic tree of living vertebrates (adapted from Lecointre and LeGuyader [52]). In bold the order or taxon where experimental studies provided evidence that signs of consciousness (emotion, sensory pleasure, and play behavior) and paradoxical sleep were present “yes” or absent “no”.

The question of when in phylogeny did consciousness emerge, was also asked by Rial et al. [4], who studied the structure of sleep, and by Aarhem et al. [52]. Both teams also raised the possibility that consciousness might have been a quantitative (progressive) process rather than qualitative (threshold). Their conclusions on the first question was that “consciousness should have appeared in amniotes”, i.e., the same as ours. In the data presented above, the presence of consciousness is suggested not from behavioral decisions or even “intelligence,” – like computers that can behave and possess artificial intelligence but may not be considered as having consciousness (see McFarland [18]) – but rather from signs in the animals that exist properties indicative of consciousness defined above as a four-dimensional mental state.

Are there signs of consciousness before Amniotes? Slugs displayed aversion learning [53], Lymnaeas [54,55] and terrestrial mollusks [56,57] displayed operant conditioning of escape behavior. Yet the most striking performance was that of cephalopods who were described as playing [50] and as being able to learn by looking only [58].

These observations lead to three possibilities:

- The first is that play and these other apparently signs of consciousness, actually do not necessitate consciousness. True consciousness emerged actually with Amniotes.
- Another possibility is that elements of consciousness already showed by Mollusks and Fish are the results of convergence only, as there is a clearcut absence of any sign of consciousness among Amphibians. Thus, these early elements did not evolved to the full four-dimensional consciousness displayed in Amniotes, possibly by lack of a large enough nervous system.
- The last possibility, as suggested by Rial et al. [4], is that consciousness emerged quantitatively in phylogeny as early as Mollusks, but became exploded only with Amniotes.

If that were the case, then there would remain to find an explanation to the total absence of any sign of consciousness in Amphibians early late entails implicitly that the process was more likely to have been qualitative rather than quantitative.

The existence of consciousness in an animal does not imply that behavioral responses are rational in those animals that possess a mental space. On the contrary, this mental space may simulate several possible lines of action and use the feelings they evoke to decide which response is best. For example, hibernating mammals increase their caloric stores in the autumn, but this is not a rational choice that they make to avoid starvation during the winter. Their behavior is driven not by reason but by a fear-like emotion: a negative perception of insufficient food intake at that time of year [59]. Dictionaries provide no precise term for this kind of non-rational mental modeling when the response is purely reflexive. It may be appropriate to use mentalist terminology, i.e., emotions, feelings, etc., but only for Amniota. For other Tetrapoda and below, we should describe behavior only in terms of behavior only. Fear is clearly lacking in such organisms. Their behavioral responses that can be mimicked in artificial models [60], should be described in a way that does not imply consciousness. When a clam, for instance flees away from a predator, it does not “fear”. In the case of fleeing we would suggest the use of a new word from the Latin: *timor*, to describe such non-cognitive behavioral response that precedes consciousness in phylogeny.

Consciousness may have emerged because of the increasing complexity of life in a terrestrial environment [2]. In this new adaptive landscape, existence required more and more stimulus-response pathways; eventually, a point was reached where it became more efficient, in terms of speed and flexibility, to route all decision making through a single mental space. Within this space, different possible responses would be compared and judged

according to the degree of pleasure they evoked, the aim being to maximize pleasure and to minimize displeasure. The hedonic dimension of consciousness thus became a common currency in decision making to select the final behavioral path [61,62]. It proved to be so successful that it was passed on to all descendants of these early Amniota.

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