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Consciousness without cortex

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Abstract

Sensory consciousness — the awareness and ability to report subjective experiences — is a property of biological nervous systems that has evolved out of unconscious processing over hundreds of millions of years. From which brain structures and based on which mechanisms can conscious experience emerge? Based on the body of work in human and nonhuman primates, the emergence of consciousness is intimately associated with the workings of the mammalian cerebral cortex with its specific cell types and layered structure. However, recent neurophysiological recordings demonstrate a neuronal correlate of consciousness in the pallial endbrain of crows. These telencephalic integration centers in birds originate embryonically from other pallial territories, lack a layered architecture characteristic for the cerebral cortex, and exhibit independently evolved pallial cell types. This argues that the mammalian cerebral cortex is not a prerequisite for consciousness to emerge in all vertebrates. Rather, it seems that the anatomical and physiological principles of the telencephalic pallium offer this structure as a brain substrate for consciousness to evolve independently across vertebrate phylogeny.

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Introduction

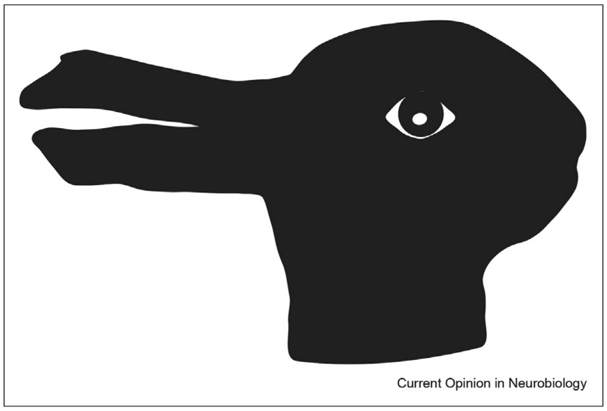
The evolution of our consciousness — the awareness and ability to report our subjective experiences ('being conscious of') [1] — is one of the greatest riddles in biology. Consequently, we ponder whether commonalities in conscious experience are shared across species. If so, how could it possibly result from the workings of the brain?

A key methodological approach to advancing the scientific study of consciousness is the identification of underlying neural markers using a combination of sophisticated behavior and intracranial neurophysiological recordings. Such techniques have been explored in humans [2–5], as well as our closest relatives in the animal kingdom, nonhuman primates [6–10]. These studies exploit the perception of ambiguous stimuli that remain constant in their physical appearance but elicit very different internally generated percepts. Classic examples of such ambiguous stimuli are puzzle pictures (also known as 'flip–flop' images): in the famous 'duck–rabbit image', we have the vivid percept of either a duck or a rabbit, even though the image itself does not change (Figure 1). Experimental techniques to create such ambiguous stimuli causing alternating percepts include binocular rivalry [5–7], temporal masking [3], flash suppression [2,9], and perceptual threshold approaches [8,10].

As an objective marker of sensory consciousness, a proportion of cortical neurons recorded in primates have been shown to modulate their activity in relation to the subject's alternating conscious percept for physically identical stimuli. This neuronal pattern signifies a neural correlate of consciousness (NCC). Based on this body of work in human [2–5] and nonhuman primates [6–10], consciousness is therefore intimately associated with the workings of the mammalian cerebral cortex (neocortex, isocortex) and even its specific types of neurons [11].

The finding that the cerebral cortex is the brain structure from which subjective experience emerges provokes two alternative hypotheses. The first hypothesis posits that the mammalian cerebral cortex is a prerequisite for subjective experience. If so, all non-mammalian species would be precluded from having subjective experiences because they show distinctly evolved endbrains (telencephala) lacking a cerebral cortex. The alternative hypothesis predicts that the cerebral cortex is just one among other possible neural instantiations from which consciousness can spring. Accordingly, evolution could have found different neural solutions to endow animals from different taxa with subjective experiences.

Figure 1



Duck–rabbit illusion. In this ambiguous image, either a duck or a rabbit can be seen alternatingly, thus illustrating contrasting conscious percepts despite constant visual information.

Birds are among the vertebrates with an endbrain lacking a cerebral cortex; they evolved radically different endbrain structures since they diverged from the mammalian lineage 320 million years ago [12,13]. Nevertheless, some birds, particularly members of the corvid songbird family (crows, ravens, jays), show sophisticated cognitive behaviors, which suggest conscious experiences [14–18]. Indeed, recent neurophysiological recordings in behaving crows argue for consciousness without a cortex [19].

Neuronal correlate of consciousness in the crow pallial endbrain

Carrion crows were trained to report the presence or absence of visual stimuli of various intensities in a rule-based delayed detection task (Figure 2) [19]. In some trials, the stimulus was either clearly visible and the crows reported having seen it in almost all trials; in other trials, no stimulus was shown and the crows veridically reported not having perceived a stimulus (Figure 3A). In a fraction of the trials, however, the stimuli were at the perceptual threshold and barely visible, so that the crows reported perceiving the stimulus in half of the trials but failed seeing it in the other half of the trials. In this condition, the internal state of the crows determined whether stimuli of identical intensity were perceived or not (Figure 3A).

The task was designed in such a way that after the stimulus presentation period and the subsequent delay phase, but before the crows' response, a rule cue informed the crows whether or not a head movement was required to report their percept (Figure 2). This prevented the crows from preparing a motor response prior to the rule cue. This was important for accompanying neuronal recordings in which single-neuron activity related to subjective sensory experience and its following accessibility could be explored in the absence of motor preparation.

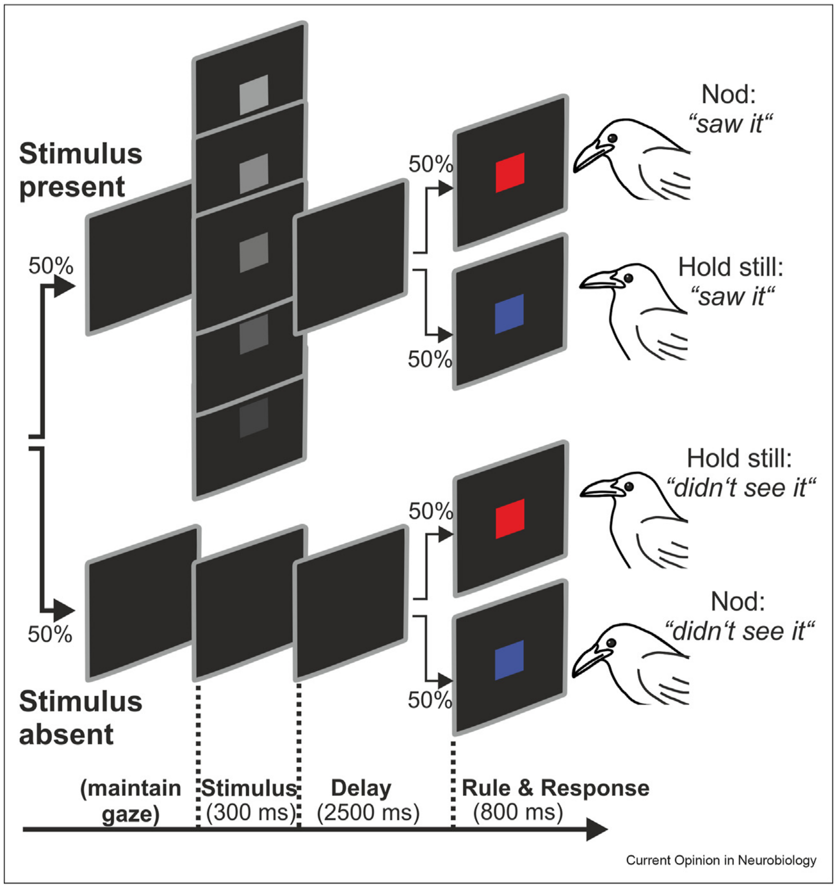
While the crows performed the task, the activity of single neurons was recorded from an associative endbrain area termed the nidopallium caudolaterale (NCL) (Figure 3B). Based on anatomical connectivity patterns and its importance in high-level cognition in birds [20–23], the NCL is suggested as an avian analog of the mammalian prefrontal cortex (PFC) [17,20]. Indeed, NCL single-neuron activity correlated with the crows' perception of stimulus presence or absence and revealed an avian neuronal correlate of sensory consciousness [19]. Despite the identical intensity of stimuli in near-threshold trials, only those stimuli that the crows later reported as having perceived elicited activity changes. Moreover, such neurons also responded in trials in which no stimulus had been displayed but the crow reported the percept of a stimulus. Both of these neuronal response patterns reliably predicted the crows' conscious percept about whether or not they had been aware of a stimulus.

Interestingly, this percept-related neuronal activity needed time to emerge (Figure 3C). During stimulus presentation, neurons responded mainly in agreement with the variable intensity of the stimulus and only mildly to the crows' later reported conscious percept. During the subsequent delay period, however, many neurons responded according to the crows' report rather than to stimulus intensity. Neuronal population analyses showed that NCL neurons switch from initially mainly representing stimulus intensity to predominantly encoding the crows' subjective experience later in the trial and before a required behavioral report.

Conscious processing in crows and the global neuronal workspace hypothesis

The finding of an initial representation of stimulus intensity that switches to an encoding of sensory consciousness a few hundred milliseconds after stimulus onset in the crow NCL is reminiscent of effects reported in the primate cerebral cortex. While initial activity is mainly involved in unconscious vision, activity correlating with consciousness is delayed relative to stimulus onset activity [5,3,24–26]. This effect is captured by the 'global neuronal workspace' (GNW) hypothesis that has been developed for neocortical neurons in the primate brain [27–29]. The GNW postulates that only sensory activity that is strong enough to coherently activate a widely distributed network of workspace neurons (the GNW) can access awareness [28]. If external stimuli cause sufficient activation, the GNW becomes activated via a non-linear 'all-or-nothing' activation process termed 'ignition'. Evidence suggests this ignition emerges in higher brain centers. A recent

Figure 2



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Rule-based delayed detection task used to investigate neuronal activity related to subjective sensory experience and its lasting accessibility in crows. In this visual detection task, crows were trained to report the presence or absence of stimuli after a brief delay. In 50% of the trials (bottom row), no stimulus was shown (blank screen). In this case, the crows had to report that they had not perceived anything by holding still when a red rule cue was shown, but by moving the head when a blue rule cue was displayed. In the other 50% of the trials (top row), stimuli of varying intensities were shown. While some stimuli were salient and easy to detect, others were at the perceptual threshold and difficult to detect; for these ambiguous stimuli, the internal state of the crows determined whether stimuli of identical intensity were perceived or not. For stimulus trials, the crows had to report that they had perceived the stimulus by moving when a red rule cue was shown but by holding still when a blue rule cue was displayed. Adapted from the study by Nieder et al. [19].

monkey study showed that while both perceived and unperceived stimuli caused activity in visual areas V1 and V4, only the perceived ones elicited sudden, strong, and lasting activity in the PFC [10]. The PFC, as the apex of the cortical processing hierarchy, plays a key role in the GNW because of its massive interconnectedness with upstream brain areas and its ability to broadcast information in a global manner. Through ignition, information about a stimulus becomes sustained and broadcasted back via recurrent interactions between various brain areas.

Given the similarity in connectivity and function of the avian NCL with the primate PFC, the NCL may very well constitute the avian brain region of such an ignition process. If and how global broadcasting of information in the GNW after ignition takes place in the avian brain has to be explored by simultaneous multi-site recordings. If realized, a two-stage process in awareness as proposed by the GNW could turn out to be a general and evolutionarily stable principle of how sensory consciousness is achieved not only in the primate cerebral cortex but also in the pallium of advanced vertebrates in general.

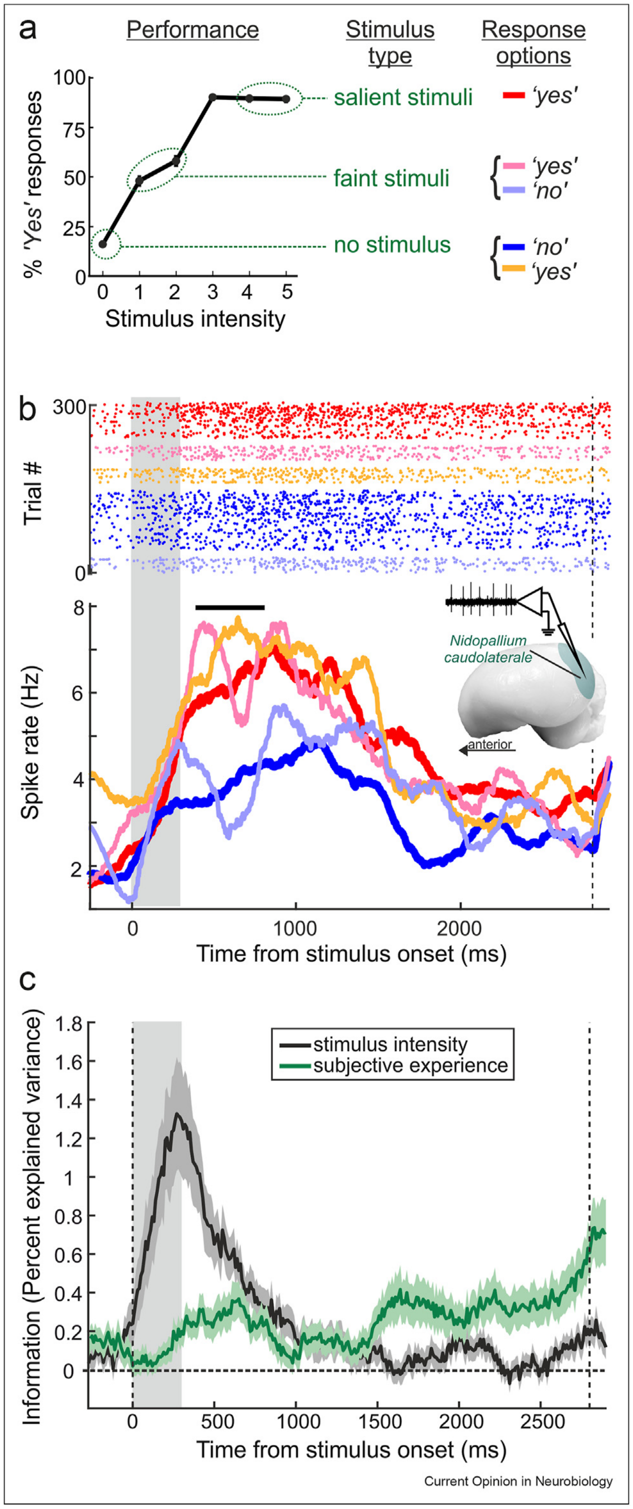
Independent evolution of endbrain integration centers enabling consciousness in birds and mammals

What is the evidence that the nidopallium of birds and the neocortex of mammals constitute evolution's independent solutions to the common problem of high-level and conscious processing? After all, both structures emerge early in embryonic development from a part of the telencephalon (endbrain) termed the 'pallium' (from Latin *mantle*) [30]. However, several lines of evidence suggest that the specific intelligence centers and circuits in birds and mammals emerged based on convergent evolution.

First, territories of the pallium giving rise to similar high-level cognitive functions in mammals and birds are different (Figure 4). Specifically, the destinies of the four pallial sub-regions (the medial, dorsal, lateral, and ventral parts) differ drastically between mammals and birds. Mammals expanded the dorsal pallium into the neocortex (isocortex or cerebral cortex), which constitutes their highest brain integration center [31]. In contrast to mammals, the ventral pallium evolved as the dominating pallial territory in birds (and sauropsids in general). It forms a large, elongated ridge that protrudes into the ventricle and is therefore called the dorsal ventricular ridge (DVR). The anterior DVR develops into a number of nuclear territories that account for most of the avian telencephalon [32] and exhibit the same neuron count as primates with much larger brains [33].

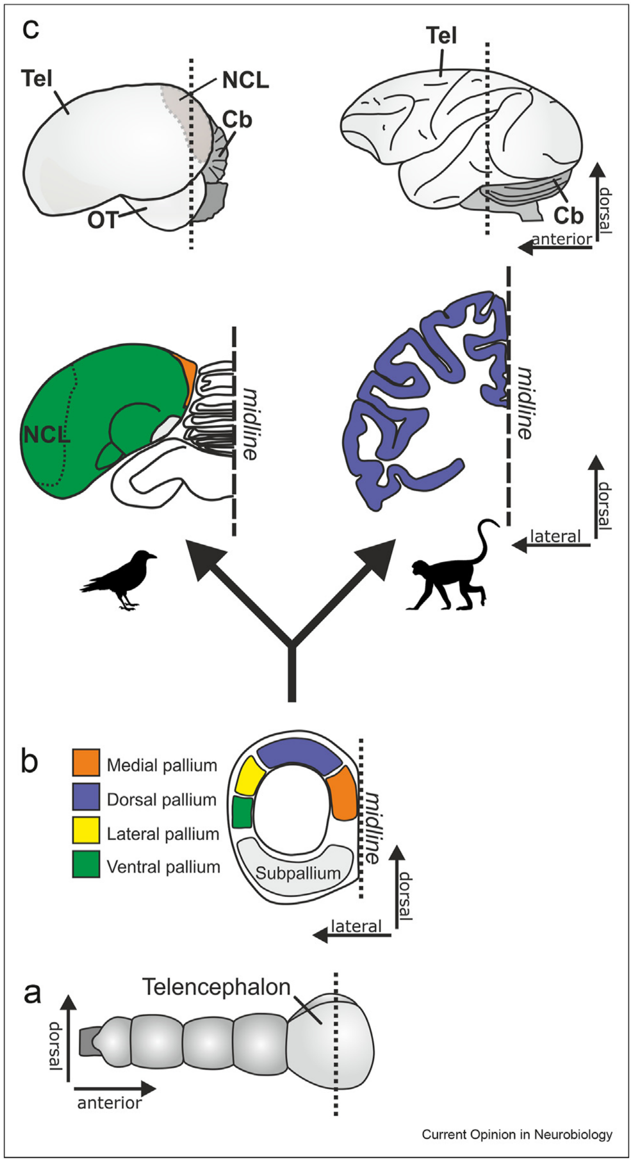
Second, the mammalian neocortex (derived from the dorsal pallium) and the dominant avian telencephalic pallium (derived from the ventral pallium) exhibit distinct neural architectures. The mammalian neocortex shows a unique lamination with six layers; pyramidal projection neurons with apical dendrites and local neurons form orderly, stacked layers that run parallel to the brain's surface [30]. In the primate lineage, in particular, associative cortical territories are enlarged and give rise to complex cognition. In birds, however, the anterior DVR develops into a number of nuclear subdivisions termed the hyperpallium, entopallium, arcopallium, mesopallium, and nidopallium. The mesopallium and nidopallium in the avian brain assume the functions of associative neocortical regions in mammals. While sensory input areas in the avian pallium show a layer-like organization, the large associative areas of the nidopallium (of which the NCL is a part), an enigmatic

Figure 3



Behavioral performance of a crow and neuronal responses from its NCL related to sensory consciousness. (**a**) Psychometric functions of a crow performing the rule-based delayed detection task (shown in Fig. 2). Trials were grouped into salient-stimulus, faint-stimulus near-threshold=, and no-stimulus trials. The different response options ('yes'/'no') for each trial group are color coded and depicted on the right. Error bars (very small) indicate the standard error of the mean. (**b**) The activity of an NCL neuron in relation to the crow's behavioral responses. Top panels depict dot raster histograms (every line is a trial, every dot is an action potential); bottom panels represent the corresponding averaged and smoothed spike density histograms. The vertical gray shading indicates the presence of the stimulus (onset at 0 ms), the vertical dotted line signifies the end of the delay. The color code represents neuronal activity for the crow's different behavioral response categories, which are shown under 'response options' in (a). Reddish colors signify all trial categories in which the crow reported perceiving a stimulus; blueish colors represent trial types in which the crow subsequently reported stimulus absence. Significant activity differences between 'stimulus present' and 'stimulus absent' trials are seen in the first half of the delay period. The inset shows a lateral view of a crow brain depicting the nidopallium caudolaterale (shaded) in the telencephalon. (**c**) Sliding-window percent explained variance (ω^2) analysis quantifying the information about the stimulus intensity and subjective percept. To quantify how much information about the physical stimulus and the subjective experience was carried at each trial moment by the activity of the entire population of recorded NCL neurons, the percent explained variance for stimulus intensity and 'yes/no' response was calculated. Adapted from the study by Nieder et al. [19]. NCL, nidopallium caudolaterale.

Figure 4



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Divergent evolution of the telencephalic pallium in birds and mammals. (**a**) Lateral view of idealized early embryonic formation of the five brain vesicles with the telencephalic hemispheres at the anterior pole. (**b**) Coronal sections through the telencephalon (at the level of the dotted line) early in embryonic development. The idealized layout of the telencephalon represents the hypothetical ancestral vertebrate condition with the four pallial regions (color coded) forming the roof of the telencephalon. (**c**) *Top row:* Lateral views of the brains of a crow (representing birds, left) and a rhesus macaque (representing mammals. right). *Bottom row:* Coronal sections (at the level of the dotted lines in the top row) of the crow (*left*) and macaque brains (*right*). The nidopallium (NCL, nidopallium caudolaterale) originating from the ventral pallium encodes subjective experience in crows, whereas the cerebral cortex emerging from the dorsal pallium gives rise to sensory consciousness in monkeys (and mammals in general). Tel, telencephalon; NCL, nidopallium caudolaterale. Adapted from the study by Nieder [53].

structure that evolved most distinctly in birds and, therefore, defies comparison with the mammalian neocortex [34], explicitly lacks such a cortex-like architecture [35]. This suggests that a cortex-like structure is not a prerequisite for consciousness.

Third, even within the same ancestral subdivision of the pallium, one-to-one homologies between mammals and sauropsids (reptiles/birds) cell types and arrangements are absent. For instance, the extant three-layered reptilian dorsal cortex (emerging from the dorsal pallium) is thought to represent an ancestral form of the neocortex, which also evolved from the dorsal pallium. Despite this common origin, the patterns of lamination and neuronal migration in the developing dorsal pallium differ markedly between reptiles and mammals [36]. Furthermore, neuronal gene expression for glutamatergic cell types and layer types differ in the dorsal pallium of both amniote groups [35,37,38]. Therefore, not only did the architecture evolve independently in mammals versus reptiles to birds, but also in the pallial cell types.

Interestingly, despite these differences in anatomical origins and genetic foundations, the avian DVR and the mammalian neocortex converged on similar neuronal circuits [39]. However, these circuits in birds engage entirely separate classes of excitatory and inhibitory pallial neurons that have no counterpart in the mammalian neocortex [40]. Complex behavior in birds and mammals seems to require equivalent neuronal circuit implementations [41], but the nuts and bolts leading to this wiring evolved largely *de novo* in these animal taxa. Overall, these findings at different levels of observation — from embryogenesis to single-cell transcriptomics — argue for a distinct and independent origin of major pallial integration centers that enable consciousness in birds and mammals.

Why the pallium may invite representation of conscious experience

If the specific organization and cell types of the mammalian neocortex are not a prerequisite for consciousness to emerge in all vertebrates, what anatomical and functional principles offer the pallium as a brain part for consciousness to evolve across phylogeny? Four characteristics may be critical.

First, the avian pallium and the mammalian neocortex share their roles as an intermediary between sensory input and motor output. Their circuits comprise three major classes of neurons: thalamic input neurons that convey sensory information, intra-telencephalic neurons that process this information within the pallium, and output neurons that project to sub-telencephalic motor centers [38,42]. At the micro-circuit level, the avian pallium contains distinct neuronal populations that exhibit profound physiological and computational similarities with mammalian excitatory and inhibitory neocortical cells [39,40]. Pallial cell types and circuits, therefore, enable important physiological functions to support subjective experience of sensory information and to respond to such percepts in an explicit and goal-directed way.

Second, the pallium enables abstract conscious experience across modalities by merging sensory information. Besides dedicated sensory and motor regions, the pallium contains large associative areas. The evolution of higher cognitive abilities are attributed to the (parietal, temporal, and frontal) association cortices in mammals, and to the mesopallium and nidopallium in birds. They integrate multi-modal information received from primary sensory pallial areas and project in turn to pallial premotor and motor output structures [43,44].

Third, pallial circuities enable recurrent processing in which information enters cascades of feedforward and feedback projections between hierarchical processing levels. Reciprocal and reentrant connections enable information to be maintained in an active state in associative circuits and networks, thereby temporarily buffering information in the service of memory functions [45,46]. Recurrent processing also allows subjectively relevant information to re-enter previous processing units to exert top-down influences on the brain's input stages. Recurrent processing is also essential in the GNW hypothesis as it enables network ignition that triggers, amplifies, and sustains a neural representation to become consciously aware [28].

Fourth, the avian and mammalian pallium show specific neuronal connectivity patterns that enable the interplay of millions of neurons distributed in specialized processors and loops throughout many brain regions. The topological architecture of the brain connectome is widely depicted by graph theory analysis. Here, brain networks in the mammalian neocortex are characterized by modular organization, small-worldness (i.e. high local interconnectivity with short path lengths between brain regions), and highly connected and centralized hubs [47,48]. The avian pallium shows a connectome comparable to the mammalian neocortex [49,50], such that it is modular, small-world network with a connective core of hub nodes that include all major (prefrontal-like) associative areas of the avian brain (parts of the nidopallium and mesopallium) linked to executive functions. This wiring is also in agreement with the GNW hypothesis, which can operate without a layered cortical architecture but needs a modular connectome with a small-world network and major hubs embedded in multiple specialized modules [26,27]. Given the increasing evidence for convergent evolution of the major parts of the avian pallium, the shared network topologies seem to be the result of similar selection pressures in these cognitively advanced vertebrate classes.

Conclusion: interpreting the phylogenetic origins of consciousness

Because consciousness is a process rather than a structure, neurophysiological insights from behaving animals are instrumental in advancing the scientific study of consciousness. With such neurobiological markers at hand, the presence of subjective experiences has so far been demonstrated in (advanced species of) two animal taxa, namely birds and mammals. How can the emergence of consciousness in birds and mammals be reconciled in light of their independent pallial evolutions?

One possibility is that birds and mammals inherited sensory consciousness from their last common ancestor, a reptilian-like stem amniote. This would have two major consequences. First, it would date back the evolution of consciousness to at least 320 million years ago. Second, it would predict that (at least) all descended amniote vertebrates (all reptiles, birds, and mammals) are consciously aware. Given the many cognitive specializations of the avian and mammalian brains and without unequivocal demonstration of behavioral signatures of consciousness in reptiles (such as explicit working memory), this scenario seems unlikely.

A more parsimonious explanation is to assume that consciousness emerged independently based on convergent evolution on different branches of the amniote tree of life. If true, consciousness was absent in the last common ancestor of birds and mammals but evolved later in phylogeny and independently during the rise of these taxa. Extrapolating this scenario would open up the possibility that consciousness as a convergently evolved trait might even be found in very remotely related but cognitively advanced invertebrates [51,52]. Combining recordings of neuronal activity with controlled behavioral protocols will help to decipher the evolutionary roots of conscious experience in the animal kingdom.

Conflict of interest statement

Nothing declared.

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