



Introduction

Subjective experience is probably not limited to humans: The evidence from neurobiology and behavior [☆]

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Abstract

In humans, conscious perception and cognition depends upon the thalamocortical (T-C) complex, which supports perception, explicit cognition, memory, language, planning, and strategic control. When parts of the T-C system are damaged or stimulated, corresponding effects are found on conscious contents and state, as assessed by reliable reports. In contrast, large regions like cerebellum and basal ganglia can be damaged without affecting conscious cognition directly. Functional brain recordings also show robust activity differences in cortex between experimentally matched conscious and unconscious events. This basic anatomy and physiology is highly conserved in mammals and perhaps ancestral reptiles. While language is absent in other species, homologies in perception, memory, and motor cortex suggest that consciousness of one kind or another may be biologically fundamental and phylogenetically ancient. In humans we infer subjective experiences from behavioral and brain evidence. This evidence is quite similar in other mammals and perhaps some non-mammalian species. On the weight of the biological evidence, therefore, subjectivity may be conserved in species with human-like brains and behavior.

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1. Introduction

Some years ago a popular book suggested that conscious cognition emerged 2500 years ago, between the writing of the *Illiad* and the *Odyssey* (Jaynes, 1976). Jaynes' criterion of consciousness was whether Homer's heroes talked to themselves—the warriors of the *Illiad* did not, while Odysseus did. But speech is not a necessary condition for consciousness. After all, aphasics with impaired inner and outer speech show no sign of losing consciousness. This Special Issue of *Consciousness and Cognition* explores extensive evidence that consciousness is a major biological adaptation going back many millions of years.

Subjective consciousness is of course inferred from observable evidence, much like working memory or other scientific constructs like electrons (Banks, 1995). Thus consciousness is not a metaphysical absolute, but a scientific construct like any other. In humans, the standard behavioral index of conscious cognition is accurate or verifiable report. It has been used scientifically since the beginning of psychophysics in the 1820s. Accurate report is highly reliable, but of course it is subject to limitations like any other empirical measure (Baars, 1988). However, behavioral measures of conscious cognitions are reliable enough to be routinely used in optometry, audiology, and the design of video screens and audio equipment. Physicians routinely use such evidence to test patients for impaired consciousness. Thousands of human experiments use verifiable report to study conscious perception, episodic memory, explicit cognition, focal attention, and the like (Baars, Banks, & Newman, 2004). But behavioral evidence is less useful when we study the question of animal consciousness. Bees meet the “accurate report” criterion when they convey information about food sources by doing a “waggle dance.” But human-like consciousness seems implausible in bees. Thus when we look beyond the human species, brain evidence may be a more useful source of evidence.

Can we infer subjectivity in other mammals? It is an inferential leap for one person to believe in the consciousness of another. Such inferences are made routinely when physicians test head-injured patients with impaired responsiveness. But if we make such inferences to other humans, then why not to other creatures, if the objective basis is the same? It is sometimes argued that animal subjectivity is not a testable claim, but we now have a number of studies that have tested such inferences, for example, on the question of visual consciousness in monkeys (e.g., Cowey & Stoerig, 1995). When we include other kinds of sensory awareness (especially touch, hearing, and pain) the circle of conscious animal species seems to grow larger. Non-mammals have been studied in less detail, but the range of conscious species will likely expand as we learn more.

2. Articles in this issue of *Consciousness and Cognition*

This issue is dedicated to the memory of Donald R. Griffin (see the obituary by Speck, 2005). Donald Griffin devoted his life to field studies of animals, and took intense criticisms from scientific colleagues when he began to address the question of animal consciousness—initially phrased as “animal cognition.” He was a scientific pioneer of outstanding courage and integrity, and we owe him a great debt of gratitude.

Jaak Panksepp is another modern pioneer, in his case in the study of the brain substrates of emotion in humans and other mammals. He has made many contributions to understanding the mammalian social attachment system associated with the region surrounding the cerebrospinal aqueduct,

called the peri-aqueductal grey (PAG). This brainstem region is of fundamental importance in mother–infant attachment, and appears to be involved in such behavioral events as separation distress cries in mothers and infants. Brainstem regions are of course phylogenetically old, and Panksepp makes a case that conscious emotional feeling states have a long biological history. One of Panksepp's famous discoveries is the existence of high-frequency distress cries in newborn rat pups separated from the mother; another is the reward value of tickling and social play in rats. Panksepp is the author of the landmark volume *Affective Neuroscience* (1998), which lays out a coherent brain-based framework for emotion. For this special issue he has written two papers. His major empirical case is made in “Affective Consciousness: Core Emotional Feelings in Animals and Humans”; a second article in this issue is a commentary called “Toward a science of ultimate concern.” It pursues the ethical implications of the evidence for consciousness and emotions in animals. How do we deal with a world in which animals as well as humans experience pain and pleasure?

Bjorn Merker is a Swedish neurobiologist who also conducts field work with Gibbons in Indonesia and experimental studies of music. Merker has recently published a significant article on the functional implications of neocortical layer structure (Merker, 2004). In this article he suggests one of the few serious evolutionary hypotheses for the biological origins of consciousness. As he points out, our conscious experience of the world is relatively stable compared to the sensory input. We constantly change our visual gaze, head orientation, body motion and the like, without noticing a change in the world. Self-other discrimination in motion perception has been thought to be fundamental since Helmholtz pointed out that the eye can be moved by gentle external pressure, and the world will be seen to jump. Yet much larger endogenous eye movements do not result in consciously experienced changes in the world. Such self-other discrimination is needed even for earth worms being investigated by a curious dog. The worm must distinguish between the friction of its own movements compared to being licked by a dog. One is a danger to survival; the other is a sign needed to keep moving.

One implication of Merker's point is to notice that consciousness may originate in the intersection between decision processes and sensory input. Humans make decisions based on conscious alternatives, though shaped by unconscious biases. Numerous recent studies show that conscious, but not unconscious sensory input activates executive regions of prefrontal and parietal cortex (Frackowiak, 2004). In order to make decisions, one must have a reasonably stable representation of the current state of the world. Perhaps one function of consciousness is to facilitate this interaction between world and self.

Banks (1995) has suggested that understanding the functional role of consciousness may also give us a line of evidence on its emergence. Franklin's commentary proposes such a functional generalization of Merker's argument, suggesting that consciousness may be a distant pre-mammalian development (2005). Franklin also argues that an analogue of consciousness may be implemented in non-biological hardware.

Seth and Baars (2005) pursue the function of consciousness from the perspective of Neural Darwinism (ND), an influential theory of brain function developed by Gerald M. Edelman and colleagues (e.g., Edelman, 1993). While Edelman has repeatedly described ND as the brain basis for consciousness, this article posits a set of specific objective criteria for consciousness and explores the adequacy of ND for their understanding. It may therefore be one of the most detailed evaluations of Edelman's hypothesis regarding consciousness, coming to the conclusion that ND fares rather well by the criteria discussed.

Developing empirical hallmarks for poorly understood empirical questions is a standard goal of science. In neuroscience the empirical criteria for neurotransmitters were a hot topic of debate some decades ago, leading to the discovery of acetylcholine and a host of other chemicals that met those standards. Perhaps the major reason for confusion about consciousness is the absence of an agreed-upon set of empirical indices. Seth, Baars, and Edelman (2005) therefore propose a set of 17 testable aspects of consciousness that command widespread agreement among scientists. Others have been proposed by Edelman (2003) and Crick and Koch (2003).

Edelman, Baars, and Seth (2005) apply this approach to the question non-mammalian consciousness. For reasons discussed in this Introduction, the case for mammalian consciousness is quite compelling, using objective indices available today. It is always possible, of course, that there is some distinctive human brain feature that excludes consciousness in other species. However, we have two centuries of neuroanatomical evidence and 70 years of EEG studies of waking, sleeping, and dreaming. In addition, we now have much greater insight into the phylogeny of nervous systems as well as its genetic basis. Brain homologies that were highly controversial a few years ago are now widely accepted, because the genetic codes are known to be the same across species. Non-mammals have less obvious homologies, but still share basic classes of neurons, neurotransmitters, and even types of connectivity that may potentially resemble the human neocortex. Although our ignorance about the brain basis of consciousness continues to be vast, it is not infinite. What we know today suggests that consciousness is a basic biological adaptation, with an evolutionary basis like any other.

Living organisms are characterized by functional redundancy, as pointed out by Edelman and Gally (2001) and Price and Friston (2003). (The technical term is “degeneracy.”) We have two lungs, two cortical hemispheres, four heart chambers, and many regenerating regions of the liver. That suggests that consciousness, like other major adaptations, may have multiple functions, and that we should not become trapped into looking for only one. A closely related example is the case of sleep, whose function is not at all agreed on at this time. Sleep probably has many functions, including circadian timing of gene expression, possible stress reduction, and perhaps others, such as detoxifying glutamate products that accumulate during the waking state. We argue below that there is an indisputable association between waking consciousness and goal-directed survival and reproductive behavior. Its biological primacy is therefore hard to dispute.

Valli et al. (2005) take the functional debate another step. REM dreaming¹ is a state closely related to waking consciousness. The EEG of REM dream states is hard to distinguish from waking, and people can even learn to signal on cue from REM dreams. While skeletal muscles are typically paralyzed during REM, eye movements are not, and can be performed on contingent voluntary control. Finally, REM dreams can be reported, as we know from virtually universal human experience. They therefore meet the standard behavioral criterion of consciousness. REM emerges with early mammals, and Valli et al. (2005) suggest that the function of dreams is to simulate, and therefore prepare to deal with, threatening situations. These authors make creative use of dreams from traumatized children as an empirical basis for their hypothesis.

¹ The term “REM dreams” is used here because the previously accepted association between physiological REM and dream reports has come under considerable question in recent years. These comments refer to physiological REM that is also reflected in classical dream reports.

Finally, Greenspan and Baars explore some reasons why the question of consciousness in animals and people was expelled from science after 1900. The seminal role of Jacques Loeb, Ivan P. Pavlov, and other physical reductionists is explored. It is interesting that the experimental evidence we use today to explore the brain basis of conscious experience was well known to William James and Charles Sherrington. For example, binocular rivalry has been one of the major experimental techniques for exploring consciousness in recent years (see below). Much of the evidence known before 1900 is not very different from today's findings, yet we are currently seeing some 5000 articles per year citing the word "consciousness" in the biobehavioral literature, after a century of virtual taboo. The reason for the long taboo is therefore somewhat puzzling.

3. The rediscovery of consciousness

Charles Darwin wrote that "Consciousness appears to be the product of complexity of organization," an hypothesis that continues to draw serious scientific attention today (e.g., Edelman & Tononi, 2000; Tononi & Edelman, 1998). In the 19th century scientists like Darwin treated consciousness as an obvious scientific topic. Research on conscious sensory perception, conscious and unconscious influences on memory, selective attention, and even hypnosis began in 1800s. The 1400 pages of William James' *Principles of Psychology* (1890/1983) provide a guide to the rich domain of empirical knowledge gathered during that period. It is filled with facts that have since been rediscovered, and which are the subject of much current research (e.g., Baars, 1986, 1988; Baars et al., 2004).

Yet in the years before 1900 the openminded scientific attitude toward human and animal consciousness began to change. Thomas Henry Huxley, known as "Darwin's Bulldog" for his public defense of biological evolution, suggested that consciousness might be a useless by-product of normal brain functioning. He wrote that "Consciousness would appear to be related to the mechanism of the body simply as a (side) product of its working, and to be completely without any power of modifying that working, as the (sound of) a steam whistle which accompanies the work of a locomotive is without influence upon its machinery." (quoted in James, 1890/1983, p. 135). The empirical phenomena of consciousness, which are plentiful and easy to obtain, became entangled in the snares of the mind-body problem, a set of philosophical conundrums that are not subject to empirical test. Further, consciousness came to be seen, in the words of the American behaviorist John B. Watson, as "nothing but the soul of theology." It soon fell victim to a culture war between science and religion.

In biology C. Lloyd Morgan proposed the "Lloyd Morgan Canon," claiming that anthropomorphic generalizations about animals are dubious in principle (Morgan, 1896). I.P. Pavlov's work on conditional associations in dogs was interpreted to mean that psychological concepts like volition were meaningless, and that learning could be automatic, without conscious involvement. Both of these interpretations are now known to be false (e.g., Baars, 1986, 1988). But Pavlov's work was very much in tune with the times, and H.G. Wells, for example, welcomed Pavlov as "a star which lights the world, shining above a vista hitherto unexplored." (quoted by Skinner, 1976). Behaviorism was celebrated as soon as it was proclaimed, launching the influential careers of John B. Watson and B.F. Skinner in the United States, and logical positivist philosophers in Britain and elsewhere.

The early 20th century saw a massive scientific purge of consciousness and related ideas—including purpose, mental imagery, emotional feelings, unconscious processes, attention, meaning,

thinking, and inner speech. Consciousness came to have the status of a scientific taboo. A hundred years of useful empirical discoveries were forgotten. Behaviorists popularized several standard criticisms of 19th century consciousness science; but those criticisms have now themselves come under serious question (e.g., Blumenthal, 1979; Hilgard, 1987). They now appear to be almost entirely erroneous.

Since the decline of behaviorism, hundreds of facts about consciousness described in James' *Principles* have been rediscovered (Baars, 1986, 1988; Baars et al., 2004). Indeed, nineteenth century findings about topics like sensory psychophysics have continued to accumulate in the last hundred years without serious controversy. No one can have a simple eye examination today without benefiting from psychophysical methods first developed in the 1820s. Psychophysics was considered to be the scientific study of conscious sensations, and indeed that is how we are once again seeing it.

Yet we are still recovering from a century in which consciousness became a taboo. Obviously, for those who doubt that humans are conscious, the question of other animals cannot be addressed with an open mind. The evidence is now extensive that behavioristic skeptics were wrong. Today some 5000 articles per year cite the term "consciousness" in the scientific literature. The importance of consciousness in humans, as assessed by objective evidence, is beyond empirical dispute. What about other animals?

4. Behavioral and brain evidence

It is essential to distinguish between "intelligence" (as problem solving) and "consciousness" (as wakeful alertness and conscious perception, including the perception of pain and pleasure). We know of hundreds of differences between humans and other mammals in problem-solving tasks, ranging from word retrieval to migratory travel. Problem-solving tends to be species-specific. Early in life humans all over the world are able to learn a very large vocabulary, demonstrating a distinct species-specific capacity. Pigeons, on the other hand, excel in finding their way in air space, far beyond unaided human abilities. Throughout the animal kingdom, different brains support high evolved species-specific abilities. Yet the fundamental brain mechanisms of conscious alertness and of conscious sensory perception are not limited to a few animal species. They have extremely wide distribution among vertebrates and perhaps more widely. Species differences such as the size of neocortex seem to be irrelevant to wakefulness and perceptual consciousness. To stay close to the established evidence, this review is limited to waking alertness and perceptual consciousness in mammals, including humans.

5. Behavioral indices of consciousness: Accurate report

In humans, the standard observational index of consciousness is "accurate or verifiable report" (e.g., Baars, 1988, 1998; Baars et al., 2004). In humans reports of conscious experiences do not have to be verbal; pressing a button, or any other voluntary response, is routinely accepted as adequate in research. Reporting responses are equally useful in animals.

Humans are extraordinarily good in detecting conscious sensory events. Seeing a single star on a dark night has been calculated to require no more than a single stream of photons activating a single retinal receptor, that is, the lowest physical amount of light energy. Likewise, in a very quiet place humans can hear a background hiss due to the random motion of air molecules in the outer ear canal; that, too, is a stimulus at the lower physical limit of auditory stimulation. Seeing a star and hearing noise are provably conscious events in humans, because they meet the standard operational definition of accurate report; thus these extraordinary sensory abilities are in some sense capacities of consciousness. Animal sensory capacities are likewise remarkable, and can be reported by way of overt behavior just as clearly as humans can tell us about their conscious visual or auditory experiences. In primates, birds, and marine mammals that can use artificial symbols like sign language, gestures or computer keyboards, referential accuracy is well established.

6. The “commentary key” as evidence for mammalian consciousness

Skeptics sometimes question whether the ability of monkeys and cats to accurately report sensory events really involves conscious perception. That hypothesis can be tested in a number of ways. Recent research in macaques and other species is especially remarkable, because it allows us to ask if the animals studied respond to conscious events differently than they do to comparable brain events that are unconscious. Weiskrantz (1991) and Cowey and Stoerig (1995) have developed a “commentary key” method for the macaque, allowing it to give a behavioral comment on a previous response. This reflects the idea that human reports of conscious experiences are shared comments about those experiences. When a child exclaims, “Mommy, airplane!” s/he is making a public comment about a conscious visual event, telling an outside observer what was just experienced. The commentary key is especially useful in the study of cortical blindness, where humans can make accurate discriminations while claiming that they do not actually see the discriminated targets consciously. Cortical blindness is a condition in which the first cortical projection area (V1) of the primary visual pathway is damaged. In the occluded part of the field humans report a loss of conscious visual qualities like stimulus color, motion, and location. Yet there is excellent evidence that such properties of the visual stimulus are still processed by the visual brain, as shown by forced-choice responses. Thus blindsight patients can sometimes point to the location of a visual object, and detect motion and color, while strongly denying that they have normal visual experiences of those features.

A remarkable study by Cowey and Stoerig (1995) made use of a commentary response to test whether macaques with cortical blindness lose conscious visual qualia like color and motion, which humans report losing with similar brain damage. The macaque’s visual brain resembles the human one in a number of respects. Careful lesion studies show that the macaque behaves much like a human blindsight subject when selected parts of area V1 are removed. But can we be sure that the “blindsighted” macaque has also lost visual conscious qualities, the qualia discussed by philosophers, such as color, motion, and texture? Cowey and Stoerig make this case, using a behavioral commentary key, which allows the monkeys to make a metacognitive comment about their discriminative responses. Like a human blindsight subject, the blindsighted macaque can choose accurately between colors, for example. The commentary key allows it to signal whether its accurate behavior has a corresponding conscious qualitative experience—specifically,

whether a stimulus in the occluded visual field can be distinguished from a blank display in the intact field. In the event, macaques did not learn to discriminate between the two, just as if a human blindsight patient were saying, “I can’t tell the difference between input in my blind field and a completely blank input in my sighted field.” This is in effect a denial of visual qualities. Thus the commentary key apparently provides an equivalent of the reportability criterion in humans.

7. Other behavioral evidence

A number of other behavioral sources of evidence suggest consciousness. For example, mere distractibility in animals indicates a limited capacity for competing sensory streams, a well-established feature of conscious but not necessarily unconscious input processes (e.g., Baars, 1988, 1998; Baars et al., 2004). Simply presenting a distracting stimulus when an animal appears to be orienting to an event of interest creates competition between the two sources of information. Such competition is the standard method for assessing limited conscious capacity. When a giraffe bends down to drink from a water hole, it cannot at the same time monitor what its offspring are doing, whether a predator is in the neighborhood, or whether another giraffe is showing unexpected signs of social or sexual competition. Animals routinely “catch each other unawares” during such moments of distraction; many predation strategies are based on prey distractibility. Likewise, in humans, moving our eyes and ears to a source of stimulation leads to conscious experiences. Such receptor orienting can be observed in other mammals at every moment of the waking day. The same may be said for exploratory behavior, the willingness of animals to work for novel or biologically significant information. Finally, animals show unmistakable behavioral signs of sleep, drowsiness, and alertness that correspond to distinct conscious states in humans.

Scientists have been extremely cautious before attributing consciousness even to animals that closely resemble humans in their abilities and brain functions. There is an effective consensus today that consciousness can be attributed in the case of visual perception in macaque monkeys, using the very rigorous criteria illustrated above. The weight of evidence in these cases seems so clear at this time that we may begin to relax our current high demands for proof to some degree. For example, it seems likely that perceptual consciousness may become routinely accepted, even in mammals that do not communicate by way of referential symbols like sign language. In the coming years, as the pattern of brain and behavioral evidence grows, we may begin to attribute consciousness on the basis of a mammal’s ability to match and discriminate between classes of stimuli, combined with evidence about the underlying brain events. It has been known for decades that a vast range of animals show this ability. It is effectively equivalent to saying, “I hear a tone, and can match it with the same tone an octave above; but I can distinguish between that tone and another one a half-tone up in the octave scale.” Such descriptive responses appear equivalent to reports of conscious events in humans.

8. Electrical activity

It has been known since the late 1920s that there is a major difference in scalp electrical activity (EEG) between waking consciousness and deep, unconscious sleep, as reported by human

subjects. These EEG phenomena apply to humans and other mammals alike, so much so that mammalian EEG studies are often applied to humans. In all mammalian species studied waking shows fast, irregular, and low-voltage field activity throughout the thalamocortical core. In contrast, deep sleep reveals slow, regular, and high-voltage field activity. Thus the electrical activity of the thalamocortical core in waking appears to support reports of conscious experiences in humans. But the underlying brain activity is so similar in humans, monkeys, and cats, that these species are routinely studied interchangeably to obtain a deeper understanding of states of consciousness.

The specific neuronal activities underlying these global differences in EEG are now increasingly understood. During unconscious sleep, slow-wave global EEG appears to reflect highly regular and coordinated burst-pause firing patterns in many billions of individual neurons in thalamus and cortex. In contrast, waking EEG reflects irregular firing in the same billions of single neurons, as well as rapidly changing periods of gamma coherence between them. (Destexhe, Contreras, & Steriade, 1999). The regular burst-pause pattern of neurons during slow-wave sleep is highly synchronized, with effective zero-lag correlations between individual neurons at a distance of a centimeter or more. Significantly, the same pattern of slow-wave, synchronized EEG appears in other states of global unconsciousness such as general anesthesia, coma, and epileptic “states of absence” (Baars et al., 2004). In all these cases human beings do not report events that are conscious during the waking state.

All mammalian species studied so far show the same massive contrast in the electrical brain activity between waking and deep sleep. Thus we have some seventy years of cumulative evidence related to brain activity during consciousness and its absence in humans and other mammals.

9. Neuroanatomy of consciousness

In years past it was commonly said that consciousness must be some vague and non-specific aspect of the human brain. In fact, the waking state can be abolished by less than cubic centimeter lesions in the brainstem reticular formation and even smaller bilateral cuts in the intralaminar nuclei of the thalami (Bogen, 1995; Moruzzi & Magoun, 1949). In contrast, very large volumes of cortex can be lost without impairing the state of consciousness. Entire hemispheres are routinely removed surgically without loss of consciousness.

While the sleep–waking cycle is controlled by basal brain “spritizers” that distribute neuromodulating transmitters throughout the forebrain, in humans and other mammals the contents of perceptual consciousness depend on cortex. There may be species differences in this respect, with visual contents being in part dependent on the tectum in other mammals (the colliculi). But in all mammals the state of consciousness seems to require only small anatomical areas, the brainstem reticular formation, intralaminar nuclei of the thalamus, and basal neuromodulatory nuclei.

10. The thalamocortical (T-C) complex

In humans the thalamus and cortex are crucial for supporting the contents of consciousness (Edelman & Tononi, 2000). Thalamus is often considered to be an extension of cortex, an added

sandwich of interacting layers that controls most traffic to and from cortex. Local damage to cortical sensory regions, like the fusiform gyrus for face perception, results in a loss of conscious knowledge about faces but not about other visual features like color, location, or size. If the intralaminar nuclei of the thalamus are lesioned bilaterally, the conscious state is lost. By comparison, large lesions to cerebellum, basal ganglia, and spinal cord do not impair either conscious contents or state. Cerebellar damage can cause paralysis but not loss of consciousness. Lesion evidence on these points is supported by stimulation experiments using electrodes, transcranial magnetic stimulation (TMS), and microdialysis. It is also reflected in functional brain imaging. The evidence is therefore very strong that the T-C system supports consciousness. That is why many neuroscientists consider the T-C system to be the “seat” of conscious experience, and have done so for at least a century.

What about the T-C system in other animals? All mammals have a highly developed T-C system, suggesting that they must be conscious. Mammals are 100–200 million years old. Although we cannot directly observe ancestral forms of mammals, by studying skulls and gene conservation across species, it certainly seems that the fundamental T-C system has not changed much in 100–200 million years. Contrary to the Jaynes hypothesis, therefore, it seems that at least some types of consciousness are not merely 2500 years old, but closer to 100 million years. Notice that brainstem mechanisms like the reticular formation are also extremely ancient phylogenetically, going back at least to early vertebrates. Thalamic structures like the intralaminar nuclei also exist in mammals generally. Both these facts suggest that the brain anatomy of conscious wakefulness is very ancient indeed.

11. Visual consciousness in human and mammalian cortex

In the last 20 years we have made considerable progress on understanding perceptual consciousness in humans and other mammals. We have already discussed studies of blindsight in the macaque, suggesting that these primates have qualitative conscious visual experiences that closely resemble human visual experiences. Along the same lines, in a landmark series of multiple-neuron recording studies, Logothetis and colleagues have used binocular rivalry at different levels of visual analysis to track neurons responding to both conscious and unconscious input features in the occipito-temporal lobes of the macaque (Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). Binocular rivalry involves presentation of two incompatible visual stimuli, one to each eye. Only one stimulus becomes visually conscious in the sense of being reportable, but the unconscious stimulus still evokes appropriate feature cell activation in visual cortex, starting with the first visual projection area and succeeding to more and more elaborate feature-detecting neurons. Rivalrous pairs of visual stimuli can be designed to activate each level of visual feature analysis in the ventral temporal cortex. By experimentally counterbalancing stimulus conditions between the two eyes, one can rule out stimulus and eye effects, and focus only on those neural processes that are due to consciousness of a stimulus in either eye. Binocular rivalry experiments can be designed, therefore, to tease out the effects of visual consciousness

For example, a downward flow of stairstep lines can be presented to the right eye, along with an upward flow to the left eye. While only one eye’s input becomes conscious at any given moment, some motion-sensitive neurons in area MT (V5) respond to a conscious stimulus, while others fire

to a competing unconscious stimulus. Likewise, right-diagonal lines can be presented to the right eye, and left-diagonal lines to the left eye, thereby activating neurons in areas V1 and V2 that are sensitive to edge orientation. Finally, different objects can be presented to each eye, creating competing streams of input into object-recognition neurons in the anterior pole of the lower temporal cortex (area IT), and in the superior temporal sulcus (STS). Thus each level of visual feature analysis can be interrogated with a distinct set of binocular stimuli, one conscious and the other not.

Earlier work showed that binocular rivalry activates small numbers of cells in early visual cortex, where single visual features are represented, such as color, motion, line orientation, and spatial frequency. Some of these early cells respond to the “conscious eye” while others respond to unconscious input in the “unconscious eye.” More than half of the cells at early levels of visual analysis do not respond to either stream. However, [Sheinberg and Logothetis \(1997\)](#) demonstrated that this pattern changes dramatically toward the anterior end of the visual ventral stream, where whole objects are represented in inferotemporal cortex (area IT). In this region 90% of neurons responded to conscious, but not to unconscious visual input.

Area IT therefore appears to be the best current candidate for a distinctive locus of visual consciousness in cortex, because it clearly distinguishes between the conscious and unconscious input stream, and unlike earlier regions it massively favors the conscious stream. Since IT represents whole visual objects, it involves the integration of many specific visual features into a single, integrated representation. Nevertheless, conscious vision still appears to be crucially dependent on other parts of the brain, including earlier visual areas, other parts of cortex, and subcortical regions such as the thalamus.

The macaque is often chosen for these studies because its visual brain and abilities so closely resemble the human case. Findings from macaque vision studies are routinely found to generalize to humans. The opposite must be true as well: If humans are visually conscious, given the same kind of brain, the same kinds of results from studies of single neurons, and the same overall psychophysical parameters of vision, it becomes plausible to say that macaques and their close relatives must be visually conscious much as humans are.²

12. Neurochemistry

In all mammals, waking, sleeping, and dreaming are controlled by brainstem nuclei that widely project their axons to the forebrain, secreting neuromodulators widely to the forebrain. [Hobson \(1997\)](#) writes that “in waking, the aminergic systems of the brain stem are spontaneously, continuously, and responsively active; in REM (rapid eye movement state), they are shut off by an active inhibitory process that is probably gaba-ergic. As a function of this shut-down of aminergic systems in REM, the cholinergic systems of the brain stem become disinhibited and excite the brain with strong tonic and phasic activation signals. The net result is that, in REM sleep, the brain is aminergically demodulated and cholinergically hypermodulated.” (p. 392). Again, the fact that

² The most obvious difference between humans and other mammals, of course, is the great expansion of frontal cortex. While cetaceans have comparable brain size, their anterior cortices are homologous with parietal rather than prefrontal regions. The closest cortical homologies among mammals therefore seem to apply to perceptual regions that are located in the posterior half of cortex in humans.

neuromodulation of conscious and unconscious states is controlled by brainstem nuclei suggests an ancient evolutionary origin. Current evidence suggests that all mammals without exception have similar fundamental brainstem mechanisms.

High-dose general anesthesia often shows a slow-wave pattern of EEG similar to deep sleep, though often mixed with other waveforms. While different anesthetic agents seem to have quite different mechanisms of action, recent findings indicate that they may have similar global effects in the thalamocortical core. Thus [Alkire, Haier, and Fallon \(2000\)](#) have found evidence for a thalamocortical switch in general anesthesia across different anesthetic agents.

13. Functional evidence: In mammals, all goal-directed survival and reproductive behavior takes place during the conscious waking state

Mammalian locomotion, hunting, evasive action, exploring, sensing, actively attending, learning, eating, grazing, nursing, mating, social interaction, and all other goal-directed survival and reproductive actions take place only during waking, as defined by EEG and other indices. Perceptual consciousness, as defined objectively by recent brain research, only takes place during waking periods. It therefore appears that brain activity that supports consciousness is a precondition for all goal-directed survival and reproductive behavior in humans and other mammals. The biologically fundamental nature of the conscious waking state is beyond serious question.

Another hint of the fundamental biological nature of waking consciousness is the recent finding that wakefulness triggers the expression of early-immediate genes in rats ([Cirelli, Pompeiano, & Tononi, 1996](#)). Early-immediate genes are highly conserved among species, and appear to be needed for fundamental functions such as learning. This kind of basic biological evidence suggests a long evolutionary development, leading to recognizably conscious and unconscious states in humans and other species ([Baars, 1987, 1993](#)).

Not so long ago it was common for some observers to claim that consciousness might be an epiphenomenon, with no causal role at all (e.g., [Block, 1995](#)). On the weight of the evidence, however, it seems that waking consciousness involves a basic biological adaptation with many survival functions.

14. Consciousness beyond mammals

What about non-mammals? The gross anatomy of bird brains they seems different from mammals. Like most non-mammals, birds have collections of nuclei rather than the beautiful fiber radiations of the thalamus into cortex. But gross-level nuclei could still have neuronal connectivities that are similar to the T-C system. At the level of neurons there is interesting evidence suggesting homologies. Some birds certainly pass the behavioral test. Irene Pepperberg's African Grey Parrot Alex is able to use spoken words accurately, which is another way of satisfying the accurate report criterion. Ravens spontaneously perform gaze-sharing (looking in the same direction to see an "intersubjective" object). Other birds bury nuts for the winter, and can find them very accurately when the visible scenery has changed very much. That is another measure of accurate report.

So the evidence is very strong for mammals, and a little less so for birds. What about large-brained invertebrates, like squid or octopi? How about fast-moving reptiles like lizards, or at a larger brain scale, Komoda Dragons? We need more evidence, but these questions are becoming ripe to be studied.

15. Summary

Cumulative evidence suggests that consciousness is a fundamental biological adaptation. The known brain correlates of consciousness appear to be ancient phylogenetically, going back at least to early mammals. In all mammals alertness and sensory consciousness are required for the goal-directed behaviors that make species survival and reproduction possible. In all mammals the anatomy, neurochemistry and electrical activity of the brain in alert states show striking similarities.

After more than seven decades of discoveries about waking as well as sensory consciousness, we have not yet found fundamental differences between humans and other mammals. Species differences such as the size of neocortex seem to be irrelevant to the existence of alertness and sensory consciousness, though different mammals obviously specialize in different kinds of sensory, cognitive and motor abilities.

Skeptics sometimes claim that objective evidence for consciousness tells us little about subjective experience, such as the experience of conscious pain. Scientifically, however, plausible inferences are routinely based on reliable and consistent patterns of evidence. In other humans we invariably infer subjective experiences from objective behavioral and brain evidence—if someone yells Ouch! after striking a finger with a hammer, we infer that they feel pain. The brain and behavioral evidence for subjective consciousness is essentially identical in humans and other mammals.

On the weight of the objective evidence, therefore, subjective experience would seem to be plausible in all species with human-like brains and behavior. Either we deny it to other humans, or, to be consistent, we must also attribute it to other species that meet the same objective standards.

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