The biological cost of consciousness.

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Abstract

Some philosophers maintain that consciousness as subjective experience has no biological function. However, conscious brain events seem very different from unconscious ones. The cortex and thalamus support the reportable qualitative contents of consciousness. Subcortical structures like the cerebellum do not. Likewise, attended sensory stimuli are typically reportable *as* conscious, while memories of those stimuli are not so reportable until they are specifically recalled.

Reports of conscious experiences in normal humans always involve subjectivity and an implicit observing ego. Unconscious brain events are not reportable, even under optimal conditions of report. While there are claimed exceptions to these points, they are rare or poorly validated.

Normal consciousness also implies high availability (rapid conscious access) of the questions routinely asked of neurological patients in the Mental Status Examination, such as common sense features of personal identity, time, place, and social context. Along with "current concerns," recent conscious contents, and the like, these contents correspond to high frequency items in working memory. While working memory contents are not immediately conscious, they can be rapidly recalled to consciousness.

The anatomy and physiology of reportable conscious sensorimotor contents are ultraconserved over perhaps 200 million years of mammalian evolution. By comparison, full-fledged language is thought to arise some 100,000 years ago in homo sapiens, while writing, which enables accelerated cultural development, dates between 2.5 and 6 millennia. Contrary to some claims, therefore, conscious waking precedes language by hundreds of millions of years.

Like other major adaptations, conscious and unconscious brain events have distinctive biological pros and cons. These involve information processing efficiency, metabolic costs and benefits, and behavioral pros and cons. The well-known momentary limited capacity of conscious contents is an example of an information processing cost, while the very large and energy-hungry corticothalamic system makes costly metabolic demands.

After a century of scientific neglect, fundamental concepts like “conscious,” “unconscious,” “voluntary” and “non-voluntary” are still vitally important, because they refer to major biopsychological phenomena that otherwise are difficult to discuss.

1.0 Introduction

The scientific study of consciousness has been debated for more than a century, in part because of the difficulty of verifying conscious experiences in humans and other species. However, both technical and conceptual advances have now clarified the evidence, and viable hypotheses have emerged, so that in 2005 the journal *Science* listed "the biological basis of consciousness" as one of the major open questions in science. Well-known scientists like Francis Crick and Gerald M. Edelman have advanced significant ideas about the brain basis of consciousness, and discussion of non-human consciousness has also found increasing acceptance in neurobiology. (Edelman, 1989; Crick & Koch, 2003; Edelman et al, 2010). Mammals share the corticothalamic system that supports reportable conscious experiences in humans. Avian homologies may exist for the corticothalamic complex. (Kaas & Preuss, 2003). Some cephalopods have rodent-like brain size, high neuroanatomical complexity, and flexible problem-solving capacities, suggesting that they may have conscious cognition, assuming that such processes are of ancient origin, or that, like lensed eyes, they may exhibit parallel evolution. (Seth et al, 2005).

Humans are our best-studied species when it comes to conscious contents, since we can communicate our experiences using speech. However, language is much more recent than consciousness as such. Language-related symbolic artifacts appear in the archeological record perhaps 100,000 years ago, and the outside estimates are perhaps twice that long. The mammalian brain, which prominently features the corticothalamic core and its characteristic circadian states, is closer to 200 million years of age, and may well emerge even earlier. If we include reptiles, like salamanders, which have (iso) cortex and thalamus, conscious events may go back even earlier.

In contrast, human aphasics who are deprived of language, or people who never developed language, still show the expected behaviorial and neuronal features of conscious waking and sleep. Judging by corticothalamic anatomy and physiology, sensorimotor aspects of consciousness emerge long before language.

It is useful to divide human conscious experiences into "primary" (sensorimotor) and "higher-order" (language-dependent) types. Higher order consciousness is thought to flourish mainly in humans. It excludes purely sensory and motor events but includes autobiographical memories, esthetic skills and experiences, self-awareness, prefrontal inhibition of limbic impulses, and adult semantics and syntax. The posterior and motor cortex (and corresponding thalamic nuclei) are involved in primary consciousness, while linguistic and semantic regions of the frontal and temporal lobes supports many higher-order functions. While the boundary between primary and higher-order consciousness is not precise, the distinction is often useful.

Both primary and higher-order conscious events are reportable under well-established conditions. Indeed, all of our knowledge of sensory psychophysics depends upon such reports. In the macaque, “match to sample” tasks have been used to report sensory events, especially for vision and memory tasks. Macaques and humans have strikingly similar visual psychophysics, and the methodology for eliciting that information is also similar. In non-linguistic species “voluntary match to sample reports” provide a useful functional analogue for human verbal reports.

If such reports are combined with the known anatomy and physiology of conscious brains, the circle of proven conscious species may expand beyond humans, primates, and even mammals.

1.1 Neuroanatomy and physiology.

The visible anatomy of the brain has been studied in detail since the Renaissance. Medical students have learned for generations that bilateral lesions of the human cerebellum do not severely impair the flow of reportable conscious experiences, although fine motor control is lost. While the scientific understanding of these brain structures continues to be refined, these observations still stand.

While circadian states of the corticothalamic (T-C) are regulated by basal brain nuclei, Steriade (2006) and others maintain that this very large region can be viewed as a single integrated oscillatory medium, ranging from single cells to entire cortical hemispheres. The T-C core is distinguished by a very high level of parallel-interactive organization, quite different from the highly modular organization of the cerebellum. The T-C core is believed to sustain high levels of informational integration and differentiation, analogous to the worldwide web. (Tononi, 2004).

The T-C core appears to be the primary organ of learned adaptation in humans and other mammals. In general, the waking (conscious) state is well-adapted to goal-relevant tasks like sensory perception, learning, exploration, path-finding, infant-mother interactions, and species-specific problem-solving (such as food finding), while SWS is adapted for the consolidation of learned memory traces acquired during waking. "Active sleep," associated with dream reports in humans, shows waking-like EEG along with skeletal muscle inhibition characteristic of SWS. Brain imaging of human dream activity shows high BOLD levels in limbic (emotional and appetitive) and visual regions (Dang-Vu et al, 2010).

Cortex and thalamus take up about 80% of the volume of the human cranium, consisting mostly of white matter fibers emerging from multi-layered arrays of neuronal cell bodies. The nuclei of the thalamus are folded neuronal arrays that closely mirror cortical regions. Major input, output, and internal pathways together create the largest parallel-interactive biological structure known. The corticothalamic (T-C) complex may use about 20% of the total energy intake, which cannot be interrupted without causing cell death (Baars and Gage, 2010).

Circadian states alter the dominant electrophysiological regime of cortex and thalamus, between waking, slow-wave sleep and REM dreams. Waking is optimized for learning and voluntary control. Slow-wave sleep enables consolidation of information acquired during the preceding waking period. Hundreds of genes are expressed differently in different circadian states.

In the waking brain, therefore, conscious contents, as assessed by human voluntary reports and their analogues in animals, are distinctly associated with cortex and thalamus, while unconscious information processing occurs sub-cortically, in the cerebellum, basal ganglia, brainstem, etc. In humans, at least, subcortical structures do not directly underlie conscious contents, though neural activity triggered in the body and sensorium is reflected in consciousness via thalamic and cortical projections. Many central nervous system functions are never conscious, even during the waking state. For instance, hypothalamic and vestibular receptors do not result in distinctive conscious contents, while the classical receptor pathways often do.

The corticothalamic complex therefore appears to enable conscious experiences "as such." However, not all cortical contents are reportable. The so-called “dorsal stream of vision” (occipito-parietal) is known to have egocentric and allocentric visuotopical maps, but unlike ventral visual events, these cannot be reported voluntarily. Dorsal stream maps can have dramatic effects on conscious vision, as in the case of parietal hemineglect. However, they do so indirectly, presumably when the two visual streams are combined in the medial temporal lobe. Such interactions between conscious and unconscious sensory streams are believed to occur in other sensory systems as well.

There are probably no entirely conscious tasks; all studied tasks involve both conscious and unconscious elements.

1.2 Electrophysiology.

EEG “arousal" has been the basic electrophysiological index of waking consciousness in humans and related species. It is the appearance of fast, irregular, and low-voltage EEG across the mammalian cortex, as well as in deeper brain structures. In healthy animals EEG arousal is always accompanied by signs of behavioral arousal, including alert posture, receptor orienting, vigilant scanning of the surroundings, social signaling, physiological signs of the orienting response (including widespread autonomic responding), voluntary and emotional activities, and well-timed, context-sensitive behavior. (Baars and Gage, 2010)

Scalp EEG sacrifices all but 0.1 percent of the electrical field amplitude of the cortex, so that implanted subdural electrodes are far superior as a recording tool, supplemented by a variety of sophisticated in vivo instruments, ranging from MRI and fMRI to voltage-sensitive dyes. In vivo experimental interventions also include chemical, electrical, and electromagnetic field stimulation.

Since waking-like cortical EEG also occurs during REM dreams, EEG arousal is not a sufficient sign of normal waking by itself. It is useful to add at least one more easily observable index, such as voluntary responding to stimulation.

In general, healthy humans and other mammals are arousable by intense stimulation at all times. During unconscious sleep behavioral arousal still occurs in response to intense stimulation, like loud sounds, calling someone's first name, or pressure on the thumb, a common test for coma. Failure of stimulus-evoked behavioral arousal is a sign of pathology, except in the case of general anesthesia.

Slow wave sleep (SWS) is the only natural unconscious state, characterized by regular, high amplitude delta waves in the corticothalamic system (2-4 Hz). However, slow background oscillations occur at all times, at < 1 Hz. These slow oscillations are not easily visible in the scalp EEG.

Dreaming states are often but not always signaled by rapid, stereotyped eye movements (REM). Classical REM dreams show waking-like EEG. During SWS massive numbers of cortical and thalamic neurons pause during the trough of the delta wave, thereby apparently blocking the free flow of neuronal firing and interaction. However, when people are awoken from SWS they may report verbal sleep mentation, which is said to be less imaginative and less visual than normative dreams. The reason for SWS mentation is unknown, but it may be that some cortical islands of waking activity can remain during behavioral sleep, especially during the peak of the repeating delta wave. Islands of normal cortical functioning are also known to occur during some epileptic seizures.

2.0 Conscious waking and sleep as biological adaptations.

The conscious state makes possible all goal-directed activities in humans. Consciousness also enables strikingly precise reports of sensory input and executive attention, which brings specific events to consciousness in much the way that voluntary eye movements enable specific visual inputs (Posner et al). Selective attention and conscious cognition enable both working memory (notably inner rehearsal) and encoding of events in episodic memory. Thus the conscious state and its stream of reportable contents, including action planning and attentional control, appear to support the great bulk of biologically significant, goal-directed behavior in humans. During sleep and dreams we can do none of these things.

2.1 Metabolic and information processing costs and benefits.

The pros and cons of sleep and waking can be divided into metabolic and information processing.

The chief information processing cost of conscious and attentional function is "limited momentary capacity," and therefore distractibility. Predators routinely make surprise attacks from hidden cover when a prey animal appears to be distracted by food or by spoor-following. Distraction is itself a function of limited focal processing capacity. Voluntary attention is also a limited capacity function, so that voluntary selection of one or another potential conscious event takes a significant period of time and loads limited capacity.

When humans and animals are surprised by some unexpected, significant event, it can take them many seconds to recover their previous stable orientation. In the cases of psychological trauma adaptation can take much longer. A surprising event can block conscious sensory processing by half a second or longer. While such time and processing costs are not significant in safe situations, they can make a difference between life and death in cases of predation, sexual competition, infant protection or physical accidents. These factors impact reproductive fitness, and in principle one could imagine a non-conscious animal that might not face these tradeoffs.

For example, a number of human babies are born with agenesis of the corpus callosum, so that direct communication between the hemispheres is either blocked, or it is developmentally accomplished subcortically. If humans would achieve a net benefit from having two separate streams of consciousness, one for each half of the sensorimotor hemifield, one might expect that humans without a corpus callosum obtain a net benefit in reproductive fitness. While that biological experiment appears to occur spontaneously tens of thousands of times every year, humans with binary streams of consciousness have not driven out more conventional brains. This suggests a net benefit for the otherwise remarkable limitations of having a single and narrow conscious stream in a brain that would seem to be otherwise capable of intelligent parallel processing.

Consciousness is strongly associated with sensory processes, exploratory learning and the construction of cognitive maps of the body and the environment, both through hippocampal and parietal regions. Prefrontal functions are involved in problem solving, decision making, and infant-mother attachment, as well as limbic impulse control. All these capacities are of reproductive and survival benefit.

Thus conscious processes pose both information-processing costs and benefits for mammals.

2.2 Metabolic costs.

The metabolic cost of the conscious state, and of specific conscious experiences, appears to be substantial. These costs are associated with the energetics of the T-C system, which occupies an estimated 80 percent of the cranium in humans.

2.3 Learning in primary consciousness and sleep.

While some major costs of the brain system that enables consciousness are clear enough, the positive function of consciousness has long been controversial. On the simplest observational level, however, all goal-directed survival and reproductive actions occur during the waking state, and disappear during sleep, when the inhibition of skeletal musculature prohibits goal-directed, cortically guided actions. Needless to say, vegetative functions and a great variety of other non-goal-directed neuronal functions continue during sleep. The sleep/waking cycle has been reliably associated with the differential expression of some hundreds of nervous system genes. These are thought to be particularly associated with learning and neuronal plasticity. Slow Wave Sleep is believed to accelerate memory consolidation via structural protein production, the replenishment of mitochondria, rebuilding neuronal and glial stores of neurotransmitters, and the like.

In rats it has been shown that three weeks of total sleep deprivation results in death due to unknown causes. The inverse, namely the induction of long-term coma-like states via general anesthetics, for example, does not have direct lethal effects, and in the case of humans, long-term coma has been known to last as long as eleven years while still allowing for recovery of consciousness. However, in these cases it is not certain whether momentary periods of non-behavioral waking may have occurred on a regular basis, a phenomenon that is now thought to be common enough to suggest a specific diagnosis for coma-like intermittent waking, the so-called Minimally Conscious State (MCS).

Because sleep and waking are mutually enhancing states, and seem to reflect the same underlying brain structures, the fact that sleep deprivation leads to rapid death while waking deprivation does not should not be interpreted to mean that sleep is a biological necessity but waking is not. Counter to that runs the observation that no goal-driven survival and reproductive actions occur in mammals outside of the waking state.

2.4 Reproductive fitness.

Vocalization, as in speech and song, and the associated arts of drumming and rhythmic social dancing, have been thought to arise as a mechanism of sexual selection. They are certainly used that way by human cultures. In some primates, like gibbons, vocalization is used for sexual as well as dominance signaling. However, vocal display also attracts attention from unwelcome enemies and sexual competitors. The ability to "narrow-cast" rather than broadcast sounds is therefore plausibly a safer way to attract attention from potential mates.

The brain regions for language, like Broca's and Wernicke's areas, are thought to be crucial for "higher-order consciousness" (Edelman, 1989), which make very fast cultural development possible for humans. However, these cortical regions have long evolutionary histories long before the primates. Lateralization of sound production is found in guinea pigs as well as birds. The putatively “language-related” gene FOX P2 is now known to exist in reptiles as well as mammals.

In humans, speech and other frontal lobe capacities may have co-evolved. They are plausibly the crucial enabling capacities for cultural development. Thus speech, song, dance, and other symbolic forms of expression, and their biological correlates such as executive overriding of limbic brain regions, the use of symbolic signaling for group identity, and the like, all define a very large domain of empirical study, and can only be mentioned here in passing.

3.0 Pathologies of sleep and waking.

In general, we do not have a foolproof objective index of conscious (i.e., subjectively normal) and unconscious states. While scalp EEG, skeletal muscle tone, voluntary eye movements, and voluntary responding to questions and stimuli are extremely useful, they are by no means perfect indices of brain states.

A great deal of medical and basic research is focused on sleep disorders. It should be pointed out that there are numerous waking disorders as well. Because the word "consciousness" has been viewed with some suspicion, we may be missing crucial aspects of mental disorders or the dementias because we do not consider them to be disorders of waking consciousness. All of the DSM Axis I disorders, for example, are also deficits of voluntary control over covert or overt brain activities.

Anything that impairs normal waking consciousness increases risk to survival and reproduction. While waking consciousness has its own informational and metabolic costs, biological risk due to the loss of consciousness is vastly greater. During natural sleep and dreaming all goal-directed activities are blocked. Before going to sleep animals seek safe shelter underground, in denses bushes or rock formations, hollows and trees, or among other group members. Sleeping animals are attuned to danger signals that trigger arousal, which may vary from species to species, and both seasonally and situationally. Thus the presence of predators during the day may also trigger more awakenings to potential dangers during sleep.

3.1 Coma, anesthesia, and the epilepsies.

In the last decade, the diagnosis of irreversible coma, as assessed by EEG and behavioral unresponsiveness, has come under serious question. Up to 40% of coma or Persistent Vegetative State (PVS) patients may be in an intermittently conscious state. For that reason the diagnosis of "Minimally Conscious State" (MCS) is being advanced as a more precise and ethical alternative to PVS. Some medications have also been reported to improve or even reverse diagnosed coma.

On the other end of the continuum, apparent general anesthesia may hide mid-operative awakenings that can be recalled afterwards by patients, even if the attending anesthesiologist may not detect them.

The appearance of coma may hide underlying periods of consciousness, most spectacularly in the case of "locked in syndrome," where the patient is normally conscious while skeletal muscle control is widely inhibited. Voluntary eye movements have been used to enable paralyzed patients to communicate by foveal fixation on the letters of a keyboard. Some locked-in patients have carried on web-based conversations over long periods of time.

The epilepsies show mixtures of conscious and unconscious events, voluntary control and non-voluntary automatisms, as well as variations in the spread of brain areas that are recruited by seizure activity. Epilepsy is also associated with mystical and other non-ordinary conscious experiences.

Epileptic unconsciousness mimics SWS in many respects, including slow, high-amplitude, widespread, hypersynchronous scalp EEG. These are important frontiers for current research.

4.0 Higher-order consciousness.

Culture, self-awareness, language, music, technology, science, and the arts all depend upon language and related aspects of higher-order consciousness. The frontal lobes --- classically called “the organ of civilization “ --- are still some of the least well-understood areas of the cortex, because of their complexity and variability under different task conditons.

4.1 Speech.

The speech regions of cortex almost certainly co-evolved with specialization of the vocal tract, which makes human speech probably the fastest and most precisely controlled flow of sequential movements in the animal repertoire. This co-evolution plausibly occurred over long evolutionary epochs.

Broca's area is almost always lateralized, with some 90 percent of humans using the left hemisphere for the production of speech. Auditory speech perception appears to be bilateral, though the dominant hemisphere is believed to be have better temporal auditory discrimination while the non-dominant side may excel in the emotional and metaphorical interpretation of speech.

The loudness, segmental length and auditory resonances of vocalization are also good surrogates for lung capacity, strength, reproductive capacity, mental alertness, youth and muscular vigor, and the availability of food, as well as clan size, gender and social dominance.

The most important point for the present purpose, however, is that speech as an evolutionary development appears to greatly accelerate cultural evolution, including "higher order consciousness," which Edelman (1989) suggests includes shared meanings and abstractions, the entire vocabulary of human languages as a set of cultural discoveries, and indeed science, the arts, and technology. Indeed, even today the size of one's vocabulary is a good predictor of intelligence, which may reflect the capacity for mental effort as shown by BOLD activation of the prefrontal cortex.

About 6 millenia ago vocal speech was transformed into widespread writing systems, as in the case of China, Egypt, Sumer, India and the Middle East. About 2.5 millenia ago, phonemic and syllabic writing systems greatly simplified the encoding of vocal speech into written symbols. Widespread writing enabled multi-generational cultural memory among extended populations, leading to city states and all their attendant sociological and cultural complexities. Thus over the last 3-6 millenia cultural evolution has increased much faster than biological evolution, leading both to benefits and difficulties.

Thus vocal speech and its related evolutionary functions, like song, dance, executive control and social coordination, produce many novel conscious contents, including concepts, beliefs, symbolic expressions, individual and shared fantasies, musical forms, dancing, and the like, which become socially shared as the speaking brain evolves.

4.2 Self-awareness, flow and absorption.

Lucid dreaming occurs when subjects are aware they are dreaming. During REM dreaming (with waking-like EEG), trained lucid-dreaming subjects can hear auditory stimuli, and can count up to ten in inner speech, signaling the beginning and end of the ten-second period using agreed-upon voluntary eye movements. This self-aware type of dreaming has been widely reported informally, and the ten-second period corresponds well to the typical decay time of short-term memory during waking. The commonly reported experience of dream paralysis may in fact be spontaneous lucid dreaming, in which subjects realize that their limb and head muscles are inhibited, which is part of the normal physiology of sleep and dreams. When people try (cortically) to move their muscles, and they cannot move, they may feel unpleasantly paralyzed. However, dream paralysis is not a disorder but plausibly a self-aware period of normal dreaming.

Self-awareness in general may depend upon the frontal lobes. Thus lucid dreaming is in a sense the opposite of drowsy or sedated states, when people have waking sensory abilities but little executive control or self-awareness. Experiences of "conscious flow" as reported by high-functioning athletes or artists may also involve "frontal hypometabolic" states. High levels of theta and alpha power have been found in such states. High-functioning individuals commonly report a drop in unneeded self-consciousness during flow states, such as distracting worries about one's own performance.

5.0 Summary and conclusions.

Conscious waking and its variety of reportable contents appears to be biologically ancient and widespread. All reportable sensory and executive motor events involve cortical and often consciously-mediated processes. Like other biological adaptations, conscious waking, sleep, and dreaming appar to have distinctive costs and benefits.

Conscious waking allows for all explicit, goal-directed actions to occur. Waking may be optimized for learnng, and most of what we know about the sensory system comes from human and animal "behavioral reports" during the conscious waking state. Slow-wave sleep may be optimized for memory consolidation, while the role of classical REM dreams remains unresolved.

Metabolically, waking, sleep and dreaming depend upon the thalamus and cortex, which together occupy some 80 percent of cranial capacity, a very large biological investment. From an information processing perspective both conscious waking and sleep have survival and reproductive costs, consciousness because of the well-known limited momentary capacity of conscious contents, which place animals at risk of accidents or predation during moments of distraction. Sleep renders animals unresponsive to biological dangers and opportunities, and apparently unable to learn.

While philosophical debates continue, the scientific key is to compare conscious and unconscious brain states and reportable vs. unreportable contents. These are relatively easily observable, and allow us to gain a third-person perspective on what has traditionally been described from a subjective point of view. Over the past decades a very large empirical and medical literature has emerged using such comparisons.

The medical sciences have never adopted behavioristic strictures against consciousness, because its everyday relevance in the hospital and clinic is indisputable. In science, concepts like subjective consciousness and volition are also indispensable.

Primary or sensorimotor consciousness provides the biological foundation of mammalian environmental learning. Cultural evolution is crucially dependent upon frontal lobe functions like language and executive control. The explosion of cultural technologies in the last 6-100 millennia is therefore dependent upon both primary and higher-level consciousness.

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