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Animal consciousness: a synthetic approach

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Despite anecdotal evidence suggesting conscious states in a variety of non-human animals, no systematic neuroscientific investigation of animal consciousness has yet been undertaken. We set forth a framework for such an investigation that incorporates integration of data from neuroanatomy, neurophysiology, and behavioral studies, uses evidence from humans as a benchmark, and recognizes the critical role of explicit verbal report of conscious experiences in human studies. We illustrate our framework with reference to two subphyla: one relatively near to mammals – birds – and one quite far – cephalopod molluscs. Consistent with the possibility of conscious states, both subphyla exhibit complex behavior and possess sophisticated nervous systems. Their further investigation may reveal common phyletic conditions and neural substrates underlying the emergence of animal consciousness.

A synthetic framework for studying animal consciousness

Although Darwin proposed that animal and human minds alike are the products of natural selection [1], questions of animal consciousness were largely neglected throughout the 20th century (but see Griffin [2]; note the term ‘animal’ is used here to mean ‘non-human animal’). This neglect may have arisen in part because, seemingly, only humans are capable of accurately describing their phenomenal experience. However, there is now abundant and increasing behavioral and neurophysiological evidence consistent with, and even suggestive of, conscious states in some animals. We will use humans as a benchmark for the development of new empirical criteria for further investigation. Here we apply this approach to birds and cephalopod molluscs, subphyla that exhibit complex cognitive faculties and behaviors and have strikingly elaborate brains. These two subphyla are examples of highly distinct lineages, and their study provides an excellent opportunity to examine how conscious states might be instantiated in very different nervous systems. While we do not resolve this issue here, we propose that its examination lies within the reach of contemporary neuroscience.

Humans as a benchmark

The notion that consciousness can be engendered in different nervous systems by a variety of underlying mechanisms suggests a need to examine constraints, and therefore to synthesize behavioral, neurophysiological, and

neuroanatomical evidence. Human studies involving the correlation of *accurate report* with neural correlates can provide a valuable benchmark for assessing evidence from studies of animal behavior and neurophysiology. A constraint on this strategy is that the capacity for accurate report of conscious contents implies the presence of *higher-order consciousness*, which in advanced forms may require linguistically-based narrative capability. This is in contrast to *primary consciousness*, which entails the ability to create a scene in the ‘remembered present’ [3] in the absence of language. Primary consciousness may be a basic biological process in both humans and animals lacking true language.

Various properties of human consciousness can be identified at the neural, behavioral, and phenomenal levels [4]. Neural correlates of human consciousness include the presence of thalamocortical signaling, fast, irregular,

Glossary

Accurate report: a first-person account of what an individual is experiencing, made without the attempt to mislead. Accurate report, which can be given through language or related varieties of voluntary response, has been critical in the investigation of conscious states in humans. In animals without the faculty of natural language, forms of behavioral report acting through other motor channels might be examined to determine the possible presence of high-order discriminations suggesting conscious states.

Binocular rivalry: this occurs when the two eyes are each simultaneously presented with a different image. Rather than seeing both images superimposed on one another, the subject sees one image first, then the other, in an alternating sequence. For example, if one eye is presented with parallel vertical stripes and the other with parallel horizontal stripes, rather than seeing an overlapping ‘weave’ of vertical and horizontal stripes, the subject sees first one orientation of stripes, then the other [83].

Explanatory correlates of consciousness: Conventional approaches within consciousness science have emphasized the search for so-called ‘neural correlates of consciousness’: neural activity having privileged status in the generation of conscious experience [7]. However, the transition from correlation to explanation requires an explanation of how particular neural correlates *account for* specific properties of consciousness. Searches for explanatory correlates of consciousness attempt to provide this link [11,14].

Primary consciousness: this refers to the experience of a multimodal scene composed of basic perceptual and motor events. Primary consciousness is sometimes called perceptual or phenomenal consciousness, and it may be present in animals without true language.

Higher-order consciousness: this, by contrast, involves the referral of the contents of primary consciousness to interpretative semantics, including a sense of self and, in more advanced forms, the ability to explicitly construct past and future narratives [3]. The presence of higher order consciousness or metacognition should not be assumed to be necessary for the ascription of primary consciousness, though it may be constitutively required for advanced forms of self-consciousness and consciousness of consciousness (Box 2).

Transitive inference: the ability to connect two or more separate relations, and is widely regarded as a fundamental process in reasoning. Such abilities have been demonstrated in certain birds. For example, in experiments involving the relative ranking of objects presented in pairs, pigeons were able to determine that B>D after they had separately learned that A>B, B>C, C>D, and D>E, while great tits have been observed to deduce complex social dominance rankings [30].

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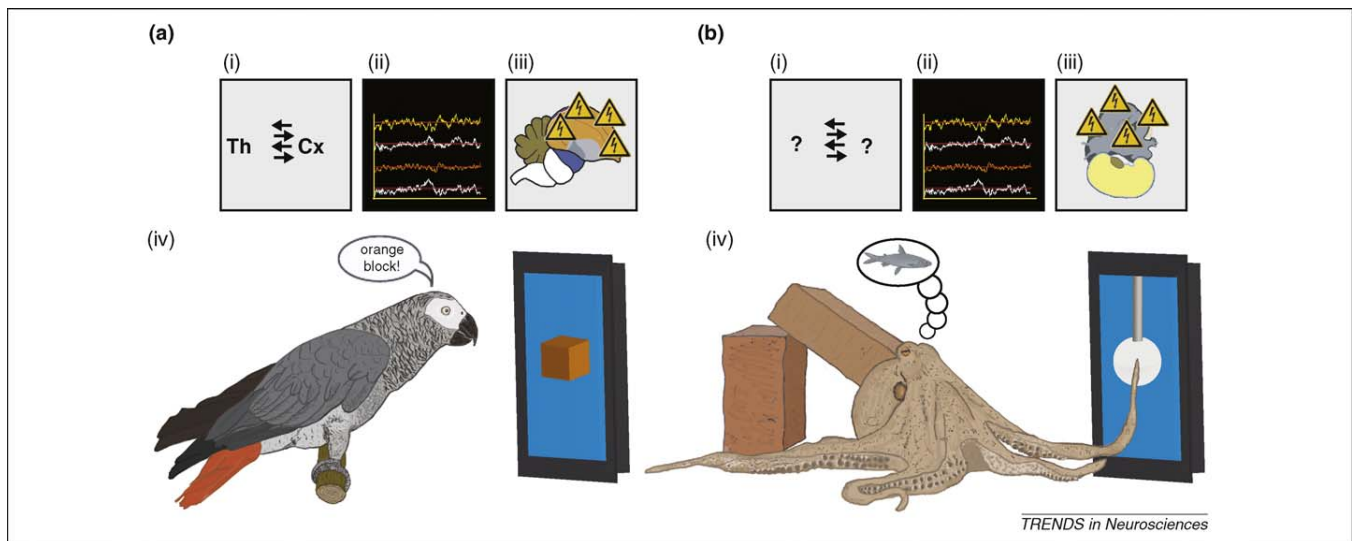


Figure 1. The investigation of possible conscious states in non-human species as disparate as birds (a) and cephalopods (b) can be informed by searching for neural properties that have been correlated with consciousness in humans, including reentrant signaling between thalamus and cortex (a, i) or putative functional analogs (b, i), fast, irregular, low-amplitude EEG signals (a and b, ii), and widespread electrical activity in cortex (a, iii) or functionally analogous structures (b, iii). Such processes in animals can best be related to consciousness when they can be correlated with accurate reports. Relevant forms of report include vocalizations in the case of African grey parrots (a, iv) or coloration and body patterning in the case of cephalopods (b, iv). In the figure, an African grey parrot and a common octopus (*O. vulgaris*) respond to salient artificial stimuli presented on video displays: an orange block in a discrimination task (a, iv) and a white ball that has been previously associated with food (herring) during training (b, iv) (see Box 1).

low-amplitude electroencephalographic (EEG) signals, and widespread cortical activity correlated with conscious contents [5–7]. At the behavioral level, consciousness has been associated with behavioral flexibility [8], rational action [9], and certain forms of conditioning [10]. These can be related to cognitive properties involving widespread access and associativity [8], multiple discriminations [11], and the capacity for accurate report [5]. These properties can be mapped to a variety of functions related to consciousness [12]. At the phenomenal level, human consciousness involves the presence of a sensorimotor scene, the existence of a first-person perspective, the experience of emotions, moods, and a sense of agency [13–14].

Using humans as a benchmark, behavioral, cognitive, and neural properties can be employed as empirical criteria informing the ascription of conscious states to animals (Figure 1). The application of this approach requires that: (i) at least some of these properties reliably occur in both humans and animals; (ii) human brain areas responsible for consciousness can be seen to be integrated with those areas responsible for accurate report of phenomenal experience; and (iii) neural evidence that can be correlated with phenomenal properties of consciousness must in addition *account* for those properties.

In humans, explicit verbal, or linguistic, report of a conscious experience is sometimes taken as a ‘gold standard’ in the sense that it guarantees the presence of consciousness. However, many creatures, including infants, most animals, and aphasic human adults, are constitutively unable to produce linguistic reports. The production of such reports is therefore too limiting a criterion for the ascription of consciousness in general. Importantly, accurate report may exploit behavioral channels other than language, for example lever presses or eye blinks (Box 1). However the ability to provide such report nonetheless implies the presence of higher-order (meta-

cognitive) access to primary conscious contents, which may not be constitutively required for primary consciousness. Our approach therefore recognizes that the mechanisms responsible for primary consciousness may be distinct from those mechanisms enabling its report.

The extent to which neural evidence can account for phenomenal properties is particularly important with respect to those properties that are common to most or all conscious experiences. For example, in humans, every conscious scene is both integrated (i.e. ‘all of a piece’) and differentiated (i.e. composed of many different parts) [11]. Therefore, finding neural processes that themselves exhibit simultaneous integration and differentiation would help to *explain*, and not merely correlate with, the corresponding phenomenal property. Such neural processes can therefore be considered to be ‘*explanatory correlates of consciousness*’ [14], and because they are explanatory, their identification in animals is more suggestive of the presence of corresponding phenomenal properties than is the identification of neural correlates *per se*. In this view, conscious states are neither identical to neural states nor are they computational or functional accompaniments to such states; rather, conscious states are entailed by neural states in much the same way that the spectroscopic response of hemoglobin is entailed by its molecular structure [6].

The presence of voluntary behavioral responses is another candidate ‘gold standard’ for the ascription of consciousness. However, the absence of such responses in humans does not necessarily imply absence of phenomenal experience. For example, in a recent study of a patient in a behaviorally unresponsive vegetative state, brain activity related to volition was taken as persuasive evidence of residual consciousness [15]. Conversely, behavior that appears to be volitional could be attributed widely among animals on the basis of spontaneous and adaptive

Box 1. Metacognition, blindsight, and behavioral report

In seminal experiments by Cowey and Stoerig [84], rhesus macaques with lateralized lesions to the visual area V1 were trained to touch a region of a video display where stimuli appeared. These monkeys could detect and discriminate between stimuli presented within their lesioned hemifields, but they could not distinguish between regions with stimuli presented in these hemifields and regions containing no stimuli presented in their unaffected hemifields. The absence of response in the latter case has been interpreted as a 'metacognitive comment', indicating lack of awareness of the difference between the two hemifields. This could be compared to the responses of human 'blindsight' patients who claim not to see stimuli to which they nonetheless successfully respond. The plausibility of this comparison depends to a degree on the highly conserved neuroanatomy between macaques and humans. When adapted in conjunction with an improved understanding of neural analogs and homologs between mammals and other subphyla, the 'commentary key' paradigm suggested by Cowey and Stoerig [84] provides a valuable experimental platform. For example, 'avian blindsight' might be inducible by lesioning the ectostriatum, the avian brain area analogous to mammalian V1 (Figure 2). Although the optic tracts of many birds are nearly completely decussated (>99%) to opposite hemispheres of the brain, precluding hemifield arrangements analogous to those in monkeys and humans, and the avian brain lacks a corpus callosum, evidence of interhemispheric switching [85] suggests that binocular rivalry might be achieved under appropriate experimental conditions.

Metacognitive comments on the presence or absence of stimuli in occluded hemifields could be made through vocalizations previously entrained to those stimuli.

Similar approaches can be envisaged in cephalopod molluscs if functional analogs to mammalian visual cortex can be discerned (Figure 1). For example, we suggest a version of the 'attentional blink' paradigm, a phenomenon observed when human subjects are presented with a rapid sequence of co-located visual stimuli. A subject will fail to observe a secondary salient target stimulus occurring within this succession if it is presented between 200 and 500 ms after the first stimulus [83]. In an octopus presented with a serial stream of stimuli containing a 'blink' stimulus, the chromatophore system [86,87] or other components of body patterning [88] might provide a channel for experiments to explore similar effects. For example, an octopus could be presented with a serial stream containing an image of an octopus displaying chromatophore patterns associated with aggression in succession with patterns associated with mating display. Variation in responses to the second target, if presented in close temporal proximity to the first, would be suggestive of a 'blink.' Such 'psychophysical' experiments must recognize that cephalopod vision is substantially different from vertebrate vision. Most cephalopod molluscs are color-blind [89], but many are known to perceive polarized light and make subtle discriminations based on this capacity [90,91].

behavioral responses. Therefore, apparent voluntary behavior at best provides a weak criterion for the ascription of consciousness. In addition, conditions such as the vegetative state underscore the point that consciousness should not be confused with arousal or inferred directly from the existence of distinct sleep/wake cycles. States resembling deep sleep have been observed in many animals, including *Drosophila melanogaster* [16] and *Caenorhabditis elegans* [17]; conversely, female killer whales and dolphins and their newborn calves may not sleep for periods of four to six weeks *postpartum* [18].

Mammalian consciousness: extending the benchmark

Mammals, particularly primates, share with humans many neurophysiological and behavioral characteristics relevant to consciousness, and therefore represent a relatively uncontroversial case for the ascription of at least primary consciousness [5]. In a classical example, Logothetis *et al.* trained rhesus macaque monkeys to press a lever to report perceived stimuli in a *binocular rivalry* paradigm [19] (Box 1). Neurons in macaque inferior temporal (IT) cortex showed activity correlated with the reported percept, whereas neurons in the visual area V1 instead responded to the visual signal. This suggests a critical role for IT in visual consciousness. These observations are consistent with evidence from humans subjected to binocular rivalry while being examined via magnetoencephalography (MEG). The results from these studies suggest that consciousness of an object involves widespread coherent synchronous cortical activity [20]. This correspondence between monkeys and humans provides an example of how benchmark comparisons across humans and animal species can be made. With this in mind, we now explore the application of benchmark comparisons to two widely divergent animal subphyla: birds and cephalopod molluscs. We are aware of the pitfalls of making facile comparisons and implying that homologies exist in the absence

of strong evolutionary evidence. In each case, we will present behavioral evidence first, and then present evidence based on neural architecture and dynamics.

Building a case for avian consciousness*Avian cognition and behavioral capabilities*

Feats of avian memory [21,22], tool use and manufacture [23], deception [24], and vocal learning and performance [25,26], the capacity of some species to employ lexical terms in meaningful ways [27], and evidence for higher order discriminations in some birds [27,28], collectively support the functioning of nervous systems as sophisticated as those of most mammals.

Episodic and working memory capabilities are implied by the sophisticated food caching behaviors of corvids (e.g. jays, jackdaws, magpies, rooks, crows, and ravens) [23] and by laboratory-based demonstrations of *transitive inference* and delayed-match-to-sample in pigeons and great tits [29]. African grey parrots, magpies, and ring doves have shown the ability to track periodically hidden and displaced objects; such object constancy certainly requires working memory [30]. In addition, spatial learning, though obviously implied by navigation during flight, has been shown explicitly by hooded crows learning to negotiate a radial maze [31].

Studies of avian tool use and manufacture imply not only elaborate memory and learning substrates, but also the ability to make sophisticated discriminations and to plan behaviors before executing them. For example, New Caledonian crows have been observed to fashion hooked-wire tools to retrieve food from a glass cylinder, sometimes flying to a distant perch to bend the wire before returning to the cylinder [23]. Similarly, wild crows are known to fabricate tools from twigs and leaves in order to extract insects from holes in trees [23]. In addition, a variety of avian species, including Japanese quails [32] and European starlings [33], may be capable of social or observa-

Review

tional learning (but see Zentall [34] and Heyes [35]). Perhaps most notable are instances in which scrub jays re-cached food in private after their initial caching was witnessed by conspecifics [30], and observations of ravens challenging conspecifics that witnessed caching activities while ignoring 'naïve' birds [36]. These behaviors suggest that some birds may be capable of theory of mind.

The avian vocal channel

While the foregoing cognitive capabilities are suggestive of conscious states, the most promising avenue for investigating avian consciousness may involve the study of species capable of vocal learning, which enables a highly flexible form of accurate report. The capacity for some form of vocal learning is shared by at least six animal groups, including cetaceans, bats, parrots, songbirds, hummingbirds, elephants, and possibly even mice and some other rodents [37]. In birds, vocal learning enables sophisticated song learning and production, mimicry of sounds, and, in the psittacines (parrots), word production, comprehension, and naming [27]. For example, African grey parrots were able to name objects, having acquired vocabularies roughly equivalent to those of some language-trained chimpanzees (albeit after years of training and reinforcement) [38]. Indeed, by naming objects in categorization paradigms, these animals appeared to produce accurate reports of sophisticated discriminations they were making. 'Alex', a principal subject of many of these experiments, when presented with an altered array of objects, seemed able to make a judgment to the effect that – 'I know that something in this perceptual scene has changed, and here is what has changed'. This finding suggests an ability to make discriminations about putative primary conscious states that appears to resemble some form of higher order consciousness [27,28].

Avian neural structures and processes homologous to those of mammals suggest possible neural substrates for both consciousness and its report

On what structural bases might avian vocal behavior be related to structures underlying human verbal accurate report? Supporting evidence could come from shared neural mechanisms. One example may be the neural substrate for motor learning in mammals and that for song learning in some birds. Much of the neural basis for song learning in oscines (songbirds) and psittacines resides in an anterior forebrain pathway involving the basal ganglia, in particular, a striatal nucleus called Area X [39] (see Figure 2). The anatomical and physiological properties of neurons in Area X closely resemble those of neurons in the mammalian striatum. Specifically, the four neuronal phenotypes found in mammalian striatum are also present in Area X. A notable difference is the presence of a fifth neural phenotype in Area X – but not in mammalian striatum – that is similar to cells found in the mammalian globus pallidus. Area X may therefore comprise a novel mixture of striatal and pallidal anatomies, but it is nonetheless recognizably homologous to the direct striatopallidothalamic pathway of the mammalian basal ganglia [39]. A similar circuit has been reported in the anterior forebrain of the budgerigar, a parrot [40].

Together, these findings strongly suggest common functional circuitry underlying the organization and sequencing of motor behaviors related to vocalization in birds and mammals capable of vocal learning. However, whether in some birds this circuitry is embedded within a broader network homologous to that underlying human verbal report remains to be determined.

Another avenue for exploring non-mammalian consciousness is to identify structural and functional homologs to mammalian thalamocortical systems. Vertebrate nervous systems follow a highly conserved body plan that emerged with the first chordates more than 500 million years ago. Consequently, many vertebrate neural structures can be traced to common origins in specific embryological tissues. Avian homologs of subcortical structures, such as the hypothalamus and pre-optic area, are relatively easy to recognize. Although the identity of the avian neural homolog of mammalian isocortex remains controversial [41,42], comparative embryological studies suggest that the basic underlying neuronal composition and circuitry of the mammalian cortex were established within clustered arrangements of nuclei long before the appearance of the distinct six-layered mammalian cortex [43]. In particular, the nuclei comprising the dorsal ventricular ridge (DVR) of the developing avian brain contain neuronal populations homologous to those present in different layers of the mammalian neocortex. These include neurons receiving thalamic input, as well as cells projecting to brainstem and spinal cord neurons. The neurons of the avian DVR and mammalian cortex are nearly identical in both their morphology and constituent physiological properties [44].

Structural homologies can also be identified using molecular and immunohistological techniques. In particular, neurotransmitters, neuropeptides, and receptors specific to particular neuronal populations within mammalian brain regions have been localized to homologous avian brain regions. For example, both AMPA receptor subunits and the pallidal neuron/striatal interneuron marker Lys8-Asn9-neurotensin8–13 (LANT6) are found in the neurons of both mammalian and avian basal ganglia [45,46]. Finally, gene expression patterns similar to those of mammals have been identified in the avian brain. For example, a comparison of homeotic genes involved in early brain development in chick and mouse embryos has revealed robust structural homologies between parts of the avian telencephalon and mammalian cortex [47].

Deep avian–mammalian homologies have also been revealed by examining functional properties of neuronal populations within particular brain regions. The avian anterior forebrain pathway may be functionally analogous to the mammalian cortico-basal ganglia-thalamocortical. This is suggested by the presence of both inhibitory and excitatory pathways in the medial nucleus of the avian dorsolateral thalamus (DLM), as well as by functional similarities between neurons in the DLM and mammalian thalamocortical neurons. Similarities have also been found among the excitatory and inhibitory circuitry of birds and mammals, particularly in the serotonergic, GABAergic, and dopaminergic systems [48].

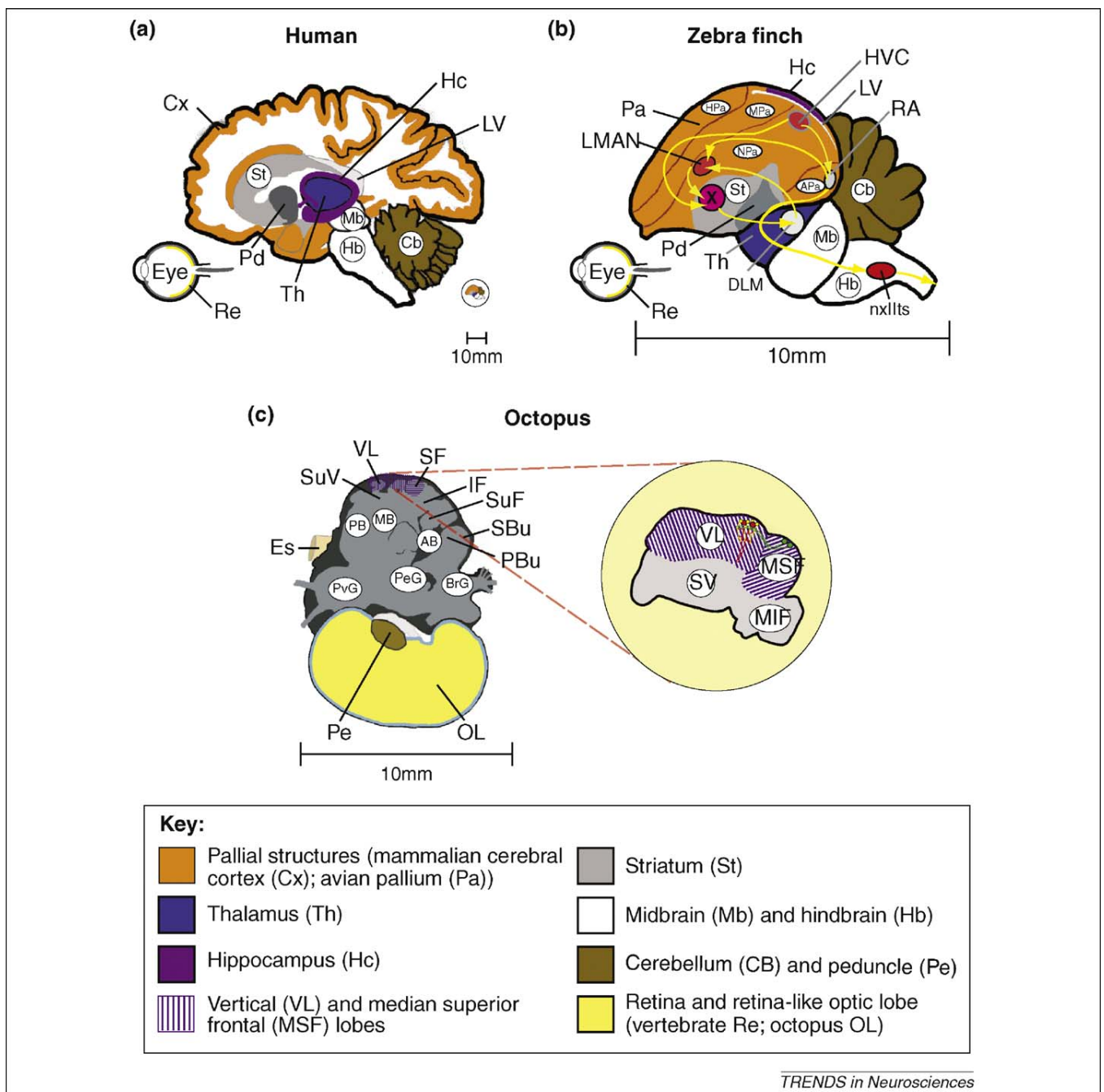


Figure 2. Avian and mammalian brains contain homologous structures and similar functional circuitry; the complex nervous systems of coleoid cephalopods may exhibit some functional circuitry analogous to those of higher vertebrates. **(a)** Midline sagittal section of a human brain showing major structures, including those involved in generating conscious states (e.g. cortex, thalamus, and basal ganglia). **(b)** Midline sagittal section of the brain of a zebra finch, a songbird. Major neural structures are shown, including those with mammalian homologs. Also shown is a greatly simplified schematic of the anterior forebrain pathway for song learning (yellow arrows) involving components of the basal ganglia, including the striatal nucleus Area X ('X' in filled red circle). The circular inset to right of human brain shows zebra finch brain to scale for comparison. **(c)** Midline section of the brain of an octopus (*O. vulgaris*). Most major lobes and ganglia are shown. Vertical (VL) and median superior frontal (MSF) lobes (purple hatched lines), containing circuitry critical for long-term memory, are shown in a magnified view in circular inset on right. The key (bottom of figure) shows color-coding of major brain regions to indicate homology or functional and/or structural analogy. Other regions of human and avian brains are labeled: LV, lateral ventricle; Pd, pallidum. Pallial divisions of the avian cerebrum are indicated as follows: HPa, hyperpallium; MPa, mesopallium; NPa, nidopallium. Components of the avian anterior forebrain pathway are indicated as follows: DLM, medial nucleus of the dorsolateral thalamus; HVC, higher vocal center; LMAN, lateral magnocellular nucleus of the anterior neostriatum; nxlts, tracheosyringeal portion of hypoglossal nucleus; RA, robust nucleus of the archistriatum. Major lobes and ganglia of the octopus brain are indicated as follows: AB, anterior basal lobe; BrG, brachial ganglia; Es, esophagus; IF, inferior frontal lobe; MB, median basal lobe; MIF, medial inferior frontal lobe; PBu, posterior buccal lobe; Pe, peduncle; PeG, pedal ganglia; PB, posterior basal lobe; PVG, palliovisceral ganglia; SuV, subvertical lobe; SBU, superior buccal lobe; SF, superior frontal lobe; SuF, subfrontal lobe. Scale bars are shown at the bottom of each brain section.

In addition to neuroanatomy, electrophysiological studies are critical in establishing functional homologies between avian and mammalian nervous systems. Currently, however, common properties of mammalian thalamocor-

tical neurons, such as low-threshold calcium (Ca^{2+}) spikes and slow oscillations, have not yet been found in birds [49]. Nonetheless, similarities between the waking EEG patterns of birds and mammals, as well as slow wave electrical

activity recorded during avian sleep [50], are suggestive of neural dynamics that might support conscious states in birds.

The existence in birds of structural and functional homologies to mammalian thalamocortical systems is certainly consistent with the presence of higher cognitive faculties and perhaps consciousness [30,51]. Nevertheless, a compelling case for avian consciousness cannot be made solely on the strength of relevant neuroanatomical and neurophysiological resemblances. Nor are descriptions of avian behaviors that imply sophisticated cognitive capabilities sufficient to make such a case. New experimental strategies are needed for the evaluation of possible conscious discriminations in awake, behaving birds. The findings obtained from studies of Alex the African grey parrot encourage the development of such strategies. Even more challenging though are approaches to investigating conscious behavior in invertebrates.

Searching for consciousness in invertebrates: The cephalopod case

The richness of cephalopod behavioral repertoires

In addition to possessing large brains, cephalopod molluscs have extremely flexible behavior and highly developed attentional and memory capacities that may be suggestive of conscious states [52]. The performance of some cephalopods (particularly *Octopus vulgaris*) in several learning and memory paradigms (e.g. flexibility, persistence of memory traces, contextual learning) [53] is formidable, and comparable in sophistication to that of some vertebrates. Octopuses can make discriminations between different objects based on size, shape, and intensity [54,55], classifying differently shaped objects in the same manner as vertebrates ranging from goldfish to rats [55]. Octopuses are also capable of finding the correct path to a reward in a plexiglas maze and can retrieve objects from a clear bottle sealed with a plug [56,57]. In another striking study, 'naïve,' or 'observer,' octopuses watched conditioned

animals ('demonstrators') choose between two simultaneously presented objects that differed in contrast only; the observer octopuses later made the same contrast choices in isolation and without any explicit conditioning [58]. Although controversial [59–62], this finding suggests that octopuses are capable of observational learning, a faculty previously thought to be unique to highly social animals.

Finally, distinct capacities for short- and long-term memory have been shown in both the octopus and the cuttlefish [53,63]. In a maze containing obstacles that were changed *ad libitum*, octopuses could remember these changes and adjust their movements accordingly. Interestingly, the octopuses in this study appeared to pause and deliberate about the layout of the maze before proceeding [64].

Cephalopod brains: complex nervous systems distant from the vertebrate line

The organization of invertebrate nervous systems diverges so greatly from those of vertebrates such as birds and mammals that, until recently, sophisticated cognitive capabilities had rarely been ascribed to invertebrate species (see Figure 2). Bees [65,66], spiders [67,68], and the cephalopod molluscs [52] are notable exceptions.

Of all cephalopod molluscs, the octopus has the largest population of sensory receptors. These receptors communicate with a nervous system that, in adults, may contain between 170 million and 500 million cells, most of which are neurons [69,70]. In the brain of one genus of squid, *Loligo*, at least 30 distinct nucleus-like lobes have been identified [71]. The optic lobe, the largest of the fused central ganglia, contains as many as 65 million neurons. In addition to processing visual input, the optic lobe plays a critical role in higher motor control and the establishment of memory [69]. A number of other lobes may be functionally equivalent to vertebrate forebrain structures [69], though their organization bears little resemblance to the

Box 2. Animal selves

Animal selfhood can be conceived at many levels. A primitive or 'core' self may depend on self-modeling processes that use sensorimotor predictions to guide behavior leading to the emergence of a 'point-of-view' [13]. Core selfhood may arise from the complexity of the sensorimotor coordination and proprioception needed to support adaptive behavior [77]. It may also depend on 'feelings' or emotional states mediated by interoceptive representations of bodily states [92,93] related to homeostatic control of low-level drives for (at least) air, water, food, and pain avoidance [94,95].

Advanced selfhood involves the emergence of the subjective 'I' of higher order consciousness, and, in its most elaborated form, the ability to understand the world from the perspective of another. Basic requisites for a subjective 'I' are suggested by 'mirror self-recognition' (MSR) experiments, in which, for example, animals spontaneously use a mirror to examine an otherwise inaccessible body region [96]. MSR has been demonstrated in primates, including chimpanzees, orangutans, and (less conclusively) gorillas [96,97]; evidence suggestive of MSR has also been elicited from Asian elephants [98], dolphins [99], and magpies [100]. Even in chimpanzees, however, the prevalence of MSR behavior is only about 75% [101].

Even though animals lacking higher order consciousness cannot construct a subjective 'I,' taking humans as a benchmark suggests new experimental approaches. For example, combining virtual reality with tactile feedback can lead to a displacement of the first person

perspective to a place outside the physical body, similar to spontaneous 'out-of-body' experiences [102]. This displacement, possibly due to a disruption of self-modeling, can be validated both by accurate report (e.g. 'I see myself from behind'), and by indirect behavioral evidence (e.g. subjects move in directions reflecting their perceived location). Similar results obtained from animals would suggest that they, too, possess a body-centered locus of experience.

Recent neuroimaging results have exposed new self-related neural processes in humans that may prompt similar searches in animals. Activity in the human 'default network' is correlated with stimulus-independent thought and self-related conscious content [103], and is anti-correlated with sensitivity to external somatosensory stimuli [104]. The right insular cortex appears important for self-consciousness [105], with anterior subregions possibly supporting explicit representations of feeling states underlying higher-order self-representations [92]. Hypoactivation of insula has been reported in humans with 'depersonalization disorder,' involving reduced subjective validity of the self [106]. Identification of animal analogs to these processes would require demonstration of very close homologies so far not achieved. Indeed, the thalamocortical pathway conveying interoceptive signals to the right anterior insula appears to be unique to primates [92], suggesting important species-specific differences as well as commonalities to be kept in mind when considering animal consciousness.

laminar sheets of mammalian cortex. In particular, the vertical, superior frontal, and inferior frontal lobes of octopus, squid, and cuttlefish are involved in memory consolidation [63,72,73]. In experiments in which the vertical lobe of *Octopus vulgaris* was lesioned, the ability to learn visual discriminations was severely impaired, but long-term memory consolidation remained intact [63]. Removal of the median inferior frontal lobe caused memory deficits that compromised learning [54,74]. Taken together, these studies suggest that some regions of the octopus frontal and vertical lobes are functionally comparable to regions of mammalian cortex (see Young [75] for a review).

Radical differences between cephalopod nervous systems and those of vertebrates are exemplified by the parallel, distributed architecture of the octopus locomotor system. The number of neurons in the tentacles of the octopus collectively exceeds the total number in the central fused ganglia of the brain itself [70]. A detached octopus arm will ail in a realistic manner when stimulated with short electrical pulses [76], suggesting pseudoautonomous control of some locomotor behavior patterns and hinting at a sophistication of sensorimotor coordination rivaling that of many vertebrates. This elaborate bodily representation in the service of sensorimotor coordination for adaptive behavior (e.g. locomotion, camouflage, mimicry) might support a 'core selfhood' [77] (see Box 2), a tantalizing concept as applied to cephalopods.

With regard to neuropharmacological and physiological properties, the cephalopod nervous system contains many of the major neurotransmitters that are found in mammalian brains [69,78]. In particular, the presence of dopamine (DA), noradrenaline (NA), and serotonin (5-HT) receptor subtypes that resemble those found in vertebrates may reflect the presence of circuitry similar to vertebrate excitatory and inhibitory pathways. As is the case with functional avian neuroanatomy, application of immunohistochemical and genetic techniques may help to determine the cephalopod functional analogs to neural regions in mammals that show correlated activity during conscious behavior. An encouraging indication is the recent identification of a cephalopod ortholog to the *Foxp2* gene, which in birds and humans has been implicated in motor function related to song and language production, respectively. Notably, *Foxp2* expression has been observed in the adult octopus chromatophore lobes [79].

What can be said of neurodynamics in cephalopod brains? Examination of octopus vertical lobe slices has identified long-term potentiation (LTP) of glutamatergic synaptic field potentials similar to those found in vertebrates [80]. More directly related to possible conscious states, electrophysiological studies have identified EEG patterns, including event related potentials, which resemble those of awake vertebrates, and at the same time are distinct from those recorded in other invertebrates [81,82]. Identifying cephalopod EEG patterns that reflect low amplitude fast irregular activity similar to that observed during human conscious states will require determination of suitable recording sites. Optic, vertical, and superior lobes of the octopus brain – all of which are critical to learning and memory – are relevant candidates.

The similarities discussed above by no means confirm the existence of conscious states in cephalopod molluscs, but neither do they exclude them. An intermediate effort to clarify the situation might be the pursuit of psychophysics in cephalopods, an approach not yet represented in the literature (see Box 1).

Concluding remarks

Approaches to animal consciousness require both clear theoretical frameworks and relevant experimental evidence. We have suggested that a useful approach is to synthesize neuroanatomical, neurophysiological, and behavioral evidence, using humans as a benchmark. We recognize that a distinction between primary and higher-order consciousness implies that mechanisms underlying putative primary conscious states might be distinct from, though possibly overlapping with, mechanisms allowing its accurate report, such that absence of evidence need not be evidence of absence in regard to animal consciousness.

Within this framework we find that birds exhibit rich cognitive and behavioral capabilities consistent with conscious states, including working memory, social learning, planning, and possibly even insight during problem solving. These capabilities are complemented by substantial anatomical homologies and functional similarities with mammals in the thalamocortical systems that are associated with consciousness. The case for cephalopod molluscs is currently much less clear. However, abundant evidence of sophisticated learning and memory faculties and rich behaviors, as well as early indications from studies of cephalopod neurophysiology, suggest at least the possibility of conscious states.

Given the profound gaps that remain in the neuroanatomical characterization of both subphyla, many basic questions remain concerning the existence, form, and prevalence of non-mammalian consciousness (see Box 3). Future progress in addressing these questions will require elaboration of behavioral paradigms designed to assess complex discriminatory behavior associated with consciousness. Vocal learning in birds provides a particularly promising avenue for achieving this objective (Box 1). In all cases, theoretical developments are necessary to facilitate the transition from correlation to causal explanation [14]. Such a transition will allow attribution of animal consciousness to be based causally on neural properties rather than on indirect behavioral report. Finally, we note that work on animal consciousness may help in assessing

Box 3. Outstanding questions

- How can we distinguish the neural mechanisms underlying accurate report from those underlying primary consciousness?
- Can degrees of consciousness be established among different species?
- What invertebrate neural structures and mechanisms may be analogous in function to mammalian thalamocortical systems?
- What function does consciousness serve in adaptive behavior?
- When did consciousness appear in the course of evolution?
- How might a synthetic approach facilitate the study of consciousness in other phyla (i.e. reptiles, amphibians, and bony and cartilaginous fish)?
- What ethical implications would emerge if convincing evidence is obtained for widespread animal consciousness?

consciousness in humans incapable of report, including infants and patients in vegetative and minimally conscious states.

Acknowledgements

We are grateful to Drs. Graziano Fiorito, Joseph Gally, and Michael Beaton for their critical reading of the manuscript. We also thank Dr. Fiorito and Dr. Erich Jarvis for generously providing material used to design the cartoons of octopus and avian nervous systems, respectively, presented in Figure 2. Finally, we are indebted to Dr. Heidi Junger for her keen insights and assistance in the design of both figures. The work of D.B.E. is supported in part by DARPA (ONR Grant N00014-08-1-0728) and by the Neurosciences Research Foundation. A.K.S. is supported by EPSRC Leadership Fellowship EP/G007543/1.

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