

THERE ARE NO KNOWN DIFFERENCES IN BRAIN MECHANISMS OF CONSCIOUSNESS BETWEEN HUMANS AND OTHER MAMMALS

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Abstract

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Recent scientific findings indicate that consciousness is a fundamental biological adaptation. The known brain correlates of consciousness appear to be phylogenetically ancient, going back at least to early mammals. In all mammals, alertness and sensory consciousness are required for the goal-directed behaviours 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 cumulative discoveries about waking and sensory consciousness, we have not yet found any 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.

Sceptics 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 behavioural and brain evidence – if someone yells ‘Ouch!’ after striking a finger with a hammer, we infer that they feel pain. The brain and behavioural 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 equally plausible in all species with human-like brains and behaviour. Either we deny this experience to other humans (which is rarely done) or, to be consistent, we must also attribute it to other species that meet the same objective standards. It seems that the burden of proof for the absence of subjectivity in mammals should be placed on the sceptics.

Keywords: animal awareness, animal welfare, attention, consciousness, waking

Global scepticism about consciousness in the 20th century

Charles Darwin (1838-1840) wrote that ‘consciousness appears to be the product of complexity of organization’, a hypothesis that continues to draw serious scientific attention today (eg Tononi & Edelman [1999]). In the 19th century, scientists like Darwin treated consciousness as an undeniable scientific topic. Research on conscious sensory perception, conscious and unconscious influences on memory, selective attention and even hypnosis began in the 19th century. The 1300 pages of William James’ *The Principles of Psychology*

(1890/1983) provide an extraordinary guide to the riches of empirical knowledge about consciousness that was obtained during that period. They are filled with facts that have since been rediscovered, and which are the focus of much current research (eg Baars [1986, 1988, 1997]; Baars & Newman [in press]).

Yet in the years before 1900, the open-minded scientific attitude toward human and animal consciousness began to change. Thomas Henry Huxley, known as Darwin's bulldog for his public defence of evolution, suggested that consciousness might be a useless by-product of normal brain functioning. He wrote (quoted in James [1890/1983 p 135]) 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.

The *empirical* phenomena of consciousness, which are plentiful and easy to obtain in a reliable fashion, became entangled in the snares of the mind-body problem, a set of philosophical conundrums that appeared to be impossible to settle. Further, consciousness came to be seen, in the words of the American behaviourist John B Watson (1925), as 'nothing but the soul of theology'. It soon fell victim to a culture war between science and religion. Scientists rejected it as a snare and a delusion.

In biology, C Lloyd Morgan proposed the 'Lloyd Morgan Canon', claiming that anthropocentric 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 (eg 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 in Skinner [1976]). Behaviourism 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 was forgotten. Behaviourists popularised several standard criticisms of 19th century consciousness science, but those criticisms have now themselves come under serious question (eg Blumenthal [1979]; Hilgard [1987]). They appear to be almost entirely erroneous.

Since the decline of behaviourism, hundreds of facts about consciousness described in James' *Principles* have been rediscovered (Baars 1986). Indeed, 19th century findings about topics like sensory psychophysics have continued to accumulate in the last 100 years without serious controversy. No one can have a simple eye examination today without benefiting from psychophysical methods first developed in the 1820's. 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 the topic of consciousness became a scientific taboo. Obviously, for those who doubt that humans are conscious, the question of consciousness in other animals cannot be addressed with an open mind.

Thesis

The evidence is now massive that behaviouristic sceptics were wrong. The functional importance of consciousness in humans, as assessed by objective evidence that has accelerated in the last 2 decades, is beyond serious empirical dispute. Further, in the last 70 years of cumulative research on the brain basis of consciousness, we have found no convincing evidence for any essential difference between humans and other mammals in regard to the existence of waking alertness and perceptual consciousness.

What is this evidence?

The evidence: brains support consciousness across a wide range of species

It is essential first to distinguish between ‘intelligence’ (ie problem solving) and ‘consciousness’ (ie wakeful alertness and conscious perception, including the perception of pain and pleasure). We know of hundreds of differences between humans and other mammals in intelligent problem-solving tasks, ranging from word retrieval to migratory travel. Such problem-solving abilities are highly species-specific. Early in life, humans all over the world are able to learn a very large word vocabulary, rapidly retrieving the right words from thousands of possibilities on demand. Human word learning and word retrieval demonstrate a unique 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 many hundreds of such distinctive species-specific abilities. Yet the fundamental brain mechanisms of conscious alertness and of conscious sensory perception are not limited to one or a few biological species. They have an extremely wide distribution among vertebrates and invertebrates. Species differences such as the size of neocortex seem to be irrelevant to the existence of 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. But these points are likely to apply beyond mammals as well.

Operational definition of consciousness: accurate report

In humans, the standard observational index of consciousness is ‘accurate, verifiable report’ (eg Baars [1988, 1997, 1998]). 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 at 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, ie 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 behaviour 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.

The 'commentary key' as evidence for consciousness

Sceptics 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 rhesus macaque (*Macaca mulatta*), allowing it to give a behavioural 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, 'Mummy, aeroplane!' 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 (blindsight), 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 part of 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 colour, 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 colour, 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 colour and motion, which humans with similar brain damage report losing. The macaque's visual brain resembles the human one in a number of respects. Careful lesion studies have shown 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 colour, motion and texture? Cowey and Stoerig make this case, using a behavioural 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 colours, for example. The commentary key allows it to signal whether its accurate behaviour 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 my 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.

Other behavioural evidence for consciousness

Many other behavioural sources of evidence indicate the existence of consciousness. For example, mere distractibility in animals indicates limited capacity for competing sensory streams, a well-established feature of conscious but not unconscious processes (eg Baars [1988, 1998]). 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 waterhole, it cannot at the same time monitor what its offspring is doing, whether a predator is in the neighbourhood, 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 behaviour, the willingness of animals to work for novel or biologically significant information. Finally, animals show unmistakable behavioural 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 (see, *The 'commentary key' as evidence for consciousness*). There is an effective consensus today that consciousness can be attributed in the case of visual perception in macaques, using the very rigorous criteria discussed 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 behavioural 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 shows 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.

Thus, we do not really need advanced brain monitoring techniques to show that mammals are conscious. Yet such techniques clinch the case for animal consciousness beyond any reasonable doubt, as we shall see.

Electrical brain activity of waking consciousness

It has been known since the late 1920's 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 animal EEG studies are routinely assumed to apply 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 well understood. During unconscious sleep, slow-wave global EEG appears to reflect highly regular and coordinated burst-pause firing patterns in many billions of individual neurones in thalamus and cortex. In contrast, waking EEG reflects irregular firing in the same billions of single neurones, as well as complex interactions between them (Destexhe *et al* 1999). The regular burst-pause pattern of neurones during slow-wave sleep is highly synchronized, with effective zero-lag correlations between individual neurones at a distance of a centimetre or more. Significantly, the same pattern of slow-wave, synchronized EEG appears in other states of global unconsciousness such as general anaesthesia, coma and epileptic 'states of absence'. 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 electrical brain activity between waking and deep sleep (eg Bressler & Freeman [1980]; Freeman [1991]; Steriade [1995]; Rechtschaffen & Siegel [2000]). I have not been able to find a single exception to these findings reported among mammals. Thus we have some 70 years of highly consistent evidence related to brain activity during consciousness and its absence in humans and other mammals.

Neuroanatomy needed for waking consciousness

In years past it was commonly said that consciousness must be some vague and non-specific feature of the human brain. In fact, anatomically, conscious waking depends on quite small and specific parts of the brain in both humans and animals. The waking state can be abolished by less than 1cm³ lesions in the brainstem reticular formation and even smaller bilateral cuts in the intralaminar nuclei of the thalami (Moruzzi & Magoun 1949; Bogen 1995). In contrast, very large volumes of cortex can be lost without impairing waking consciousness. Entire hemispheres are routinely removed surgically without inducing coma or a loss of consciousness. It appears therefore that, anatomically, waking consciousness is not some vaguely global property of the brain; it is dependent on a few highly specific brain locations (Magoun 1962; Hobson & Brazier 1980; Scheibel 1980; Edelman 1989).

While the circadian sleep-waking cycle is controlled by brainstem mechanisms, in humans and other primates the content of perceptual consciousness seems to depend on cortex (Livingstone & Hubel 1981; Zeki 1993; Cowey & Stoerig 1995; Van Essen & Anderson 1995; Sheinberg & Logothetis 1997). There may be species differences in this respect, with visual contents being increasingly dependent on the tectum in early mammals. However, in all mammals the state of waking consciousness seems to require only two small anatomical areas, the brainstem reticular formation and intralaminar nuclei of the thalamus (Bogen 1995).

Notice that brainstem mechanisms like the reticular formation are extremely phylogenetically ancient, going back at least to early vertebrates. Thalamic structures like the intralaminar nuclei also exist in mammals generally. Both these facts indicate that the brain anatomy of waking consciousness is very ancient indeed (Magoun 1962; Edelman 1989; Rechtschaffen & Siegel 2000).

Neurochemistry of waking consciousness

In all mammals, waking, sleeping and dreaming are controlled by brainstem nuclei that widely project their axons to the forebrain, secreting neuromodulators, neurochemicals that have very wide and highly coordinated effects. Hobson (1997 p 392) 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.

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

High-dose general anaesthesia often shows a slow-wave pattern of EEG similar to deep sleep, though often mixed with other waveforms. While different anaesthetic 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 *et al* (in press) have found evidence for a thalamocortical switch in general anaesthesia across different anaesthetic agents.

The neural basis of conscious vision in the human and primate cortex

In addition to these basic findings about the *state* of consciousness, in the last 20 years we have made considerable progress on understanding the *contents* of consciousness as well, at least with regard to perceptual consciousness in the visual cortex of 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-neurone recording studies, Logothetis and colleagues have used binocular rivalry at different levels of visual analysis to track neurones responding to both conscious and unconscious input features in the ventral temporal lobe 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 neurones. Rival 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 per se (Logothetis & Schall 1989; Sheinberg & Logothetis 1997).

For example, a downward flow of stairway 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 neurones 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 neurones 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 neurones in the anterior pole of the inferotemporal cortex (area IT), and in the superior temporal sulcus. Thus each level of visual feature analysis can be interrogated with a distinct set of binocular stimuli, one conscious and the other not (Sheinberg & Logothetis 1997).

Earlier work showed that binocular rivalry activates small numbers of cells in early visual cortex, where single visual features are represented, such as colour, 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 area IT. In this region, 90 per cent of neurones 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 favours the conscious stream (Van Essen & Anderson 1995). 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 neurones, and the same overall psychophysical parameters of vision, it becomes implausible to deny that macaques and their close relatives must be visually conscious much as humans are.

Consciousness as a fundamental biological adaptation

Mammalian locomotion, hunting, evasive action by prey, 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 (Magoun 1962; Scheibel 1980; Edelman 1989). Perceptual consciousness, as defined objectively by recent brain research, only takes place during waking periods (Geschwind 1979; Livingstone & Hubel 1981). It therefore appears that brain activity that supports consciousness is a precondition for all goal-directed survival and reproductive behaviour 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 and, possibly, other species (Cirelli *et al* 1996). Early-immediate genes appear to be involved in numerous fundamental functions including learning. This kind of basic biological evidence indicates 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 (eg Block [1995]). On the weight of the evidence, however, it seems that waking consciousness involves a basic biological adaptation with many survival functions.

Can we infer subjectivity in other mammals?

It is an inferential leap for me (as the subjective self) to believe in your (the reader's self) consciousness, and vice versa. Such inferential leaps are invariably made whenever we think about other people. But if we can easily make the inference of subjective consciousness about other humans, then why not beyond that to other creatures, if the objective basis for that inference is the same? It is sometimes argued that animal subjectivity is not a testable claim, but today we have a number of widely accepted scientific studies that have tested the inference about subjectivity in visual consciousness in monkeys, for example, and were able to support the hypothesis that macaques with humanlike visual brains have similar subjective visual experiences (Cowey & Stoerig 1995). When we include other kinds of sensory awareness (smell, taste and pain, for example) the circle of subjectively conscious animal species would seem to grow larger and larger. If we take the many signs of mammalian sleep-waking cycles as evidence, no mammalian species can be excluded. Non-mammals have not been studied in as much detail, but the domain of conscious species will probably expand as we learn more.

Sceptics sometimes claim that the 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 humans we invariably infer subjective experiences from objective behavioural and brain evidence; but that evidence is essentially identical in other mammals. On the weight of the objective evidence, therefore, subjective experience would seem to be equally plausible in humans and other mammals. Either we deny it to other humans (which is rarely done) or, to be consistent, we must also attribute it to animals that meet the same objective standards. It seems that the burden of proof for the absence of subjectivity in mammals should be placed on the sceptics.

References

- Alkire M T, Haier R J and Fallon J H** Toward the unified theory of narcosis: brain imaging evidence for a thalamocortical switch as the neurophysiological basis of anesthetic-induced unconsciousness. *Consciousness and Cognition* (in press)
- Baars B J** 1986 *The Cognitive Revolution in Psychology*. Guilford Press: New York, USA
- Baars B J** 1987 Biological implications of a Global Workspace theory of consciousness: evidence, theory, and some phylogenetic speculations. In: Greenberg G and Tobach E (eds) *Cognition, Language, and Consciousness: Integrative Levels* pp 209-236. Erlbaum: Hillsdale, USA
- Baars B J** 1988 *A Cognitive Theory of Consciousness*. Cambridge University Press: New York, USA
- Baars B J** 1993 How does a serial, integrated and very limited stream of consciousness emerge from a nervous system that is mostly unconscious, distributed, parallel and of enormous capacity? *Theoretical and Experimental Studies of Consciousness, Ciba Foundation Symposium 174*: 282-90; 291-303
- Baars B J** 1998 Metaphors of consciousness and attention in the brain. *Trends in Neurosciences 21*: 58-62
- Baars B J and Newman J (eds)** *Essential Sources in the Scientific Study of Consciousness*. MIT Press/Bradford Books: Cambridge, USA (in press)
- Block N** 1995 On a confusion about the function of consciousness. *Behavioral and Brain Sciences 18*: 227-287
- Blumenthal A L** 1979 Wilhelm Wundt – the founding father we never knew. *Contemporary Psychology 24*: 547-550
- Bogen J E** 1995 On the neurophysiology of consciousness: I. An overview. *Consciousness and Cognition 4*: 52-62
- Bressler S L and Freeman W J** 1980 Frequency analysis of olfactory system EEG in cat, rabbit, and rat. *Electroencephalography and Clinical Neurophysiology 50*: 19-24
- Cirelli C, Pompeiano M and Tononi G** 1996 Neuronal gene expression in the waking state: a role for the locus ceruleus. *Science 274*: 1211-1215
- Cowey A and Stoerig P** 1995 Blindsight in monkeys. *Nature 373*: 247-249
- Darwin C** 1838-1840 Old and useless notes. In: Barrett P H, Gautrey P J, Herbert S, Kohn D and Smith S (eds) *Charles Darwin's Notebooks, 1836-1844: Geology, Transmutation of Species, Metaphysical Enquiries*. Cornell University Press: Ithaca, USA
- Destexhe A, Contreras D and Steriade M** 1999 Spatiotemporal analysis of local field potentials and unit discharges in cat cerebral cortex during natural wake and sleep states. *Journal of Neuroscience 19*: 4595-4608
- Edelman G** 1989 *The Remembered Present: a Biological Theory of Consciousness*. Basic Books: New York, USA
- Freeman W J** 1991 The physiology of perception. *Scientific American 264*: 78-85
- Geschwind N** 1979 Specializations of the human brain. *Scientific American 241*: 180-201
- Hilgard E R** 1987 *Psychology in America: a Historical Survey*. Harcourt Brace Jovanovich: New York, USA

- Hobson J A** 1997 Consciousness as a state-dependent phenomenon. In: Cohen J D and Schooler J W (eds) *Scientific Approaches to Consciousness: the XXVth Carnegie Symposium on Cognition*. L Erlbaum Ass: Mahwah, USA
- Hobson J A and Brazier M A B (eds)** 1980 *The Reticular Formation Revisited: Specifying Function for a Non-specific System*. Raven Press: New York, USA
- James W** 1890/1983 *The Principles of Psychology*. Holt: New York, USA/Harvard: Cambridge, USA
- Livingstone M S and Hubel D H** 1981 Effects of sleep and arousal on the processing of visual information in the cat. *Nature* 291: 554-561
- Logothetis N K and Schall J D** 1989 Neuronal correlates of subjective visual perception. *Science* 245: 761-763
- Magoun H W** 1962 *The Waking Brain, 2nd edition*. Thomas: Springfield, USA
- Morgan C L** 1896 *Habit and Instinct*. Arnold: London, UK
- Moruzzi G and Magoun H W** 1949 Brain stem reticular formation and activation of the EEG. *Electroencephalopathy and Clinical Neurophysiology* 1: 455-473
- Rechtschaffen A and Siegel J M** 2000 Sleep and dreaming. In: Kandel E R, Schwartz J H and Jessel T M (eds) *Principles of Neuroscience* pp936-947. McGraw Hill: New York, USA
- Scheibel A B** 1980 Anatomical and physiological substrates of arousal. In: Hobson J A and Brazier M A B (eds) *The Reticular Formation Revisited: Specifying Function for a Non-specific System* pp 55-66. Raven Press: New York, USA
- Sheinberg D L and Logothetis N K** 1997 The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences, USA* 94: 3408-3413
- Skinner B F** 1976 *Particulars of My Life*. Knopf: New York, USA
- Steriade M** 1995 Brain activation then (1949) and now: coherent fast rhythms in corticothalamic networks. *Archives Italiennes de Biologie* 134: 5-20
- Tononi G and Edelman G M** 1999 Consciousness and complexity. *Science* 282: 1846-1851
- Van Essen D C and Anderson C H** 1995 Information processing strategies and pathways in the visual system. In: *An Introduction to Neural and Electronic Networks, 2nd edition*. Academic Press: New York, USA
- Watson J B** 1925 *Behaviorism*. Norton: New York, USA
- Weiskrantz L** 1991 Disconnected awareness for detecting, processing, and remembering in neurological patients. *Journal of the Royal Society of Medicine* 84: 466-470
- Zeki S** 1993 *A Vision of the Brain*. Blackwell Scientific: London, UK