Identifying hallmarks of consciousness in non-mammalian species

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Abstract

Most early studies of consciousness have focused on human subjects. This is understandable, given that humans are capable of reporting accurately the events they experience through language or by way of other kinds of voluntary response. As researchers turn their attention to other animals, ''accurate report'' methodologies become increasingly difficult to apply. Alternative strategies for amassing evidence for consciousness in non-human species include searching for evolutionary homologies in anatomical substrates and measurement of physiological correlates of conscious states. In addition, creative means must be developed for eliciting behaviors consistent with consciousness. In this paper, we explore whether necessary conditions for consciousness can be established for species as disparate as birds and cephalopods. We conclude that a strong case can be made for avian species and that the case for cephalopods remains open. Nonetheless, a consistent effort should yield new means for interpreting animal behavior.
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Keywords: Accurate report; Behavior; Birds; Cephalopods; Consciousness; Neuroanatomy; Neurophysiology; Octopus

1. Introduction

A scientific analysis of consciousness in non-human animals must confront a number of difficult challenges. The most obvious of these has to do with privacy and first person report. In the ab-

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sence of accurate, first person report, what criteria can be used to suggest that the necessary conditions for consciousness have emerged? Another concerns the evolution of consciousness. Is consciousness the result of natural selection and gradual emergence of various related functions?

One approach to these questions is to use evidence on the basis of human consciousness as a reference and a benchmark. Such evidence comes from humans reporting their conscious states in a wide variety of experimental paradigms, often involving non-invasive imaging techniques. For example, binocular rivalry has been examined in humans during magnetoencephalography (MEG) and definite changes in brain activity have been observed when consciousness of an object was reported (Srinivasan, Russell, Edelman, & Tononi, 1999). In general, these results implicate the thalamocortical system in the generation of conscious states. In addition, evidence from strokes and destruction of brain regions has indicated that structures such as the thalamocortical circuit and the mesencephalic reticular formation provide a necessary structural basis for consciousness. A search for homologous structures in other species and corresponding behavioral evidence is obviously warranted.

Such an anatomical benchmark, when considered in conjunction with neurophysiological recordings during rich discriminatory behavior, might, even in the absence of report, suggest the presence of conscious states in primates and other mammals. For example, a binocular rivalry paradigm—similar to that described above—has been used in monkeys. Monkeys were presented with rivalrous and non-rivalrous stimuli, and, during rivalry, the majority of neurons (>90%) recorded in the inferotemporal cortex (IT) fired in response to the perceived stimulus (the monkeys were trained to report the stimuli they perceived by pulling a lever). Conversely, these IT neurons were not responsive to the non-perceived stimulus (Logothetis, 1998). The results of this study are at least consistent with the proposal that the monkeys were conscious of certain visual stimuli.

A theoretical proposal to account for the properties and evolution of consciousness has been developed over several decades (Edelman, 1987, 1988, 1989, 2004; Seth & Baars, in press; Tononi & Edelman, 1998;). A key feature of this proposal is that consciousness in mammalian species emerged when reentrant connectivity evolved between brain areas for perception and those involved in memory. In humans, evidence for such reentry has been shown using MEG (Srinivasan et al., 1999). This proposal also distinguishes two varieties of consciousness: primary consciousness, in which percepts are united into episodic scenes, each of which is of a piece; and higher-order consciousness, which involves self awareness, the ability to reconstruct past scenes and formulate future scenes, and in humans the ability to represent both internal state and external world symbolically through language or other means (Edelman, 1989).

In this paper, we explore the possibility of primary consciousness in two disparate vertebrate and non-vertebrate non-mammalian species: birds and octopuses.[1] We explicitly avoid issues related to first person report and higher-order consciousness, except in a few instances where the evidence can be stringently assessed. While many attempts to assay animal consciousness and cognition rest almost entirely upon ethological evidence (Griffin, 1976; Griffin & Speck, 2004), we look beyond behavior to neuroanatomy and neurophysiology. We argue that the necessary conditions for primary consciousness in non-mammalian species must include the following: (1) iden-

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[1] We note that the issue of possible evolutionary prerequisites of consciousness (e.g., selective attention, learning, and perceptual categorization) in another group of invertebrates, the insects, has been taken up elsewhere (Griffin & Speck, 2004; Seeley, 1998; Wilcox & Jackson, 1998).

tification of neural structures that are the functional equivalents of cortex and thalamus; (2) neural dynamics analogous to those observed in mammals during conscious states;[2] and (3) rich discriminatory behavior that suggests a recursive linkage between perceptual states and memory (Edelman, 1987, 1989).

Sufficient conditions for consciousness are difficult to establish. By focusing on necessary conditions, our review strongly suggests that birds are excellent candidates for deeper experimental investigations into the possibility that their brains might give rise to conscious states. We use the octopus as a kind of counter example, given the fact that the cephalopod nervous system and phenotype have no resemblance at the systems level to those of humans or birds. However, it remains a fascinating speculation that consciousness of one form or another could have emerged in creatures such as octopuses, which exhibit rich behavior and discriminatory capacity, and possess complex nervous systems.

2. Avian species: Rich behavior, candidate anatomy, and physiology

2.1. Behavior

Avian species exhibit a broad range of behaviors, from simple nest-building in swallows (Winkler & Sheldon, 1993) to the fabrication and use of tools by New Caledonian crows (Hunt, 1996; Weir, Chappell, & Kacelnik, 2002); from caching of food in a hundred or more sites involving complex spatial memory capacity (Sherry & Duff, 1996) to epic migrations of thousands of miles (Lincoln, Peterson, & Zimmerman, 1998); from sophisticated song learning, song production, and mimicry—with extraordinary fidelity—of natural and artificial sounds (McCasland, 1987) to word comprehension (albeit limited), production, and naming (Pepperberg & Shive, 2001; Pepperberg & Wilcox, 2000). Underlying this last series of behaviors is the capacity for vocal learning; a capability shared by only six animal groups: humans, cetaceans, bats, parrots, songbirds, and hummingbirds (Jarvis et al., 2000).

The capacity for vocal learning in the three groups of birds might provide leverage to test for avian conscious states. In particular, song production in song birds might act as a channel for something like accurate report, given an appropriately designed experiment. As a model for such an experiment, consider the study of "blindsight" in *Rhesus macaques* by Cowey and Stoerig (1995; see also the discussion in Seth, Baars, and Edelman, this issue). Monkeys with lesions to one-half of the striate cortex (V1) could learn to detect visual stimuli, and make discriminations across such stimuli, when these stimuli were presented in the visual hemifields that had been rendered "cortically blind" (i.e., those hemifields contralateral to the lesioned half of V1). In these trials, the monkeys were trained to touch the region of a video screen where stimuli appeared. However, the monkeys were not able to distinguish between stimuli in the cortically blind hemifield and blank displays in the unimpaired hemifield, a result which can be interpreted as a report by the monkey that it could not perceive any difference between the two hemifields. Finally, when

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[2] Bullock (1993, 2003) has noted the lack of comparative physiological studies that address the evolution of complex neural dynamics.

all stimuli were located in the unimpaired hemifield, the monkeys were able to make both types of discrimination with few errors. It is possible that birds trained to vocalize to a particular stimulus could be lesioned in a similar fashion and tested in a similar way.[3]

In addition to lesion experiments, one might employ an electrophysiological paradigm similar to that used by Logothetis (1998) on behaving monkeys. Logothetis found that the majority of neurons in the monkey IT fired in response to the percept (as defined by a behavioral report), while neurons in V1 responded to the signal (Logothetis, 1998). The question arises whether similar results might be obtained when ambiguous stimuli are presented to birds. Such experiments would of course require the identification of neurons in the avian brain analogous to those in the mammalian striate cortex.

One might more easily assay necessary conditions for consciousness if the test subject is a parrot capable of reproducing human speech. Indeed, some of the most impressive demonstrations of complex avian behavior have come from the laboratories of cognitive psychologists studying avian problem-solving abilities and symbolic capacity. Pepperberg and her colleagues (Pepperberg & Shive, 2001; Pepperberg & Wilcox, 2000) have shown that African grey parrots are capable of performing naming tasks after acquiring vocabularies equivalent to those of some of the chimpanzees employed in language-training projects. These chimpanzees had learned up to a couple of hundred lexical terms after many years of rigorous training and reinforcement (Gardner & Gardner, 1969; Premack & Woodruff, 1978; Premack & Premack, 1984).[4]

Although the concept of accurate report in humans or something analogous in monkeys (Cowey & Stoerig, 1995; Logothetis, 1998) was not explicitly mentioned in studies demonstrating categorization and naming of objects by parrots (Pepperberg & Wilcox, 2000; Pepperberg & Shive, 2001), the subjects of these studies seemed able to produce something very much like reports of the discriminations that they made; sufficiently rich object naming can be considered a form of accurate report.

Pepperberg has in fact suggested that parrots may possess primary consciousness; what she has referred to as "perceptual consciousness" (Pepperberg, 1998). Moreover, the fact that Pepperberg's parrot, Alex, seems to be able to make a judgement to the effect that, "I know that something in this perceptual scene has changed, and here is what has changed," when presented with an altered array of objects (Pepperberg & Wilcox, 2000; Pepperberg & Shive, 2001) seems to demonstrate the ability to make discriminations about discriminations. Such an ability may be considered a feature of higher-order consciousness that complements primary consciousness (Seth, Baars, & Edelman, in press). Indeed, this kind of meta-cognition has been taken by some authors to be the royal road to identifying animal consciousness (Smith, Shields, & Washburn, 2003).

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[3] Lesioning the ectostriatum (the avian brain area analogous to V1 in the mammalian tectofugal pathway; see Nguyen et al., 2004), might disrupt early visual processing in birds. We note also that avian optic tracts are nearly completely decussated (>99%) to opposite hemispheres of the brain, and thus birds do not have the same type of hemifield arrangement as monkeys and humans (Güntürkün, 2003).

[4] The most impressive non-human symbolic capacity so far has been shown in captive pygmy chimpanzees (bonobos) by Savage-Rumbaugh. One individual, Kanzi, acquired several hundred lexical terms and responded to requests or queries through the use of a keyboard containing arbitrary symbols (Savage-Rumbaugh, Rumbaugh, & McDonald, 1985, 1986).

2.2. Anatomy

The overall organization of the vertebrate central nervous system, like that of other organ systems and tissues reflects a highly conserved body plan that emerged early in the history of the chordates, perhaps 520 million years ago (Smith, 1999). Developmentally, many brain structures in lower vertebrates (i.e., reptiles and lizards), birds, and mammals can be traced to common origins in specific embryological tissues. Identifying likely structural homologies across different classes and orders is often not a problem. For example, comparative studies of non-mammalian vertebrate auditory and visual pathways at the level of both constituent cell populations and tissues led Karten (1997) to propose that the sensory systems of all amniotes are similarly organized. In fact, the work of Karten (1991, 1997) and others (Kuan, Elliot, Flavell, & Rakic, 1997; Medina & Reiner, 2000; Nguyen et al., 2004) strongly suggests that much of the neuronal properties and circuitry that underlie the mammalian cortex were in place within nucleated or clustered arrangements long before the evolutionary appearance of the distinct six-layered mammalian cortical mantle. Additionally, the somatomotor circuitry within the avian dorsal pallium appears to be homologous to the mammalian basal ganglia–cortico–thalamic loop (Medina & Reiner, 2000). Interestingly though, the lamination of the avian wulst[5] does not appear to be homologous to the layered organization of the mammalian cortex (Medina & Reiner, 2000). Moreover, the identification of avian homologues to structures such as mammalian isocortex remains contentious (see Aboitiz, 1999a & 1999b and Faries, 2004 for reviews of the subject). Nevertheless, it is clear that data from comparative developmental molecular and histological studies will soon resolve such outstanding issues.

Although it is uncertain when consciousness first emerged in the vertebrate line, it is plausible that it appeared independently at least twice, sometime after the divergence, 300 million years ago, of the *anapsid* and *synapsid* reptilian lines that led to birds and mammals, respectively (Kardong, 1995) (see Fig. 1). While it remains unclear whether any reptile, extant or extinct, is, or was, capable of conscious awareness, the divergence of vertebrates leading to mammalian and avian species is suggestive if evidence can be accumulated to support homologous structures or similar analogous arrangements in birds.

From a gross anatomical perspective, avian brains are distinguished from those of mammals by the division of the telencephalon into structures resembling nuclei which lack the laminated cortical mantle characteristic of mammalian brains. Additionally, the avian optic tectum and cerebellum are more elaborated than their mammalian homologues. Regions that presumably serve more basal functions, such as the hypothalamus and pre-optic area, are relatively easy to recognize. Other regions, such as the amygdala and hippocampus, are not so easily identified through visible structural homologies. However, new techniques exist which hold the promise of allowing the identification of deeper homologies that may not be apparent from examination of gross structure. For example, it has been proposed that the avian anterior forebrain pathway is functionally analogous to the mammalian corticobasal ganglia–thalamocortical loop (Luo, Ding, & Perkel, 2001). This claim is supported both by observations that the medial nucleus of the avian dorsolateral thalamus (DLM) contains inhibitory, as well as excitatory, pathways and that neurons in

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[5] A portion of the avian telencephalon believed to be functionally analogous to mammalian isocortex is referred to in some publications as the Wulst; other studies refer to this area as a division of the hyperstriatum (Karten, Hodos, Nauta, & Revsin, 1973; Medina & Reiner, 2000).
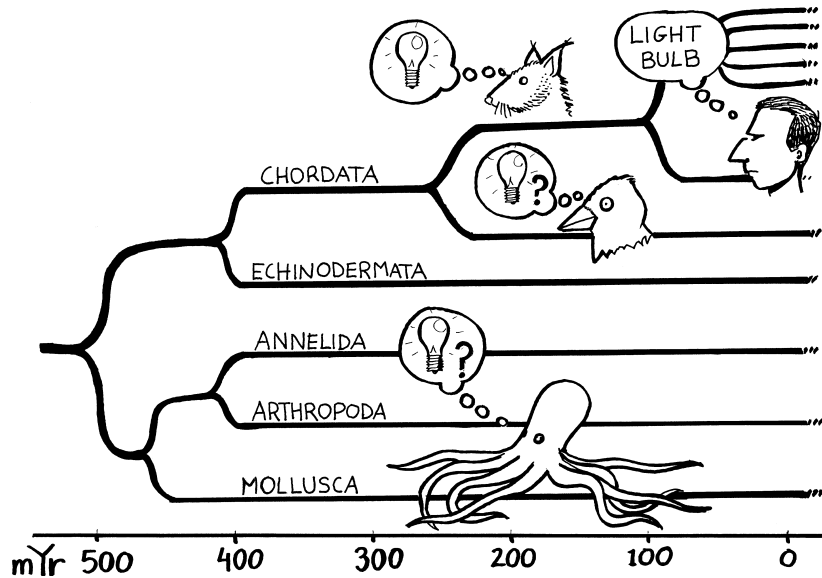
Fig. 1. The phylogeny of consciousness. Primary consciousness probably appeared early in the mammalian radiation; it is widely acknowledged to be present in members of the order Primates. Neuroanatomical, physiological, and behavioral data suggest that consciousness may have also emerged independently in the avian lineage. On the basis of rich behavioral repertoires and complex nervous systems, we suggest that the possibility of conscious states warrants future investigation in members of the *cephalapoda*, an invertebrate group that includes the octopus. Higher order consciousness, which emerged as a concomitant of language, occurs in modern *Homo sapiens* and may or may not be unique to our species.

the DLM exhibit functional properties similar to those of thalamocortical neurons (Luo & Perkel, 1999, 2002). However, the electrophysiological studies of mammals which have identified common properties of thalamocortical neurons, such as low-threshold Ca^{2+} spikes and slow oscillations (McCormick & Huguenard, 1992), have not yet been adequately reproduced in birds.

In some instances, identification of certain regions of the avian brain can be accomplished through molecular or histological means; that is, by identifying functional molecular markers such as neurotransmitters, neuropeptides, and receptors that are specific to certain cells known to reside in particular regions of the mammalian brain (Naftolin, Horvath, & Balthazart, 2001; Wada, Hagiwara, & Jarvis, 2001). Comparison of the expression patterns in chick and mouse embryos of certain homeotic genes critical to brain development has yielded evidence of structural homology between parts of avian telencephalon and mammalian cortex (Medina & Reiner, 2000). In a number of instances, the conservation of certain evolutionarily ancient vertebrate neurochemical systems has also enabled researchers to use immunohistochemical techniques to identify regions of the avian brain that are homologous to known mammalian neural structures. For example, avian brain structures corresponding to regions of the mammalian limbic system were identified by in situ binding[6] of an antibody to the steroid metabolizing enzyme estrogen synthe-

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[6] Immunohistochemistry is a technique in which an antibody to a protein that is uniquely expressed in cells of a particular structure is used to label that structure.

tase (aromatase), which in mammals is specific to certain cells in the limbic system (Naftolin et al., 2001).[7]

In another instance, cloning portions of cDNAs[8] of known mammalian glutamate receptors led to the identification of a large number of these receptors that are also expressed in songbirds. In situ hybridizations in mouse and zebra finch brains using probes based on these cDNA clones revealed that the expression of glutamate receptors in cerebellar, midbrain, and thalamic expression is highly conserved; basal ganglia and pallial patterns also exhibited a high degree of conservation. The authors of this study, noting that structural topological differences have prompted some to relegate avian brains to a lower functional status, suggest instead that avian and mammalian brains evolved in parallel to become functionally similar (Wada et al., 2001). Additionally, the appearance of novel brain functions can be correlated with the occurrence of certain genomic changes over the course of evolution, such as exon duplications[9] in pre-existing regionally expressed neural genes (Alvarez & Sutcliffe, 2002). Indeed, from neurochemical and underlying genetic perspectives, lower vertebrates, birds, and mammals all exhibit certain homologous excitatory and inhibitory systems, including the serotonergic (Jacobs & Azmitia, 1992) and GABAergic (Anadon, Adrio, & Rodriguez-Moldes, 1998; Brandon, 1985; Mann & Enna, 1980; Seiler, 1980) systems, and, in the case of birds and mammals, the dopaminergic system (Durstewitz, Kröner, & Güntürkün, 1999). The evidence suggests that there is very robust conservation of structure, a conclusion that is easily lost if one confines oneself to gross anatomical and histological studies alone.

Certain of these techniques may extend to regions for which structural homologues are difficult to identify. For example, structures such as the amygdala and hippocampus have been discerned in non-mammalian vertebrates as disparate as lampreys, goldfish, and birds through a number of methodologies, including the integration of comparative embryological data into parsimony-based phylogenetic analyses (Striedter, 1997), lesioning and behavioral response experiments (Portavella, Torres, & Salas, 2004), and comparative studies of gene expression patterns during development (Puelles, 2001; Puelles et al., 2000). Comparative histological studies have demonstrated that the primordium which gives rise to the hippocampus in mammals also exists in the developing lamprey, implying a very ancient origin (Rovainen, 1979; Polenova & Vesselkin, 1993). Indeed, comparative studies of gene expression have shown that most of the major domains of the vertebrate brain were present in the earliest vertebrate ancestor (Murakami et al., 2001; Niedert, Virupannavar, Hooker, & Langeland, 2001; Shimeld & Holland, 2000).

Taken together, the foregoing make it increasingly likely that a potent combination of immunohistological techniques applied to fixed brain tissue and reporter gene-based labeling applied in vivo will enable researchers to relate much of avian neuroanatomy to well-characterized regions of the mammalian brain. This will be absolutely critical for locating and recording from structures that might interact in the same manner as cortex and thalamus in mammals during the conscious state.

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[7] Estrogen synthetase is a known marker for a [small] population of cells in the limbic system.

[8] cDNA is complementary to messenger RNA (mRNA) and is translated into the constituent amino acids of a given protein.

[9] Exons, the protein coding regions of genes, have been duplicated frequently within the genes of many organisms over the course of evolution.

2.3. Physiology

In addition to identifying anatomical structures in avian brains that are analogous or homologous to the mammalian cortex and thalamus, it is critical to look for correlates of neurophysiological signatures of the mammalian conscious state. One such signature would be patterns of electrical activity that reflect "...widespread, relatively fast, low-amplitude interactions...driven by current tasks and conditions" (Seth et al., 2004, p. 5). In this context, it is suggestive that waking avian EEG patterns resemble those of awake mammals. Moreover, slow wave electrical activity is present during sleep as well, although the overall avian EEG pattern during sleep is markedly different than that of mammals (Ayala-Guerrero, 1989; Ayala-Guerrero & Vasconcelos-Duenas, 1988; Karmanova & Churnosov, 1973).

From the above observations, one may tentatively conclude that at least some of the necessary substrates and conditions for primary consciousness exist in birds. The challenge is to devise experiments, comparable to those in species such as monkeys, to provide additional evidence.

3. The octopus: A distant case and major challenge

The evidence relevant to establishing necessary conditions for consciousness in cephalopods is much more tenuous and sketchy than for avian species. We nevertheless attempt to present this evidence, however incomplete.

3.1. Behavior

A number of behavioral studies have probed the cognitive capacities of cephalopods. Early research suggested that the octopus possessed a rich cognitive capacity. For example, the work of Wells and Young (1965, 1972) and that of Sutherland (1969) amply demonstrated the ability of the octopus to make discriminations between different objects based on size, shape, and intensity. Sutherland made the additional observation that octopuses classify differently shaped objects in the same manner as vertebrates such as goldfish and rats (Sutherland, 1969). More recent studies have tested memory and problem-solving capabilities of the octopus. These have generally involved such tasks as learning the correct path to a reward in a plexiglas maze or retrieving an object from a clear bottle sealed with a plug (Fiorito, Biederman, Davey, & Gherardi, 1998).

In general, cephalopods have been shown to be capable of an extraordinarily plastic behavioral repertoire and, from anecdotal reports of observational learning, seem to have highly developed attentional and memory capacities. Researchers have documented evidence of distinct capacities for short-term and long-term memory in the octopus and another cephalopod, the cuttlefish (Agin, Dickel, Chichery, & Chichery, 1998; Fiorito & Chichery, 1995). In studies in which an octopus was confronted with a maze containing obstacles that were changed ad libidum by the researcher, the animal was able to remember these changes and readily navigate around these obstacles. The researchers asserted that in fact the octopus seemed to "consider" the layout of the maze before proceeding (Moriyama & Gunji, 1997). The sophistication of the octopus' memory capabilities is also borne out by its ability to solve problems through observational learning (not merely through mimicry) which has been demonstrated reasonably well (Fiorito & Scotto, 1992).

A common task employed by researchers to assess the cognitive capacity of octopuses involves the presentation of a prey species, such as a crab, enclosed in a plugged jar (Fiorito, Agnisola, d'Addio, Valanzano, & Calamandrei, 1998, 1998). Initially, the octopus approaches the prey as it would under natural circumstances by immediately attacking the jar. After repeated exposure to the crab-containing jar, the octopus learns to pull the plug to obtain the crab. Pre-exposure to the jar—that is, presentation of an empty jar—does not significantly reduce the time it takes the octopus to retrieve the crab. The authors of this study point out that while the octopus appears to be solving the jar problem, it is exhibiting species-specific, predatory behavior (i.e., pouncing on the jar) which does not abate over repeated trials (Fiorito, Biederman et al., 1998). The invariance of the octopus's behavioral repertoire as it solves the jar problem suggests the absence of the kind of inhibitory pathways that might be activated in a mammal's brain as it becomes familiar with a particular task. This might therefore discourage the notion that cephalopod brains are sufficiently complex to exhibit conscious states.

The question of necessary conditions for cephalopod consciousness has not been addressed explicitly. Assuming that cephalopod anatomy becomes sufficiently well characterized to identify functional analogues of mammalian visual cortex, it might be possible to perform experiments along the lines of the 'commentary key' paradigm employed by Cowey and Stoerig (1995) on *Rhesus macaques*. In the case of cephalopods, an obvious channel for accurate report would be the remarkably sophisticated system of chromatophore organs[10] used by these animals to change the coloration and patterning of their skin during signaling behavior, mimicry, or in efforts to camouflage themselves (Hanlon & Messenger, 2002).

3.2. Anatomy

Cephalopods, particularly the octopus, have complex sensory receptors and nervous systems that, at least in numbers of constituent neurons alone, rival those of some vertebrates. The brain of an adult octopus may contain as many as 170 million cells, the vast majority of which are neurons (Giuditta, Libonati, Packard, & Prozzo, 1970). However, in contrast to avian neuroanatomy, the organization of the cephalopod nervous system presents an utterly unique set of problems for identifying necessary structural correlates of systems underlying consciousness. The search for structures in the cephalopod brain analogous to the reentrant loops of the mammalian thalamocortical system will be particularly challenging. Where would they be? (See Fig. 2) Application of biochemical and molecular methodologies that have been brought to bear on questions of functional vertebrate neuroanatomy may be useful in addressing this question.

At the level of the constituent neurons and receptor cells, the similarities between the cephalopod nervous system and its vertebrate counterpart are obvious. Indeed, the observation that giant squid axons and synapses resemble those of vertebrate neurons, first made by researchers in the mid-20th century, represented a watershed in modern neurophysiology and made possible many

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[10] These organs, which contain pigment-filled saccules capable of contraction and expansion, are actually part of the cephalopod's neuromuscular system. Unlike the chromatophores found in crustaceans and vertebrates such as fish, amphibians, and reptiles, cephalopod chromatophores are not pigment-containing cells; nor are they hormonally controlled (Messenger, 2001).

Fig. 2. Possible neuroanatomies of primary consciousness. In humans, primary consciousness is associated with the highly reentrant thalamocortical system. In birds, a functionally analogous system may involve regions of the telencephalon, the thalamus, and basal ganglia. Cephalopod neuroanatomy is currently insufficiently characterized to advance functionally analogous structures with much confidence.

of the investigations of neuronal physiology that followed (Hodgkin, 1964; Katz & Miledi, 1966; Young, 1939).

A peculiarity of the octopus nervous system is the density of neurons located in the tentacles, which taken together, exceeds the total number of neurons in the brain itself (Young, 1971). Consistent with this fact, a recent study showed that a detached octopus arm could be made to flail realistically when stimulated with short electrical pulses (Sumbre, Gutfreund, Fiorito, Flash, & Hochner, 2001). Of course, the existence of semi-autonomous motor programs is not unique to this species or even to cephalopods in general. There is longstanding evidence for the existence of central pattern generators (CPGs) in a variety of invertebrates and vertebrates (Ben, Cabelguen, Ekeberg, & Grillner, 2003; Marder & Bucher, 2001; Marder & Calabrese, 1996). However, in vertebrates, such CPGs seem to be located in the spinal cord; i.e., within the central nervous system itself (Butt, Lebret, & Kiehn, 2002; Kiehn & Butt, 2003; Kiehn & Kjaeruluff, 1998). Accordingly, in a detached vertebrate limb it is simply not possible to produce the suite of coordinated movements that is characteristic of complex vertebrate locomotion.[11] In contrast, what is striking about the octopus is the sophistication of the semi-autonomous neural networks in its tentacles and their local motor programs. These observations bear on the assessment of consciousness in the sense that they may alter the notions of embodiment and bodily representation as they have been set forth by cognitive scientists and philosophers (O'Regan & Noe, 2001). In any case, it is not likely that the question, "what is it like to be an octopus tentacle?" will ever be posed by any rational philosopher (see Nagel, 1974).

Identification of higher levels of neural organization in cephalopods poses even more profound challenges. Cell assemblies, modules, cortical columns, thalamocortical loops, blobs (well characterized in the cortex by cytochrome oxidase labeling; see Wong-Riley, 1989) and neuronal groups

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[11] Almost a century ago, it was demonstrated that electrical stimulation applied to the muscles of a detached frog leg could cause it to extend as if it were in the explosive phase of hopping (Lombard & Abbot, 1907). In a recent study, a variety of different limb movements were produced in anesthetized and decerebrate cats through electrical stimulation of different muscles, nerves, and sites in the intermediate spinal cord, as well as the dorsal and ventral spinal roots (Aoyagi, Mushahwar, Stein, & Prochazka, 2004). Interestingly, stimulation of the ventral root produced a single, backward directed movement of the limb, whereas stimulation of the dorsal root produced a single forward directed movement. In contrast, stimulation of the spinal gray matter produced movements in a variety of directions.

have been variously defined in mammals as groups of cells that share similar structure and/or function and that exist in large numbers within a particular defined region of the brain (i.e., cortex, nuclei, and ganglia) (Hebb, 1949; Izhekevich, Gally, & Edelman, 2004; Leise, 1990; Mountcastle, 1978; Szentagothai, 1975). In its most restricted definition, a column has been described as the smallest functional module of the mammalian neocortex (Mountcastle, 1978). A broader notion of the neural module, suggested by Leise (1990), would recognize large concentrations of neuropil in invertebrates as being functionally something like the so-called minicolumn (Buxhoeveden & Casanova, 2002). The validity of such an analogy remains untested, but it would perhaps be useful to search for concentrations of closely bundled elements in the cephalopod brain. Their discovery might indicate a region that has properties similar to isocortex in mammals (isocortex refers to the larger part of mammalian cortex that is relatively uniform in its histology). The layout of such modules might yield some insight into how functional neural maps are organized in the cephalopod brain.

It should be noted that the relative brain size (normalized to body mass) of many cephalopods exceeds that of many lower vertebrates, and in some cases, approaches that of some birds (Hanlon & Messenger, 2002). In the brain of at least one genus of squid, *Loligo*, at least 30 distinct nucleus-like lobes have been identified (Maddock & Young, 1987). The largest of the lobes, the optic lobes (which contain as many as 65 million neurons in some species of octopus) handle visual processing and memory establishment, as well as some higher motor control. Although they do not have the laminar architecture of mammalian cortex, it has been suggested that these lobes are analogous to the vertebrate forebrain (Hanlon & Messenger, 2002). Other neural structures that figure prominently in the establishment of memories are the vertical and superior and inferior frontal lobes. In experiments in which the vertical lobe of *Octopus vulgaris* was lesioned, the ability to learn visual discriminations was drastically impaired, but the capacity to consolidate long term memories was not affected (Fiorito & Chichery, 1995).[12] In another study, when the median inferior frontal lobe was removed, learning was severely limited due to memory impairment (Wells & Young, 1969, 1972). If it is indeed the ability of the octopus to recall that was being affected in these studies, this would suggest that at least portions of the octopus frontal and vertical lobes serve a function similar to that of parts of the mammalian cortex.

It has been noted that considerably more genetic expression occurs in the squid nervous system than in other tissues or organs (Capano, Gioio, Giuditta, & Kaplan, 1986). This is consistent with the notion that the selection for highly complex nervous systems is phylogenetically ancient. It is plausible that complex brains capable of rich and flexible behavioral repertoires began evolving in two very different radiations between 530 and 540 million years ago (see Morris, 2000; Knoll & Carroll, 1999). Cephalopod brains have been shown to contain the same major neurotransmitters that are found in the brains of mammals (Hanlon & Messenger, 2002). This suggests that, as is now the case with functional avian neuroanatomy, it may be possible to use immunohistochemistry and genetic manipulation to define those areas of the cephalopod brain that are analogous in function to neural regions showing correlated activity during waking, conscious behavior in mammals.

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[12] In this species, the vertical lobe is known to play a role in tactile memory (Young, 1983). Also, it is interesting to note that an octopus will remain quiescent when this lobe is electrically stimulated (Hanlon & Messenger, 2002).

The cephalopod radiation came to occupy many marine niches, so, not surprisingly, there is substantial interspecies variation in sensorimotor capacities and behavioral repertoires (Hanlon & Messenger, 2002). It is conceivable that, amidst such an efflorescence of diverse adaptations, and given sufficient numbers of cells and cell-types and dense enough connectivity, discriminatory capacities necessary for consciousness may have appeared as an emergent property in at least some cephalopod species (see Fig. 2).

3.3. Physiology

Apart from their extraordinary behavioral repertoires, perhaps the most suggestive finding in favor of precursor states of consciousness in at least some members of *Cephalopoda* is the demonstration of EEG patterns, including event related potentials, that look quite similar to those in awake, conscious vertebrates (Bullock & Budelmann, 1991). So far, this has been demonstrated in just one other invertebrate: the fruit fly (Van Swinderen & Greenspan, 2003). An obvious prerequisite to identifying cephalopod EEG patterns that reflect the signature of fast irregular activity, similar to that observed in human conscious states, will be to determine precisely where to record from. It is possible that the optic, vertical, and superior lobes of the octopus brain are relevant candidates and that they may function in a manner analogous to mammalian cortex. In any event, they appear to be among the substrates of octopus learning and memory (Boycott & Young, 1955; Fiorito & Chichery, 1995; Sanders, 1975; Wells, 1978). Indeed, a recent study of slice preparations of octopus vertical lobe identified long-term potentiation of glutamatergic synaptic field potentials similar to that in vertebrates (Hochner, Brown, Langella, Shomrat, & Fiorito, 2003).

Clearly, a strong case for even the necessary conditions of consciousness in the octopus has not been made. Nevertheless, the present evidence on cephalopod behavior and physiology is by no means sufficient to rule out the possibility of precursors to consciousness in this species.

4. Discussion

We began this review by suggesting that human consciousness should serve as a benchmark for studies in other species. At the same time, we deliberately excluded any extended discussion of the higher order consciousness that makes possible explicit human report of conscious states. Our aim was to inquire only whether necessary, though not necessarily sufficient, conditions for primary consciousness could be found in birds and cephalopods.

In the absence of explicit report from a first person point of view, doubt could be cast on the assumption that members of any non-human species are conscious. Such doubt may even exist in the case of primates, where part of the problem is that much of the relevant behavioral research was not initiated with any sort of generally agreed upon definition of consciousness. Over the past two decades, quite rigorous playback experiments[13] were carefully crafted and deployed to tease

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[13] For more than two decades, field researchers have employed an experimental design in which recordings were made of an individual monkey's context-specific calls (i.e., alarm calls in response to a predators, vocalizations of an infant seeking contact with its mother) and then "played back" to that monkey's social group to investigate the response of the group.

out evidence of some kind of social awareness, intentionality, or even a "theory of mind" in monkeys in the wild (Bergman, Beehner, Cheney, & Seyfarth, 2003; Cheney & Seyfarth, 1990; Seyfarth & Cheney, 2003). At the same time, sophisticated laboratory-based methodologies were also deployed to test for a theory of mind in apes (Premack & Woodruff, 1978; Premack & Premack, 1984; Savage-Rumbaugh, Sevcik, Rumbaugh, & Rubert, 1985). Although these studies clearly demonstrated a highly sophisticated social intelligence (Seyfarth & Cheney, 2003) and, some might argue, even self-awareness (Gallup, 1970) among certain primates, they did not allow the conclusion that these animals were conscious.

A synthetic approach to assessing primate consciousness requires combining behavioral evidence with neuroanatomical and neurophysiological analyses. Thus, the main point supporting the case for consciousness in monkeys and apes is that they have rich discriminatory behavior *along with* thalamocortical systems that enable complex reentrant neuronal signaling (Seth et al., 2004). Moreover, even in the absence of the semantic capabilities shown by chimpanzees and bonobos, experiments of the kind performed by Logothetis (1998) on monkeys show that higher cortical processing results in neural responses to reported percepts, not just to sensory signals. The point of the present discussion is to suggest that this sort of synthetic methodology should provide a model for researchers pursuing consciousness studies in non-mammalian species.

It has been suggested that consciousness emerged in evolution as a result of reentrant interactions between those parts of the thalamocortical system mediating perceptual categorization and those parts mediating memory (Edelman, 1989). The activity of such systems allowed enormous increases in the capacity for sensorimotor discrimination that were highly adaptive for planning of behavior. In this view, primary conscious scenes[14] *are* those higher order discriminations (Tononi & Edelman, 1998). Consistent with this proposal, in the present paper we have made a modest attempt to consider whether the necessary conditions for consciousness are met in members of non-mammalian groups such as birds and octopuses. These conditions include reentrant neural structures that are functional equivalents of cortex and thalamus; widespread, relatively fast, low-amplitude electrical brain activity driven by current tasks and conditions; and rich discriminatory behavior. While these alone are not sufficient to conclude that the members of a species are conscious, their presence suggests the emergence of evolutionary precursors or products that are necessary for consciousness.

Marshalling evidence for consciousness in birds and cephalopods such as the octopus, squid, cuttlefish, and nautilus is much more challenging than it is for mammals because of the anatomical differences (substantial in the case of the cephalopods) that distinguish the brains of these animals from those of mammals. Moreover, in the case of the cephalopods, there are formidable technical difficulties involved in designing physiological and behavioral experiments analogous to those now performed routinely on both human and non-human mammalian subjects.

In principle, there is no reason that necessary conditions for primary consciousness cannot be tested in avian species, notwithstanding the fact that the avian telencephalon contains no part exactly matching the structure of the mammalian isocortex. Avian structural and functional equivalents of mammalian thalamocortical loops appear to exist; the circuitry underlying much of vocal learning in songbirds, for example, resembles the mammalian thalamocortical pathway (Luo

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[14] What philosophers refer to as qualia, i.e. the "redness" of red, and so on.

et al., 2001).[15] It is unclear, however, whether these aspects of this circuitry are analogous or homologous to the mammalian thalamocortical loops (Puelles, 2001). At least one study has demonstrated irregular, low amplitude, brain activity in one species of bird, the parakeet (Ayala-Guerrero, Perez, & Calderon, 1988).

Of course, a case for consciousness in birds need not be contingent on the identification of structural homologies. Rather, what is crucial is evidence of functional analogies that could underlie conscious states. In the avian brain, reentrant interactions may occur between the thalamus and those parts of the telencephalon which have been characterized as the functional equivalent of mammalian cortex (Becker & Redies, 2003; Krutzfeldt & Wild, 2004; Montagnese, Szekely, Adam, & Csillag, 2004; Reiner, Laverghetta, Meade, Cuthbertson, & Bottjer, 2004). Despite some profound differences in anatomy, it is encouraging that avian and mammalian brains possess similarly organized dopaminergic systems that subserve many of the same behavioral functions (Durstewitz et al., 1999). In addition, the cholinergic, glutamatergic, and GABAergic systems that underlie song learning in songbirds seem to be homologous to the mammalian striatal pathways of the basal ganglia that are critical to motor learning (Faries & Perkel, 2002).

In contrast to avian species, anatomical and physiological studies of the cephalopods are insufficiently developed to provide evidence for the existence of the three properties of primary consciousness we have emphasized here and elsewhere (Seth et al., 2004). For example, no account of irregular, low amplitude electrical activity in invertebrates, such as the octopus, has been published. It is unclear if this is the case because of some technical obstacle, or merely because researchers have not yet attempted such recording on either live cephalopods or in vitro preparations of cephalopod nervous systems. A key challenge is to show that reentrant neural activity can be seen among reciprocal parallel pathways in the octopus brain. Absent such pathways, a completely new basis for conscious brain activity would have to be imagined. At present, there are few grounds to support this exercise.

Our aim in this paper was to set the stage for possible experiments to show neural and behavioral correlates consistent with conscious states in non-mammalian species. Current evidence makes a strong case for the possibility of such states in birds. For cephalopods, including the octopus, we believe that the question remains very much open (see also Merker, in press). It may be useful to pursue further experimentation in this distant species if only to rule out the possibility of conscious states. At the very least, a demonstration that reentrant structures are absent in cephalopods (as in insects) would confirm that comparisons with the benchmark human species are not possible.

Nearly 30 years ago, the case for awareness in animal species other than *Homo sapiens* was made explicitly and forcefully by Donald Griffin, who relied heavily on ethological observations (Griffin, 1976). But critical as they are to evaluating the presence of conscious states in diverse animal species, behavioral observations alone cannot provide sufficient evidence that the conditions for consciousness exist in any given animal. Equally important to the assessment of conscious states in non-human species is the characterization of anatomy and neural dynamics that are functionally analogous to those which are already known to underlie consciousness in humans.

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[15] Specifically, what is referred to as the anterior forebrain pathway (AFP) connects the lateral magnocellular nucleus of the anterior neostriatum (homologous to mammalian cortex), the basal ganglia, and the medial region of the dorsolateral thalamic nucleus (Luo et al., 2001).

Acknowledgments

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