Emotion and Phylogeny

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Summary: Gentle handling of mammals (rats, mice) and lizards (iguana), but not of frogs (*Rana*) and fish (*Carassius*), elevated the set-point for body temperature (i.e., produced an emotional fever) achieved only behaviorally in lizards. Heart rate, another detector of emotion in mammals, was also accelerated by gentle handling, from ca. 70 beats/min to ca. 110 beats/min in lizards. This tachycardia faded in about 10 min. The same handling did not significantly modify the frogs' heart rates. The absence of emotional tachycardia in frogs and its presence in lizards (as well as in mammals), together with the emotional fever exhibited by mammals and reptiles, but not by frogs or fish, would suggest that emotion emerged in the evolutionary lineage between amphibians and reptiles. Such a conclusion would imply that reptiles possess consciousness

with its characteristic affective dimension, pleasure. The role of sensory pleasure in decision making was therefore verified in iguanas placed in a motivational conflict. To be able to reach a bait (lettuce), the iguanas had to leave a warm refuge, provided with standard food, and venture into a cold environment. The results showed that lettuce was not necessary to the iguanas and that they traded off the palatability of the bait against the disadvantage of the cold. Thus, the behavior of the iguanas was likely to be produced, as it is in humans, through the maximization of sensory pleasure. Altogether, these results may indicate that the first elements of mental experience emerged between amphibians and reptiles. [Japanese Journal of Physiology, 49, 1–10, 1999]

Key words: stress, fever, heart-rate, reptiles, amphibians.

The notion that emotion is useful has recently emerged from a number of publications [1, 2] and has clearly been put forward by Damasio as the major adaptive factor in the human decision-making process [3]. Usefulness irresistibly evokes natural selection and, in turn, evolutionary psychology [4]. It is therefore of interest to examine this "mental feeling"¹ from an evolutionary point of view and to contribute to the debate over the emergence of consciousness in the animal kingdom [6–10].

As is also the case with any other mental event, the main difficulty in bringing emotion into the realm of science and sharing the evidence with other observers consists in obtaining observable signs of it in animals.² A comparative study of emotion has been made possible through a discovery by Brieze and de

Quijada [11] that the core temperature of rats rises during emotional stress. The recording of body-core temperature, a physiological variable, provides an objective criterion of emotion.

1. Emotional Fever

The first report of emotional elevation of body temperature was in young boxers before a competition, as well as in veteran boxers watching the same event [12]. This was confirmed by the rise of core temperature in a population of several thousand students during university examinations [13]. The same situation was also studied by Marazziti *et al.* [14] and by Brieze [15] who showed that the core temperature of the students was elevated by 0.30–0.36°C. Such a rise in core temperature is due to the emotional anxiety of

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¹ Oxford English Dictionary and Schachter and Singer [5].

² Yet, it may be pointed out that verbal responses which are usually accepted as a sign of consciousness in humans, are also a behavior.

Fig. 1. Time course of colonic and tail skin temperature of a rat receiving no other treatment than repeated gentle handling. Due to intense peripheral vasoconstriction and shivering, core temperature rose from about 36.8°C to a plateau at about 38.5°C. The vertical dashed line shows that vasodilatation occurred only once the core temperature had risen to at least 38.2°C. Then, peripheral vasomotor responses were produced so as to mirror the core temperature, thus showing that the plateau of a high-level core temperature was being regulated. This fever had no other cause than emotion (from Briese and Cabanac [18]).

the subjects. Briese and de Quijada confirmed, in rats, the existence of such a rise in core temperature as a response to emotion [11]. Mere handling was sufficient to make the rats shiver immediately and raise their colonic temperature by 1–2°C. The emotional nature of this response was confirmed by the fact that 1) no harm was done to the animals, 2) the response tended to decrease with habituation, 3) the response returned to full strength if a new rat handler replaced the experimenter the rat had been accustomed to, and 4) the response was dependent on the environmental conditions of the session [16, 17].

There are good reasons to accept that the emotional rise in core temperature is due to a resetting of the thermoregulatory set-point (i.e., it is a fever) (Fig. 1).

1) After its initial rapid rise, the core temperature of the handled animal stabilizes, as if a new regulatory set-point had been reached [18].

2) The skin vasoconstricts and facilitates the initial rise, then waves of vasoconstriction and vasodilatation take place 180° out of phase with those observed for the core temperature, thus suggesting that skin vasomotion defends the higher set-point [18].

3) Salicylate, a known antipyretic drug, prevented the rise in core temperature during handling [19–21] in the same way as it would oppose an infectious fever. Other drugs that suppress fever also inhibited emotional fever: oxprenolol [22], naltrexone [23–25], indomethacin [26], phentolamine [27]. This may be

Fig. 2. Time course of the cloacal temperature (body temperature) of one lizard *Callopistes maculatus* when taken only once a day, on separate days (control), or when taken repeatedly every 15 min for 4 h. Each dot is the mean ($\pm$ SEM) of six measurements on different days (from Cabanac and Gosselin [41]).

explained, if the mechanism raising the set-point during emotion is similar, or close to, the mechanism raising it during bacterial or viral fever.

4) Lizards, which do not shiver and can only adjust their behavior within their environment as a means to raise their body temperatures, also raised their cloacal temperature when gently handled (Fig. 2). Thus, it cannot be argued that the rise in core temperature is a passive increase in heat load due to emotional shivering. On the contrary, the lizards used their behavior as if they “wanted” to bring their cloacal temperatures into line with a thermoregulatory set-point that had been elevated during handling, and in the following minutes.

Briese has recently come out in favor of the term “emotional” to explain the elevated temperature of gently handled rats, but has argued that the elevation, at least in rats, is not due to an elevated set-point (i.e., it is not a fever but is rather a passive hyperthermia due to excessive reflex heat production) [28]. Actually, it has been shown that heat production takes place in the rat’s brown adipose tissue during emotional stress as well as in the shivering muscles [29]. Before returning to emotion and consciousness, the main topic of this article, it is therefore necessary and important to discuss briefly this problem because the method to behaviorally assay emotion would be invalidated, especially with ectothermic animals, if the higher temperature reached during emotion was not due to a resetting of the biological thermostat.

Briese’s rationale for rejecting the idea of a set-

point in rats is that their thermal preferences at night (when they are most active) apparently follow a daily cycle in opposition to their core temperature daily cycle: at night, when their core temperature went up, the rats' thermopreferendum went down although, on first sight, one would expect the preferred temperature to go up as well. Thus, apparently, the rats' behavior counterbalanced the core temperature changes and Briese sees in this behavior a reason to doubt that a set-point is driving both the core temperature and the rat's behavior. Such a conclusion, however, may be discarded for the following reasons, which pertain to the nycthemeral cycle and to the response to emotion.

1) If there is no set-point, as claimed by Briese, then there is no temperature regulation. Therefore, one may wonder what is being regulated, and why, then does the homeotherm's core temperature remain steady.

2) The nycthemeral cycle of the rats' core temperature persisted in Briese's experiments although the rats selected cooler temperatures at night. Behavioral responses are the most powerful responses of animals [30] and could have been sufficient to suppress the nycthemeral oscillation.

3) Behavior is a final common path that is shared by all motivations [31]. Access to behavior is assigned to the motivation that is strongest at a given point in time. During the night, when the rat is active, moves around and feeds, other motivations may rank higher than slight thermal discomfort.

4) One may expect that, during the active period in darkness, the rat's heat production rises due to muscular and post-prandial thermogenesis leading, not surprisingly, to a drop in the preferred ambient temperature.

5) Contrary to other functions that are serviced only by behavior, such as food and water intake, temperature regulation can use behavioral and autonomic responses to achieve a stable core temperature. Thus, temperature regulation ranks lower than other motivations when the rat has something else to do and when the environmental temperature is not very hostile. When an animal that does not possess autonomic-defence responses to regulate its body temperature is handled, it must, and actually does use (see point 7, below), its only possible response (i.e., behavior) to raise its body temperature when handled.

6) As mentioned above, during handling the pattern of the rat's skin temperature is exactly like that of a response facilitating a regulated rise in core temperature: first vasoconstriction, then waves of vasodilatation mirroring the changes in core temperature.

7) Finally, the pattern of core temperature of han-

Fig. 3. Evolutionary tree of the animal kingdom after Valentine [72] and Field *et al.* [73]. Fever has been studied in the classes listed under the phyla indicated at the top and left of the figure. This figure includes a hypothesis on the (uncertain) origin of Molluscs after the negative results obtained with Platyhelminthes. Vertebrata, Arthropoda, and Annelida responded to pyrogens by fever, whereas Gastropoda and Turbellaria did not. It is hypothesized that fever was selected before the separation of Arthropoda-Annelida from the main shaft, but after that of a common shaft Mollusca-Platyhelminthes (from Cabanac and Drolet [74]).

dled animals, for both lizards and rats, shows a plateau that would be hard to explain without a set-point. It is still unclear why the rat's core temperature would stop rising if not regulated, and why, more crucially, the lizard's core temperature would rise and then stabilize if not driven by a set-point.

Therefore, it is reasonable and safe to reject the no-set-point hypothesis and to accept that the rat, like other thermoregulators, possesses a set-point that is elevated during and by emotion (i.e., that emotional hyperthermia is a fever).

2. Phylogeny of Emotional Fever

Figure 3 presents a simplified phylogenetic tree of the animal kingdom. Bacterial or pyrogenic fevers were recorded in tachymetabolic vertebrates (mammals and birds) that can use shivering, vasoconstriction, and behavior to raise their core temperatures. Fever was also recorded in all bradymetabolic vertebrates (reptiles,

amphibians, and fish) that use only their behavior to warm themselves. To be able to raise their body temperature, the bradymetabolic animals must have access to some operant way to control their environment. The simplest experimental setting consists in placing the animal in an environment with a temperature gradient in which the subject can move and select its thermopreferendum. In addition to vertebrates, among invertebrates, fever was produced in arthropods (crustaceans, insects, and arachnids) and in roundworms, but neither in molluscs nor in flatworms. Fever is therefore a very ancient response to infection and we stand to gain by investigating emotional fever from this standpoint.

As mentioned above emotional fever was first described in humans, then in rats. Explicit or implicit emotional fevers have also been recorded in rabbits [32], mice [33], voles [34], rats [35, 36], and foxes [37]. In hamsters, the stress of living in a small cage elevated the animals body temperature by ca. 0.5°C [38]. In foxes, indomethacin, a fever antagonist, was reported as not modifying the emotionally elevated core temperature, which was therefore considered not a fever but a hyperthermia by the authors. However, careful examination of the authors' own results seems to show that indomethacin did inhibit partly the core temperature rise, but that the time course of this result was blurred by grouping of the data.

Emotional fever has also been recorded in birds. Emotion induced either by isolation or by handling raised the cloacal temperature of young fowls by $0.6\text{--}0.8^{\circ}\text{C}$ [39]. Emotion also raised cloacal temperature in pigeons from 40.8 to 42°C at the outset of experimental sessions, when their body temperature was recorded without any other intervention [40].

Since mammals and birds are prone to emotional fever, one may expect this to exist in reptiles also. Actually, the mere handling of lizards, in experiments resembling closely those conducted previously in rats, triggered an infra-red heat-seeking behavior and a plateauing of cloacal temperature about 8°C higher than the lizards' temperatures at rest (Fig. 3) [41]. As mentioned above, such a result is important because it definitively indicates the presence of fever since reptiles do not possess skin vasoconstriction and the high metabolism that would allow them to raise their core temperature autonomically. Behavior is the sole response that enables lizards to thermoregulate, and the rise in their cloacal temperature cannot be attributed to passive transient emotional heat production. Therefore, when lizards move to a warmer environment after being handled, such a behavior is a thermoregulatory response to emotion, and the best description of

Fig. 4. Time course of the colonic temperature of one frog before and after injections, at time zero, of $2.5\text{ }\mu\text{g}$ Prostaglandin E_1 , a potent pyrogen (left), and at time 180 min of the same volume of 0.9% sterile saline into the diencephalon. The frog was swimming in a 2-m long water temperature gradient in which it selected its preferred temperature. The animal was taken out of the tank and immobilized manually for the injections. It can be seen that the Prostaglandin aroused a transient fever, as seen in the frog swimming toward warmer water. The control session, however, aroused no emotional fever, although the animal had been manipulated, immobilized, and injected before being put back in the water tank (from Myhre *et al.* [42]).

it is a resetting of the thermostat at a higher value (i.e., a fever).

In lower classes of vertebrates, emotional fever does not seem to occur. Figure 4 shows that the thermopreferendum of a frog placed in a temperature gradient was influenced by intra-cerebral injection of prostaglandin, but not of saline, although the experiment required chasing the frog in the water tank, removing it, holding it tightly, and injecting the solution into its brain [42]. Further explicit seeking of emotional fever in fish confirmed that animals of this class behaviorally developed fevers in response to pyrogens, but did not produce emotional fevers [43].

Lower phyla are able to respond to pyrogens with behavioral fevers as indicated in Fig. 2, but further investigation in species further down on the phylogenetic tree would add little information since not all classes of vertebrates have emotional fever. We already possess, thus, some indication that a qualitative threshold for emotion might exist within the vertebrates between amphibians and reptiles. It would be, however, of great interest to record other signs of emotion in these various classes.

3. Other Autonomic Signs of Emotion

Some data were obtained with tachycardia and galvanic skin response.

Emotional tachycardia

Tachycardia is a well-known sign of emotion in mammals [44] including rats [26] and humans [45–49] under various emotion-arousing circumstances. An example can be found in Fig. 5 in the heart rate of a rat before and after the same stress as that capable of triggering emotional fever: a 1-min gentle handling by an experimenter. Therefore, in lizards and frogs, the criterion we chose for autonomic response to emotion was the animal's heart rate when gently handled (Cabanac and Cabanac, in preparation). Heart rate was counted telemetrically in lizards (*Iguana iguana*) and frogs (*Rana catesbeiana*) to estimate their emotional response to a gentle 1-min handling by the experimenter. To keep body temperature from influencing heart rate, the animals were maintained at steady ambient temperatures of 28 (lizards) and 23°C (frogs). Gentle handling produced, for several minutes, a significant tachycardia in lizards. Snakes also were reported to accelerate their heart rate when they were handled [50]. Such a response is similar qualitatively to that found in mammals and is consistent with the fact that reptile hearts are fully equipped with the same extrinsic nerves and reflexes as mammals. The rat example of Fig. 5 shows that the duration of tachycardia was longer in the rat than in the lizards. Such a difference might reflect a gradation in the response and would hint that a longer or shorter duration of tachycardia might reflect different sensitivities to stress in different taxonomic groups. Yet, the main point here is the existence of a significant tachycardia in lizards.

The cardiac response of frogs during and after handling was limited to a slight trend towards tachycardia (Fig. 5). This response was not statistically significant. To confirm the absence of response, the number of frogs was twice that of lizards. The weak response in frogs contrasts with the clear-cut tachycardia observed repeatedly in the lizards, which are also ectothermic, bradymetabolic animals. Thus, the absence of tachycardia cannot be attributed to bradymetabolism. In addition, amphibians are well-known for their capacity to modulate their heart rate reflexively via their vagi nerves and catecholaminergic responses (e.g., see [51–53]). The absence of tachycardia shown by frogs in response to handling is therefore likely to be authentic. However, this absence should be considered with caution because other authors have obtained moderate tachycardia on simple presentation of a stressful stimulus. CordeiroDeSousa and Hoffmann [54] recorded the heart rate of toads during the presentation of visual stimuli shaped like prey or a predator and showed that a moderate tachycardia may occur

Fig. 5. Mean heart rate (+SEM) of one rat, two lizards (*Iguana iguana*), and four frogs (*Rana catesbeiana*) before and after 1-min gentle handling of the animals by the experimenter at time zero. Heart rate was counted electronically from a telemetric EKG signal produced by an emitter implanted surgically in the animals' bodies. Each animal was tested over five sessions. Asterisks indicate a frequency significantly different from the data obtained before handling (ANOVA and post hoc tests, $p < 0.05$) (from Cabanac and Cabanac, in preparation).

in the absence of somatic manifestations; they considered this response to be a safe index of sensory reception. Wahlqvist and Nilsson [55] exercised toads on a treadmill for 15 min and the animals' heart rates rose by about 20 beats $\cdot$ min $^{-1}$, from a variable initial rate of 10/30 beats $\cdot$ min $^{-1}$, and remained steady for the duration of the exercise. When they suspended their toads above the treadmill for 15 min, heart rate was increased during the first 5 min from about 40 to 50 beats $\cdot$ min $^{-1}$. Finally Laming and Austin [56] also observed a tachycardia in frogs that was preceded by a missing beat in the case of alarm situations. It is therefore possible that the tachycardia observed in stressful situations in higher vertebrates begins to take shape in amphibians. The results in Fig. 5, however, would tend to show that this response is at best moderate and

possibly presents only as reflex anticipatory of future exercise rather than being indicative of mental emotion. Such a response might be a precursor of emotional response in higher vertebrates.

Galvanic skin response

Another autonomic response characteristic of emotion in humans is the galvanic skin response (GSR). During emotions, skin electrical resistance drops as a result of micro-perspiration (e.g., see [46, 57, 58]). This response has been investigated as a potential sign of emotion in the frog *Rana temporaria* during conspecific calls [59]. It was found that territorial calls were followed by GSR but that mating calls were not efficacious. Thus, the response exists in amphibians, at least in a rough form, but does not seem to reflect a general arousal state (i.e., a non-specific emotion) since not all calls aroused the response.

4. Pleasure in Reptiles

I started this article by pointing out that emotion is a mental feeling. It follows from that statement that animals possessing emotion have consciousness. If emotion emerged in reptiles, or between amphibians and reptiles, the latter *de facto* had consciousness also. One may hypothesize that the first mental event to emerge into consciousness was sensation and that what gave consciousness usefulness is affectivity [60]. Thus, what makes the behavior of an animal different from that of a robot is the capacity of the animal to experience pleasure and displeasure. Before the phylogenetic emergence of sensory pleasure, behavior may be understood as a mere combination of reflexes. Pleasure means cognition. The evolutionary advantage of sensory pleasure, for the animals that first had it, is that it saved the nervous system from storing astronomical numbers of potentially useful or noxious stimulus-response reflexes. Sensory pleasure added flexibility to the behavioral pattern of those possessing and it helped them pass it on to their offspring, saved the brain from storing an infinite number of rules of thumb, and provided a formidable advantage both in amount of information stored and in flexibility of the behavioral responses.

If consciousness exists already in reptiles, then it should be possible to find evidence that they possess all the dimensions of sensation, and especially affectivity [61]. An experiment was carried out to verify whether lizards experience sensory pleasure. The general experimental design was the same as that used previously with rats [62]. The lizards lived in a terrarium where a gradient of temperature was established. In the gradient, juvenile green iguanas were placed in

Fig. 6. The mean duration of individual visits to the bait, calculated for repeated identical sessions and then for the group of three animals is plotted against the ambient temperatures. In a previous experiment it was shown that lettuce was not a necessary nutrient for these lizards, which were provided with all necessary food and water under an infra-red lamp, away from the lettuce. It can be seen that the iguanas traded off the noxiousness of the cold environment against the palatability of the lettuce in a linear pattern of response (from Balaskó and Cabanac [61]).

a situation of conflict between two motivations: a thermoregulatory drive and the attraction of a palatable bait. To be able to reach the bait (lettuce), they had to leave a warm refuge, provided with standard food, and venture into a cold environment. In Experiment (1), the time interval between sessions with bait ranging from 1 to 8 d had no effect on the time spent with the bait. This result shows that the lettuce was not a necessary food, deprivation of which would have entailed compensatory behavior. In Experiment (2), as the ambient temperature at the bait decreased the lizards spent less time feeding on lettuce and visited the bait less frequently (Fig. 6). This result shows that the lizards traded off the palatability of the bait against the disadvantage of the cold. These findings support the hypothesis that a common currency makes it possible for lizards to compare two sensory modalities. It is likely that this common currency is pleasure [63], which is the decisional dimension of consciousness [60].

5. Phylogenetic Emergence of Emotion and Consciousness

Altogether, similar responses in lizards and mammals with regards to fever and tachycardia, and no or rudimentary response in frogs, would suggest that the emotional stress was present in lizards and absent in frogs. This in turn would suggest that an important qualitative phylogenetic step took place between the ancestors of present-day amphibians and those of pre-

sent-day reptiles: the emergence of consciousness. Ethological observation led Watson [64] to the same conclusion: "In the lizards, snakes, turtles, and crocodilians, the brain of the typical land living, air breathing animal was for the first time fully established. ... I like to think that this is functionally related to a kind of behavior new in the reptiles—an emergent deliberateness, almost thoughtfulness, in behavior, perhaps most vividly apparent in the lizards. Whereas a frog sits stolidly impervious until an insect passes, when its tongue flicks out suddenly to capture it in a swift reflex action, lizards are much more mobile, even curious, in their behavior. One has the impression that here is the beginning of the world view so strikingly evident in the mammals. It is as if motor programs are not mere reflex jerks but scenarios played out on the stage of an environment of which the animal is fully cognizant, peopled with objects of more or less interest to it. (p. 301)"

It may be hypothesized that such a new "world view" is due to the affective dimension of consciousness [60]. Zajonc theoretized that archaic affective system in the mind retained its autonomy from the more recent cognitive system [65]. The advantage of consciousness would thus be primarily in its affective dimension, the dimension that makes living brains different from computers and robots. Robots are purely rational; they can detect the nature or the intensity of external or internal signals. Sophisticated robots include a goal function serving as a flexible reference for the robot's behavior, but such a flexibility is limited to one function. Despite the talents of their programmers, they lack the affective dimension of thinking. Yet, when a "cue $\times$ deficit" strategy³ is included in the robot, it performs better [66]. It should be pointed out that such a function approximates the production of alliesthesia⁴ (i.e., the modulation of affectivity and motivation) in humans. The affective dimension of the conscious experience focuses the attention of the thinking agent on the relevant conscious event. The affective dimension of consciousness is therefore of paramount importance because, among all the

thoughts that compete for access to the first rank in the final common path of consciousness [67], the winners will be the most intensely pleasant or unpleasant ones.

If, as analyzed by Oatley [68], the role of consciousness is to provide infinite flexibility to the decision-making process by allowing selection of new priorities and rearranging plans in unexpected situations, then this function is fulfilled by affectivity. In the particular case of sensation, it is the affective dimension of sensation that indexes the physiological usefulness of stimuli. One may expect also affectivity to play this role in the case of emotion. Thus, we tend to perform behaviors that produce pleasurable emotions and avoid behaviors that produce unpleasant ones. With regards to animals, Panksepp [69] stated that: "These neuro symbolic affective circuits, designed to promote survival, cannot be easily captured in the non-psychological terminology of neurophysiology. I think we have no reasonable alternative but to begin using some of the ancient affective concepts that evolved early in the development of human language as labels for the many emotional systems which we need to understand in much greater detail. (p. 54)"

Emotion has recently been assumed to be an important and useful factor for humans in the decision-making process [3, 70]. Thus, the word emotion should be used to describe the mental events leading to adaptive behaviors in humans and animals. The role of emotions is to push us to act in a direction better than chance when rationality does not provide an obvious solution to the given problem [2, 71]. The existence of emotion in animals is a reasonable hypothesis. Such a hypothesis would imply that the decision-making process was emotional before it became rational. If emotion emerged early in vertebrate phylogeny with reptiles, then its perennity indirectly implies natural selection.

6. Conclusion

The experiments presented above would suggest that emotion, might have phylogenetically emerged in rep-

³A robot behaves according to its program. A cue is a signal that the robot can detect in its environment and a deficit a signal in its own state. A multiplicative function means that if one signal is zero, the total output is nil. A robot programmed with a cue $\times$ deficit function is similar to a human with alliesthesia and performs better than with other strategies.

⁴The word alliesthesia (Greek *Allos* changed and *-esthesia* sensation) is applied to the affective component of sensation, pleasure or displeasure. Alliesthesia is the faculty of a sensation to move from pleasure to displeasure and vice versa. The amount of pleasure or displeasure aroused by a given stimulus is not invariable, it depends on the internal state of the stimulated subject and on infor-

mation stored in memory. Factors that can modify the internal state and, in turn, induce alliesthesia are as follows: internal physiological variables (e.g., deep body temperature or body dehydration modify the pleasure of thermal sensation or taste of water); set points (e.g., during fever, the body temperature set-point is raised and pleasure defends the elevated set-point); multiple peripheral stimuli (e.g., mean skin temperature determines the set-point for deep body temperature and in turn generates alliesthesia); and past history of the subject (e.g., association of a flavor with a disease or a recovery from disease renders it unpleasant). Positive alliesthesia indicates a change to a more pleasurable sensation, negative alliesthesia a change to a less pleasurable one.

Fig. 7. Partial evolutionary tree of the vertebrates indicating the hypothesis presented in this article. Emotional fever was obtained in the classes reptiles, birds, and mammals, but not in fish nor amphibians. Emotional tachycardia was obtained in reptiles but not in amphibians. Hence, the hypothesis that emotion and consciousness emerged between amphibians and reptiles.

tiles or, more likely, between amphibians and early reptiles, and might have been retained thereafter through natural selection (Fig. 7). It is likely, therefore, that an important qualitative threshold separates amphibians from reptiles, birds, and mammals. Emotion is probably present in reptiles and higher vertebrates, but serious doubt is permitted as to its presence in amphibians. The presence of sensory pleasure in lizards would tend to confirm that reptiles possess conscious sensation. Emotion and sensation being conscious events, it follows that reptiles probably possess the basic elements of consciousness.

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