

## **Criteria for consciousness in humans and other mammals**

Anil K. Seth\*, Bernard J. Baars and David B. Edelman

The Neurosciences Institute  
10640 John Jay Hopkins Drive, San Diego, CA 92121

email: [seth@nsi.edu](mailto:seth@nsi.edu), [bbaars@comcast.net](mailto:bbaars@comcast.net), [dedelman@nsi.edu](mailto:dedelman@nsi.edu)  
telephone: 858 626 2000  
fax: 858 626 2099

\*Corresponding author

### **Abstract**

The standard behavioral index for human consciousness is the ability to report events with accuracy. While this method is routinely used for scientific and medical applications in humans, it is not easy to generalize to other species. Brain evidence may lend itself more easily to comparative testing. Human consciousness involves widespread, relatively fast low-amplitude interactions in the thalamocortical core of the brain, driven by current tasks and conditions. These features have also been found in other mammals, which suggests that consciousness is a major biological adaptation in mammals. We suggest more than a dozen additional properties of human consciousness that may be used to test comparative predictions. Such homologies are necessarily more remote in non-mammals, which do not share the thalamocortical complex. However, as we learn more we may be able to make “deeper” predictions that apply to some birds, reptiles, large-brained invertebrates, and perhaps other species.

**Keywords:** Accurate report, brain physiology, mammals, thalamocortical system.

*The limits of behavioral criteria.*

“Accurate report” (AR) is the standard behavioral index for consciousness in humans. Accurate report is extremely useful and sensitive in people with intact brains. For example, we can report the light of a star on a dark night, involving a flow of single photons to a single retinal receptor. This conscious event corresponds to the lower limit of physical energy. Similarly subtle percepts are reportable in audition and touch. AR can thus be highly sensitive and accurate.

Accurate report in humans is not limited to verbal responses; any voluntary response will do. For example, eye-movements have been used in cases of paralysis or lucid dreaming. Because of its many convenient features, in particular, its broad applicability across disparate sensory modalities, AR has become routine as an index of conscious experience in both scientific and clinical applications, including cases of brain damage, medical diagnosis of pain, optometry and audiology.

Yet it is not easy to apply AR across a range of species. The closest homolog is accurate behavioral report in primates, for example, the pressing of a key to deliver a comment about a previous discrimination (Cowey & Stoerig 1995). Indeed it has become standard to use AR (by matching tasks) in rhesus macaque studies of vision. This has sound justification in the fact that the macaque visual cortex has striking similarities to that of the human, from the distribution of GABA receptor subunits across visual cortical layers to retinotopy and topographic homologies in certain visual areas, as well as similar functional maps for color vision processing in both species ((Tootell et al. 2003; Brewer et al. 2002; Hendry et al. 1994) but see (Preuss & Coleman 2002; Preuss et al. 1999)) for a review of species-specific differences in the visual cortices of humans, apes, and old and new world monkeys). Phenomena like blindsight, which are often taken to be relevant to visual consciousness, are also routinely studied in the macaque (Cowey & Stoerig 1995; Stoerig & Cowey 1997). AR can also be tested by naming tasks, which have been reported in a variety of species, including primates, cetacea, and such birds as African Grey Parrots and Budgerigars (Savage-Rumbaugh 1990; Savage-Rumbaugh et al. 1993; Marino 2002; Herman et al. 1990; Herman et al. 1993; Manabe et al. 1995; Pepperberg & Wilcox 2000; Pepperberg & Shive 2001; Richards et al. 1984; Griffin & Speck 2004). For a recent review, see (Griffin & Speck 2004).

However, behavioral measures risk a slippery slope. In principle, it is difficult to make a distinction between AR and other behavioral indices of sensory categories. The ability to distinguish between, and generalize across, classes of stimuli is extremely widespread in the animal kingdom. It has been demonstrated in mammals, birds, reptiles, fish, and invertebrates including insects; it may even reside in single-celled organisms. Even computers can produce an output that resembles AR, though few scientists would call them conscious on this basis. Furthermore, stimulus categorization can take place unconsciously in humans, without accurate reportability (Milner & Goodale 1995; Merikle et al. 2001). We should therefore be very cautious about using behavioral measures alone as evidence for consciousness across species.

In this paper we look beyond behavior to the known brain physiology of consciousness. Since humans are the reference species, we sketch out three well established brain properties of human consciousness that can be readily utilized as testable criteria, and then describe a further 14 distinctive properties – including AR - associated with this physiology (Table 1). Although these additional properties are necessarily provisional and offer varying degrees of testability, we suggest that they provide a useful basis for evaluating evidence for conscious functions in other species.

Consciousness is often differentiated into primary consciousness, which refers to the presence of a reportable multimodal scene composed of perceptual and motor events, and higher-order consciousness, which involves referral of the contents of primary consciousness to interpretative semantics, including a sense of self and, in more advanced forms, the ability to explicitly construct past and future scenes (Edelman 1989)<sup>1</sup>. Current evidence would suggest that primary consciousness, at least, is highly plausible in mammals, which share a developed thalamocortical complex. This is a standard argument from homology and appears to be widely accepted among comparative neurobiologists. However, such homologies become less and less obvious among non-mammalian species. The more difficult question of consciousness in birds, reptiles and other species will therefore be discussed in a companion paper (Edelman et al. this volume).

1	<b>EEG signature.</b> Irregular, low-amplitude, and fast electrical activity in the brain ranging from 12 to 70Hz. Conscious EEG looks markedly different from unconscious states – like deep sleep, epileptic loss of consciousness and general anesthesia – which are all characterized by regular, high-amplitude, and slow voltages at less than 4Hz.
2	<b>Cortex and thalamus.</b> Consciousness depends on the thalamocortical complex, turned on and off by brainstem neuromodulation. In humans, specific conscious contents appear to be depend on cortex, shaped by subcortical regions that do not support conscious experiences in and of themselves.
3	<b>Widespread brain activity.</b> Conscious contents are associated with widespread brain activation related to the content. Unconscious stimulation evokes only local cortical activity. Conscious scenes also involve wide effects <i>outside</i> the focus of current conscious contents, as indicated by implicit learning, episodic memory, biofeedback training of autonomic and motor function, and the like.
4	<b>Wide range.</b> Consciousness has an extraordinary range of different contents – perception in the various senses, endogenous imagery, emotional feelings, inner speech, concepts, action-related ideas and “fringe” experiences such as feelings of familiarity.
5	<b>Informativeness.</b> Consciousness may fade when signals become redundant; a loss of information may also lead to a loss of conscious access. Studies of attentional selection also show a strong preference for more informative conscious stimuli.
6	<b>The rapidly adaptive and fleeting nature of conscious scenes.</b> Immediate experience of the sensory past may last a few seconds, and our fleeting cognitive present is surely less than half a minute. In contrast, vast bodies of unconscious knowledge reside in long-term memory.
7	<b>Internal consistency.</b> Consciousness is marked by a consistency constraint. For example, while multiple meanings of most words are active for a brief time after presentation, only one becomes conscious at any moment. In general, of two mutually inconsistent stimuli presented simultaneously, only one can become conscious.
8	<b>Limited capacity and seriality.</b> The capacity of consciousness at any given moment seems limited to one consistent scene (see above). The flow of such scenes is serial, in contrast with the massive parallelism of the brain as observed directly.
9	<b>Sensory binding.</b> The sensory brain is functionally segregated such that different cortical areas are specialized to respond to different features such as shape, color, or object motion. One classic question is how these

<sup>1</sup> ‘Primary’ consciousness is often used interchangeably with ‘sensory’ consciousness. While there may be some subtle differences between these concepts, for present purposes they can be treated equivalently.

	functionally segregated regions coordinate their activities in order to generate the <i>gestalts</i> of ordinary conscious perception.
10	<b>Self attribution.</b> Conscious experiences are always attributed to an experiencing self, the “observing self” as James called it. Self functions appear to be associated with several brain regions, prominently orbitofrontal cortex in humans.
11	<b>Accurate reportability.</b> Conscious contents are reportable by a wide range of voluntary responses, often with very high accuracy. The standard operational index of consciousness is based on accurate reportability.
12	<b>Subjectivity.</b> Consciousness is marked by the existence of a private flow of events available only to the experiencing subject, though much of it is available for public report.
13	<b>Focus-fringe structure.</b> While consciousness tends to be thought of as a focal, clearly articulated set of contents, “fringe conscious” events, like feelings of familiarity, the tip-of-the-tongue experience, etc., are also important.
14	<b>Facilitation of learning.</b> There is very little evidence for long-term learning of unconscious input. In contrast, the evidence of learning of conscious episodes is overwhelming. Even implicit learning requires conscious attention to the stimuli from which implicit regularities are (unconsciously) inferred.
15	<b>Stability of contents.</b> Conscious contents are impressively stable, given the variability of input that is dealt with. Even abstract contents such as beliefs, concepts, and the motivational self are remarkably stable over years.
16	<b>Allocentricity.</b> Neural representations of external objects make use of diverse frames of reference. Conscious scenes, generally speaking, have allocentric character, though they are shaped by egocentric and other unconscious frameworks.
17	<b>Conscious knowing and decision making.</b> Consciousness is obviously useful for knowing the world around us, as well as for knowing certain of our own internal processes. Conscious intentionality may be particularly well suited for voluntary decision making.

**Table 1.** Basic brain facts: *Consciousness involves widespread, relatively fast, low-amplitude interactions in the thalamocortical core of the brain, driven by current tasks and conditions.* Unconscious states are markedly different and much less responsive to sensory input or motor plans.

*Consciousness and the brain*

Physiologically, three basic facts stand out about consciousness.

1. *Irregular, low-amplitude brain activity*

Hans Berger discovered in 1929 that waking consciousness is associated with low-level, irregular activity in the raw EEG, ranging from about 20 - 70 Hz (Berger 1929). Conversely, a number of unconscious states -- deep sleep, vegetative states after brain damage, anesthesia, and epileptic absence seizures -- show a predominance of slow, high-amplitude and more regular waves at less than 4Hz (Baars et al. in press). Virtually all mammals studied thus far exhibit the range of neural activity patterns diagnostic of both conscious states.<sup>2</sup>

---

<sup>2</sup> Dreaming during REM sleep is widely thought to be a conscious state. People who wake up from REM dreams report conscious experiences, and REM EEG closely resembles waking consciousness, even though there is a blocking of sensory input to, and motor output from, the cortex. This association between REM

Evidence from single-unit studies shows that during slow-wave sleep, massive numbers of cortical neurons tend to burst at the peak of the slow wave and pause synchronously during the trough (Steriade et al. 1993). Single-neuron bursting rates in cortex do not differ greatly from waking activity; what is distinctive about slow-wave sleep therefore are the massively synchronized neuronal pauses at < 4 Hz. Synchronized, slow pauses may disrupt the rapid interactions among cortical regions that are needed for waking functions like perception, immediate memory, interaction between distant regions of cortex, inner speech, action planning, and the like. Since slow waveforms are observed in other unconscious states as well -- whether due to brain damage, anesthetics, or epileptic absence seizures -- this may reflect a common mechanism for interrupting conscious functions.

## 2. *Involvement of the thalamocortical system*

In mammals, consciousness seems to be specifically associated with the thalamus and cortex (Baars et al. 2003). Regions such as the hippocampal system and cerebellum can be damaged without a loss of consciousness *per se*. Indeed, in cases like Rasmussen encephalitis, an entire hemisphere can be surgically removed without a loss of consciousness (although a form of blindsight can occur after surgery for this condition; see (Tomaiuolo et al. 1997). Damage to the brainstem, including the thalamus, can abolish the state of consciousness; but a very local lesion in sensory cortex may delete only specific conscious features such as color vision, visual motion, conscious experiences of visual objects and faces, and the like. Such cortical damage does not disrupt the state of consciousness, but changes its contents.

To a first approximation, the lower brainstem is involved in maintaining the state of consciousness, while the cortex (interacting with thalamus) sustains conscious contents. No other brain regions have been shown to possess these properties.

## 3. *Widespread brain activity*

Recently, it has become apparent that conscious scenes are distinctively associated with widespread brain activation (Srinivasan et al. 1999; Tononi et al. 1998c). Perhaps two dozen experiments to date show that conscious sensory input evokes brain activity that spreads from sensory cortex to parietal, prefrontal, and medial-temporal regions; closely matched unconscious input activates mainly sensory areas locally (Dehaene et al. 2001). Similar findings show that novel tasks, which tend to be conscious and reportable, recruit widespread regions of cortex; these tasks become much more limited in cortical representation as they become routine, automatic and unconscious (Baars 2002).

---

and EEG is present in all mammalian species studied. For example, the activity of hippocampal cells in sleeping rats resembles the firing patterns of these cells during awake maze running, suggesting a possible neural correlate of dreaming (Louie & Wilson 2001). The lone exceptions so far are within the monotreme order, for example the echidna and the platypus. The echidna shows a kind of unitary activity pattern during sleep that is in marked contrast to the two distinct patterns of REM and non-REM sleep observable in both marsupial and placental mammals; it is characterized by both increased variable discharge in the brainstem and synchronous cortical activity (Siegel et al. 1996). While the platypus does have an identifiable REM stage during sleep, it is anomalous in that it lacks the fast pattern typical of other mammals (Siegel et al. 1999).

*Basic properties of consciousness*

Together, these first three properties indicate that *consciousness involves widespread, relatively fast, low-amplitude interactions in the thalamocortical core of the brain, driven by current tasks and conditions*. Unconscious states are markedly different and much less responsive to sensory input or endogenous activity. These properties are directly testable and constitute necessary criteria for consciousness in humans.

It is striking that these basic features are conserved among mammals, at least for sensory processes. The developed thalamocortical system that underlies human consciousness first arose with early mammals or mammal-like reptiles, more than 100 million years ago. For example, the anatomical structures involved in thirst consciousness – which include the anterior and posterior cingulate as well as the thalamus (Denton et al. 1999) -- are present in all mammals, which suggests the emergence of a form of primary consciousness just prior to the mammalian radiation. Based on brain homologies, therefore, the widespread existence of primary consciousness among mammals seems plausible. We now describe a further 14 properties of consciousness that appear to depend on this basic physiology.

4. *Range of conscious contents.*

Consciousness presents an extraordinary range of contents --- perception in the different senses, imagery, emotional feelings, concepts, inner speech, and action-related ideas. This broad range suggests that consciousness involves many interacting, yet functionally differentiated, brain regions. Visual cortex has now been shown to be involved in conscious visual events (e.g. (Sheinberg & Logothetis 1997)). Recent studies show prefrontal activity for “fringe conscious” events such as mental effort and the tip-of-the-tongue state (Maril et al. 2001). An integrative concept of consciousness therefore must involve many brain regions as well as the interactions among them, along with the ability to recruit regions such as hippocampus (for conscious episodic storage and recall) and cerebellum (for conscious feedback control of fine motor skills).

One may ask why cortical areas that seem to be neuroanatomically similar can contribute to conscious scenes in very different ways; the content of a visual experience is very different from the taste of a lemon, or the sound of a bell. These differences may be related to the fact that, although a large proportion of the mammalian cortex is rather uniform in its histology (it is sometimes called ‘isocortex’), input to different cortical areas varies greatly. For example, visual input is very different in its statistical description from proprioceptive input, or olfactory input.

Thomas Nagel famously wondered what it is like to be a bat (Nagel 1974). Certainly, the sensory experience of sonar for a bat must depend on the informational structure of sonar input, as well as on the interactions of this input with the other sensory modalities possessed by the bat. Hence, the unique physical embodiment of the bat -- its “batness,” if you will—colors its conscious existence and at the same time precludes our ever answering this query, at least to the satisfaction of some philosophers.

5. *Informative conscious contents.*

Conscious contents often fade when signals become redundant, as in the cases of stimulus habituation and automaticity of highly practiced skills (Baars 1988). Thus a loss of information may lead to a loss of conscious access. Clear brain correlates have been identified for these

effects (Raichle 1998; Stephan et al. 2002). Studies of attentional selection also show a preference for more informative stimuli (Pashler 1999).

The informativeness of consciousness has been given a formal foundation by Edelman and Tononi (Tononi & Edelman 1998; Edelman 2003). They suggest that consciousness is supported by a ‘dynamic core’, generated by reentrant neural activity in the thalamocortical system (Tononi & Edelman 1998). The concept of a dynamic core refers to a ‘functional cluster’ of neurons, the overall dynamics of which are highly ‘complex’. A functional cluster is a group of elements (neurons, or neuronal groups) that displays high statistical dependence internally, and low statistical dependence with elements outside the subset; a functional cluster ‘speaks mainly to itself’ (Tononi et al. 1998b). Complex dynamics can be assessed quantitatively by the extent to which changes in the state of any subset of the cluster make a difference to the rest of the cluster (Tononi et al. 1994). This definition of complexity is based on maximizing the mutual information among all possible bipartitions of a system, where mutual information is an information-theoretic quantity expressing the statistical dependence between two systems, or between two bipartitions of a system (see Figure 1). By definition, a complex dynamic core is also highly informative.

A complex cluster -- a dynamic core -- is both differentiated, such that small subsets tend to behave comparatively independently, and integrated, such that large subsets tend to behave coherently. Edelman and Tononi argue that this reflects the nature of conscious experience: Each conscious scene is one among an astronomical number of possibilities (differentiation), yet each is experienced as a unity (integration).

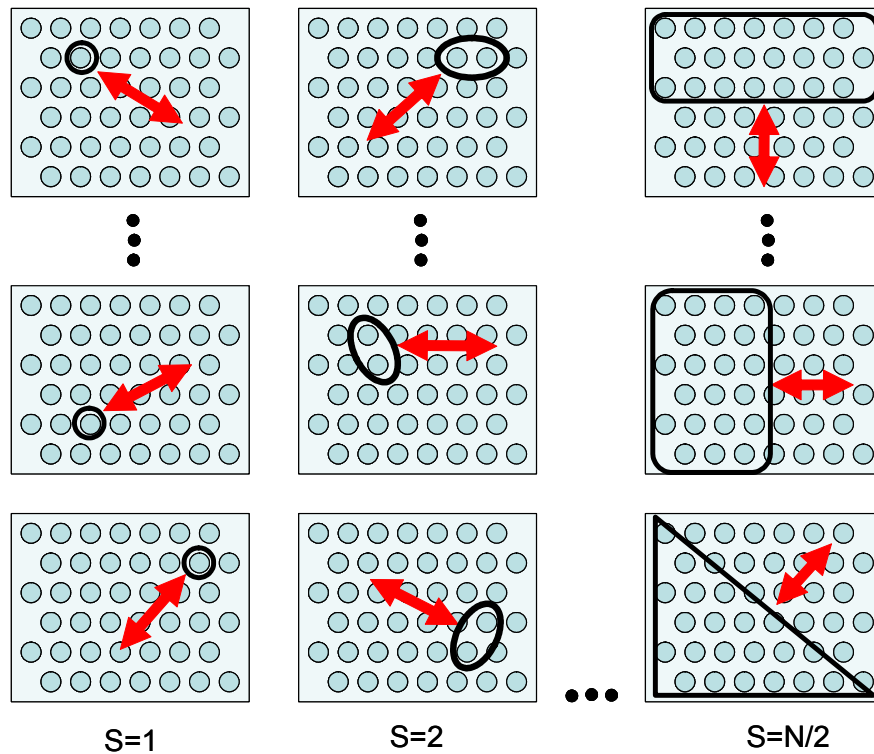
Edelman and Tononi stress that a dynamic core can only be sustained by highly reentrant neural networks like those in the thalamocortical system. Moreover, only certain functional states of such networks are highly complex in the mathematical sense; others, such as those prevalent in slow wave sleep and general anaesthesia, are significantly less complex, and perhaps for that reason, unconscious.

#### 6. *The rapidly adaptive and fleeting nature of conscious scenes.*

Consciousness is remarkable for its present-centeredness (James 1890; Edelman 1989). Immediate experience of the sensory world may last about the length of sensory memory -- perhaps a few seconds -- and our fleeting cognitive present (what Edelman calls the ‘remembered present’), though somewhat longer, is surely less than half a minute. In contrast, vast bodies of knowledge are encoded in long-term memory. They are uniformly unconscious. Both the fleeting nature and rapid adaptation of consciousness require explanation.

For conscious scenes to have adaptive value for an organism, they must have a short lifetime - enough time to recruit a broad network of neural resources to generate appropriate behavior, yet also a tendency to evolve into subsequent scenes. Consider that the state of a brain at any moment can be represented as a point on an ‘attractor landscape’ consisting of high-dimensional hills and valleys, where dimensions represent, for example, neural activities and synaptic strengths. As the state of the brain evolves over time, this point will move. A simple example is a landscape consisting of a single attractor, a deep pit in an otherwise flat plain. Brain states evolving on such a landscape would always end up in the pit, in one particular state, regardless of starting conditions. Imagine now a landscape (or manifold) with a rich topology of peaks and troughs so that a dynamic core evolving on this landscape would migrate from attractor to attractor, all the time evoking different behaviors in the organism. Conscious scenes

in this case would indeed be fleeting, their evanescence driven by the continual evolution of the dynamic core.



**Figure 1.** Neural complexity, after Figure 2 in (Tononi et al. 1998a). The figure shows an idealized neural system composed of  $N$  neuronal elements (small circles) divided into subsets of size 1 ( $S=1$ ), size 2 ( $S=2$ ), and size  $N/2$  ( $S=N/2$ ). Bold arrows indicate mutual information between subsets and the remainder of the system, where mutual information is a measure of how much one can know about the state of a subset by knowing the state of the complement. A neurally complex system is one in which small subsets of the system show high statistical independence, but large subsets show low statistical independence. This corresponds to the ensemble average mutual information between subsets of a given size and their complement, summed over all subset sizes. Neurally complex systems balance dynamical segregation - their component parts are differentiated - with dynamical integration - as larger and larger subsets of elements are considered, they become increasingly integrated.

Kelso and colleagues have used the term ‘metastability’ to describe this kind of activity (Bressler & Kelso 2001). Metastable systems can be captured by attractors, but no single attractor can dominate indefinitely. They have ‘rich intermittency’ (Friston 1997). Although the precise relation between metastability and complexity has yet to be elaborated, they are likely closely related: “Metastable dynamics is distinguished by a balanced interplay of integrating and segregating influences” (Bressler & Kelso, 2001, p.26).

Evidence from cortical electroencephalographic (EEG) recordings from humans, cats, and rabbits suggests that brain dynamics can be described in this way (Tsuda 2001; Freeman 2000; Freeman & Rogers 2003). Almost thirty years ago, metastable EEG patterns in the rabbit olfactory bulb were found to correspond to odor stimuli (Freeman & Skarda 1985), and recent studies have extended these findings to larger regions of mammalian cortex (Freeman & Rogers 2003).



7. *Internal consistency.*

Consciousness is marked by a consistency constraint. For example, while multiple meanings of most words are active for a brief time after presentation, only one becomes conscious at any given moment. The literature on dual input tasks shows without exception that of two mutually inconsistent stimuli presented simultaneously, only one becomes conscious (Baars 1988). This fact has been known for many years for selective listening, binocular rivalry, and ambiguous words and figures. Binocular rivalry in particular has become a popular topic for animal studies: Landmark work by (Sheinberg & Logothetis 1997; Leopold & Logothetis 1996) used single-unit recordings in awake-behaving monkeys to distinguish neurons in the primate visual system that correlated with the stimulus from those that correlated with the percept.

In certain clinical conditions, it is possible that the consistency constraint may no longer apply to the brain state as a whole. Severe epilepsy is sometimes treated by surgically severing the corpus callosum, the major fiber tract connecting the two cerebral hemispheres. Although post-operative patients may appear entirely normal in many circumstances, careful tests show incongruities between verbal report -- usually mediated by the left hemisphere -- and the actions of the left hand -- usually mediated by the right hemisphere ((Gazzaniga et al. 1965), but see (Plourde & Sperry 1984)). Other conditions that may involve functional disconnection within the brain include dissociative disorders, fugue states, and conversion hysteria. It is possible that future experiments will allow direct visualization of such phenomena by, for example, measuring the distribution of coherent brain activity in subjects in hypnotic dissociative states (Hilgard 1977); it may turn out that such states are accompanied by 'split' dynamic cores.

8. *Limited capacity and seriality.*

Several aspects of the brain have surprisingly limited capacity, such as the famous "seven plus or minus two" limit of rehearsable working memory (Miller 1956; Cowan 2001), and the limits of selective attention (Pashler 1997). These limits have also been studied in non-human animals. For example, (Glassman et al. 1994) showed that humans and rats have similar working memory limits when tested in comparable radial maze situations, and (Spitzer et al. 1988) correlated task difficulty in a visual discrimination task with attentional modulation of neuronal activity in macaque monkeys (see also (Chun & Marois 2002)).

While consciousness should not be identified with either working memory or selective attention, it is limited in a similar way, in that there can only be a single consistent conscious stream, or process, at any moment. Conscious seriality can be contrasted with the massive parallelism of the brain as observed directly. Events that occur in parallel with the conscious stream are invariably unconscious. Conscious seriality and unconscious parallelism are fundamental, and constrain any possible theory (Baars 1988).

Limited capacity and seriality are probably related to internal consistency. If conscious scenes are associated with global states of the thalamocortical system, such that only one such scene can prevail at any one time, it follows that these global states necessarily appear serially.

9. *Sensory binding.*

Binding is one of the most striking properties of consciousness. It is certainly among the most assiduously studied of topics in consciousness research (Crick 1984; Crick & Koch 1990; Singer

& Gray 1995; Treisman 1998; Edelman 1993). The visual brain is functionally segregated such that different cortical areas are specialized to respond to different visual features such as shape, color, and object motion. Yet consciousness of a visual scene has the property that these distinct aspects are bound together in a unified percept. Binding also appears to occur with more abstract conscious contents, such as the meaning of a phrase or even a paragraph, in which consistent discourse reference occurs, such as using the word “it” to refer to a previous noun (called deixis in linguistics). In both cases, a key question persists: How do functionally segregated regions and brain events coordinate their activities in order to generate the gestalts of ordinary conscious perception and cognition.

Most proposed solutions to the binding problem fall into one of two general classes: (i) binding through the influence of attentional processes, executive mechanisms, or superordinate maps (Shadlen & Movshon 1999; Shafritz et al. 2002); and (ii) binding through the selective synchronization of dynamically formed neuronal groups (Edelman 1993; Gray 1999; Singer 1999). The former often focuses on parietal or frontal areas, the operations of which are spatially and temporally distant from early stages of sensory processing. It has been suggested that these areas implement an executive mechanism, such as a spotlight of attention, that is able to combine visual features at specific locations in space (Treisman 1998; Shafritz et al. 2002). Advocates of neural synchrony, by contrast, suggest that sensory binding is an automatic, dynamic, and pre-attentive process: combinations of features relating to visual objects are bound by the dynamic synchronization of corresponding neuronal groups in different cortical areas.

Theories based on neural synchrony have received empirical support from neurophysiological recordings that show synchronous activity among neurons in mammalian brains (Gray & Singer 1989; Steinmetz et al. 2000; Fries et al. 2001); but see (Thiele & Stoner 2003). That this evidence derives from non-human mammals strongly suggests that sensory binding via neural synchrony may be a mechanism shared by many species.

Synchrony-based theories have also been strongly criticized. For example, Treisman suggests that although synchrony may allow the brain to ‘hold on’ to a solution to the binding problem, it does not explain how such solutions are arrived at (Treisman 1998). The lack of specific brain mechanisms for reading a synchrony-based ‘code’ has also been noted (Shadlen & Movshon 1999). Recently, theoretical models have addressed some of these concerns by demonstrating the successful categorization of multiple visual objects by the dynamic synchronization of neuronal groups (Tononi et al. 1992; Seth et al. 2004). In these models, synchronously active neural circuits form which correspond to distinct objects in the environment. The emergence and stability of these circuits depended on the presence of widespread reentrant connectivity among neural areas (Seth et al. 2004).

#### 10. *Self attribution.*

Conscious experiences are always attributed to an experiencing self, the “observing self” to which James referred (James 1890). Self functions appear to be associated with several brain regions, prominently orbitofrontal cortex in human beings.

Until now, we have focused on primary consciousness, the contents of which relate to entities in the world. While there is a clear sensorimotor “self,” -- the inferred locus of observation and agency -- ideas of the social self in consciousness usually relate to a higher-order consciousness; the capability to be conscious of being conscious (Edelman 1989).

The self as an interpreter of conscious input is very likely not limited to humans. Parietal cortex contains egocentric maps which interact with the contents of visual consciousness that depend upon “dorsal stream” regions of occipito-temporal cortex. These egocentric maps locate the perceiver’s body relative to the visual scene; they are plausibly used for interpretation of input vis-à-vis the observer, and for planning the observer’s actions relative to the visual world, as in reaching for an object. Many other brain regions may contribute to these functions, including the limbic system and its emotional input. Even lower in the brainstem, there exist appetitive systems like the hypothalamus, emotional-attachment areas such as the periaqueductal gray, and body maps such as those in the mesencephalic reticular formation. All of these arguably involve ancestral mammalian aspects of self that may also participate in a human sense of identity.

Higher-order consciousness, by contrast, flourishes in humans. At the very least, it probably requires semantic capability and, for the most developed forms of the narrative self, a linguistic capability. Edelman has proposed that a key step in the evolution of these features in hominids occurred with the development of reentrant loops connecting brain systems for language with pre-existing neural areas underlying concept generation (Edelman 1989; Edelman 2004). This enabled explicit reference to inner states, and communication of these states to others. With these mechanisms in place, higher-order consciousness could then relate current or imagined sensory content to a concept of self enriched with ideas of both past and future.

There is suggestive evidence for higher-order capabilities in non-human animals. For example, rhesus monkeys show sensitivity to the uncertainty of a discrimination (Smith et al. 2003) or of a memory (Hampton 2001). While some authors suggest that these sorts of experiment may ground the study of animal consciousness (Smith et al. 2003), such a position runs the risk of ignoring evidence for mammalian primary consciousness (Seth et al. in press).

With the possible exception of absorbed and meditative states, in which one may focus exclusively on a sensory source of information, as in driving a car with complete concentration, modern-day humans rarely experience primary consciousness in the absence of higher-order interpretations. As we discuss below, this may have some bearing on the fact that humans are generally able to explicitly report conscious events.

#### 11. *Accurate reportability.*

Accurate report (AR) is the standard behavioral index for consciousness in humans. If someone yells ‘Ouch! That hurts!’ after stubbing a toe, we infer that they feel pain. Accurate, verifiable report is so widely accepted as both an operational criterion for consciousness and a means of communicating conscious content that we risk forgetting that it must still be accounted for.

It is likely that widespread consciousness-related brain activity may contribute to explicit report, at the very least, simply by involving brain areas that are required to mobilize the machinery of report. Evidence for the involvement of prefrontal cortex in motor control and voluntary behavior is consistent with this idea (Fuster 1999). Explicit report is likely to be facilitated by the linguistic capability implicated in the emergence of a higher-order self, which for conscious humans is the normal state of affairs. It is also relevant that humans can refer to a shared social and perceptual reality from quite early in life, as when toddlers eagerly point out visible objects to their caretakers. This ‘Mommy, airplane!’ behavior is one kind of report of a conscious scene. A full explanation of reportability as an index of consciousness probably must refer to this shared social and perceptual reality for normal humans.

Although some mammals appear to be able to make verbal reports (Griffin 2001), this ability is limited. Reliance on verbal report as evidence for consciousness may therefore bias against the attribution of consciousness. As an alternative strategy, attempts have been made to elicit reliable, verifiable *non-verbal* report of conscious experience from animals. For example, the ‘commentary key’ method allows a monkey to make a behavioral comment -- or second-order discrimination -- on a previous perceptual discrimination (Cowey & Stoerig 1995; Stoerig & Cowey 1997). Following lesions to half of V1, monkeys are still able to make above-chance discriminations in the occluded visual field (localization of a visual target by pointing). However, they are not able to distinguish reliably between a stimulus in the occluded field and a blank display in an intact part of the visual field. Cowey and Stoerig argue that this amounts to a denial of visual consciousness, as if the monkey were saying “I can’t tell the difference between input in my blind field and a completely blank input in my sighted field”. By contrast, when all stimuli are presented in the intact visual hemi-field, the monkeys are able to make both discriminations accurately. This study provides a primate analog to human ‘cortical blindness’ or ‘blindsight’, a condition in which patients with V1 damage continue to make some visual discriminations, while strongly denying that they have normal visual experiences (Weiskrantz 1998).<sup>3</sup>

Of course, the interpretation of the second-order discrimination as an explicit report of a conscious visual event (or its absence) cannot be justified by the behavioral evidence alone, since discriminations about discriminations can be generated by all kinds of mechanisms. The additional factor is, of course, that monkeys and humans share a wealth of neurobiological characteristics apparently relevant to consciousness (Logothetis 2003). These similarities embolden us to interpret behavioral evidence from humans and monkeys in essentially the same way. Cortically blind human patients deny visual sensations, but intact humans explicitly report visual sensations. Cowey and Stoerig suggest that the same may also be true for monkeys.

But what are these neurobiological characteristics that are apparently relevant to consciousness? The purpose of this paper is in large measure to clarify exactly this, in a way that facilitates comparative analysis among humans, primates, and other species.

## 12. *Subjectivity and the perspective of the observer.*

Philosophers traditionally define consciousness in terms of subjectivity, the existence of a private flow of events available only to the experiencing subject. This corresponds to everyday experience, and it appears to require an explanation in a complete scientific account of consciousness. However, the peculiar position of attempting an objective, scientific description of subjective conscious scenes continues to be the source of much confusion. Various authors have proposed an ‘explanatory gap’ between scientific theory and subjective experience (Block & Stalnaker 1999; Levine 1983). Sometimes this is referred to as the ‘hard problem’ of consciousness, to be distinguished from the ‘easy problem’ of describing exactly how the brain functions, during both conscious and unconscious states (Chalmers 1995).

The aspect of *privacy* may be the most tractable of problems in consciousness research. Consciousness appears to depend on a functioning thalamocortical system; conscious scenes are thus inextricably attached to individual brains and bodies and are necessarily private.

---

<sup>3</sup> It is sometimes overlooked that the visual guided behavior of cortically blind patients, while often above chance, is considerably worse than normal.

The association of a stream of consciousness with an experiencing subject may be related to the existence of a self (whether a basic ‘sensorimotor’ self or a ‘higher-order’ narrative self). A self – an interpreter of conscious input – provides a locus for the sense of subjectivity that accompanies conscious experience. In humans that sense of subjectivity may require the interaction of posterior cortex with regions like parietal egocentric maps and orbitofrontal cortex (Baars 2002).

The qualitative feel of conscious scenes is less easily explained. Why, for example, should sensation accompany the complex activity of the thalamocortical system, but not the simple discrimination of light from dark by a photodiode? It may be that the former is sufficiently more complex than the latter (in the technical sense of “complexity;” see Criterion 5: *Informative Conscious Contents*), and that the qualitative feel of a conscious scene is a consequence of the vast amount of information disclosed by the thalamocortical system being in one given state out of an very large set of possible states (Edelman 2004; Edelman 2003; Tononi & Edelman 1998); according to Edelman and Tononi, qualia *are* these high-order discriminations.

### 13. *Focus-fringe structure.*

While consciousness tends to be thought of as a focal, clearly articulated set of experiences, an influential body of thought suggests that “fringe conscious” events, like feelings of knowing, the tip-of-the-tongue experience, and the like, are equally important (James 1890; Mangan 1993).

Fringe experiences are among the most common and significant mental events. They upset our typical ideas about consciousness, being quite unlike our experience of coffee cups or cats. Fringe experiences are “vague” - they do not have sensory qualities like color, pitch or texture; they lack object identity, location in space, and sharp boundaries in time. They do not even show figure-ground contrast. The phenomenology of the fringe seems fundamentally different from that of focal consciousness. Yet people show remarkable accuracy in fringe judgments, like feelings of knowing or familiarity (e.g. (Widner & Smith 1996; Bowers et al. 1990)). In this respect these events differ from truly unconscious knowledge, like long term memory or automatic motor skills.

Fringe consciousness may be selectively associated with prefrontal cortical areas, which have few direct projections to posterior sensory cortical areas (Baars in press). In support of this idea, a recent human brain imaging study of a canonical fringe experience, the “tip of the tongue” state, showed dominant activation in prefrontal cortex and cingulate gyrus (Maril et al. 2001).

Self-functions are frequently experienced as vague and fringe-like as well. This is consistent with the idea that the self is an interpreter of conscious experience, rather than a primary source of perceptual content. Self-functions have also been frequently associated with prefrontal cortex.

### 14. *Consciousness facilitates learning.*

The possibility of unconscious learning has been debated for decades. Indeed, conditioning studies of a (putatively) non-conscious invertebrate, the sea snail *aplysia* have become the benchmark for many researchers seeking to define the fundamental molecular and physiological properties of learning (Walters et al. 1981; Rayport & Kandel 1986). Nevertheless, there appears

to be only very limited evidence for long term learning of unconscious input (Clark et al. 2002). In contrast, the evidence for learning of conscious episodes, even without any intention to learn, is overwhelming. The capacity of conscious visual memory is enormous (Standing 1973). Even implicit learning requires conscious attention to the stimuli from which regularities are (unconsciously) inferred, and the learning of novel motor and cognitive skills also requires conscious effort.

With respect to mammals, it is well established that cortex and basal ganglia are differentially involved during learning and the expression of learned behavior, respectively (Graybiel 1995). Consider the challenge of standing on a surfboard. Thalamocortical networks, perhaps because of the complex and informative dynamics that they support, seem to be well suited to the acquisition of such a novel behavior (Seth & Edelman 2004). These complex dynamics may also correspond to conscious states (Edelman & Tononi 2000). In contrast, the expression of learnt behavior is unlikely to require the same degree of adaptive flexibility. Rather, a learned behavior should be expressed with minimal interference from other neural processes. Basal ganglia anatomy, which comprises largely of long polysynaptic chains that run in parallel, is well suited for this purpose, and the resulting dynamics are not likely to show the same complexity and informativeness of the thalamocortical networks associated with consciousness.

Of course, the basal ganglia do not act alone in the expression of learned behavior. Indeed, it may be that they implement an attentional function, reducing interference by inhibiting irrelevant sensorimotor activity in a variety of brain structures including the thalamocortical system (Edelman 2003; Jueptner et al. 1997).

Learned behavior based on conscious experience differs from the acquisition of episodic memories, which represent, or reconstruct, past conscious scenes (the moment of standing --- or falling --- from the surfboard). The acquisition and retrieval of episodic memories appears to require the interplay of the hippocampal complex and the neocortex (Ranganath et al. 2004).

15. *Stability of conscious contents relative to sensory input.*

Conscious contents are impressively stable, given the variability of input encountered by behaving organisms. In perception, the confounding influence of eye, head, and body motion is often excluded from conscious experience, as are the complex orchestrations of muscle movements required for action (Merker (in press)). Even abstract conscious contents such as beliefs, concepts, and motivations are remarkably stable over years. Indeed, fundamental beliefs often last an entire lifetime for adult humans. The same general point has been found to be true for conscious thoughts and inner speech, using thought-monitoring studies (Singer 1993). Consciousness gives access to a subjective scene that appears to be quite stable, often more so than the physical world signals that give rise to it.

It has been suggested that consciousness is the phylogenetic outcome of neural processes that ensure this stability in order to bring about effective decision making (Merker (in press)). By stripping away the confounding effects of self-motion, decision mechanisms with access to conscious scenes are better able to cope with the ongoing problem of what to do next. This point is closely related to the interaction between conscious information and executive “self” functions.

16. *Allocentricity of the objects of experience in an egocentric framework.*

Neural representations of external objects make use of diverse frames of reference. For example, early visual cortex is retinotopically mapped, yet other regions such as the hippocampus and parietal cortex show allocentric mapping, in which representations of object position are stable with respect to observer position. It seems that conscious scenes, generally speaking, have allocentric character --- they have “otherness.” Yet the otherness of perceived conscious objects exists in a framework that relates it to the perceiver. We see an apple in front of us, not an apple in abstract perceptual space. Nevertheless, the attribution of conscious contents as such is generally external. Even when we talk about ourselves, as in referring to our own moods and thoughts, we speak “as if” we are referring to something in the third-person objective reality. The “otherness” of perceived conscious objects is what philosophers often refer to as ‘intentionality,’ the property that conscious states have of being ‘about’ something (Brentano 1924-28).

There are several reasons why consciousness may be preferentially associated with object-like, intentional representations. First, allocentricity coincides with stability. A viewer-independent world is likely to be more stable than a world that constantly shifts with the perspective of the observer.

Conscious allocentricity may also be related to the distinction between ventral and dorsal visual pathways (Ungerleider & Haxby 1994). The ventral pathway, which has to do with object recognition, is closely associated with consciousness, but the dorsal pathway, which has to do with egocentric and allocentric maps, reaching and grasping, seems to be much less so. Object recognition is likely to benefit from a stable, allocentrically represented (and hence conscious) visual world, whereas reaching and grasping are viewer-*dependent* operations which are more likely to require sensitivity to the details of the position, posture, and motion of the reacher. Strikingly, beyond the fact that perceptual feature fields are mainly found in the ventral stream, neural analyses of differences in consciousness between ventral and dorsal activity are still lacking.

17. *Conscious knowing is useful for voluntary decision-making.*

Consciousness is obviously useful for knowing the world around us, as well as for knowing certain of our own internal processes. Conscious pain, pleasure, appetites and emotions refer to endogenous events. Conscious sensory perception and abstract ideas typically involve knowing the outer world; they have the property of intentionality.

The knowing function of consciousness may seem obvious. But there is also overwhelming evidence for unconscious kinds of knowledge and unconscious intentional states. Implicit learning, implicit cognition, unconscious moods, overpracticed skills, spared implicit functions after brain damage, and other kinds of unconscious knowledge are well established. Both conscious and unconscious intentionality have obvious utility in ensuring that brain operations are functionally adapted to the world.

However, conscious and unconscious states are not equivalent with respect to knowing. Many unconscious processes are not intentional; spinal reflexes, for example. Yet all conscious events -- with minor exceptions such as visual after-images and the like -- seem to involve knowing of some kind. To understand why, it is useful to recall some properties of consciousness which we have already discussed. As well as being informative, conscious scenes are rapidly

adaptive, internally consistent, reportable, referenced to a self, stable, and allocentrically represented. Furthermore, many forms of learning appear to require consciousness. Together, these properties suggest that conscious intentionality is particularly well suited to dealing with novelty, and to facilitating executive decision-making processes, in circumstances in which the automatic reactions of an organism may not suffice (Griffin & Speck 2004).

### *Putting it all together*

How, in practice, can these properties be used to test comparative predictions about consciousness? Considering this question raises the issue that the foregoing properties vary considerably in their *testability*. Those that have to do with structural homologies of neuroanatomy are relatively easy to test; it is not difficult to identify a thalamocortical complex in a monkey or in a dog (criterion #2).<sup>4</sup> It is also relatively straightforward to test for neural dynamics generated within these structures; EEG signature (#1), widespread brain activity (#3), informativeness (#5), rapid adaptivity (#6), and neural synchrony underlying sensory binding (#9), all fall into this class. These properties can therefore be treated sensibly as testable criteria.

Empirical data that pass these criteria can establish a beachhead from which the others can be evaluated. Since consciousness – whether in humans or in other animals – arises from interactions among brains, bodies, and environments, we might next consider properties that involve a behavioral component. Such properties include whether putative consciousness in an animal facilitates learning (#14), whether it can generate accurate behavioral report (#11), and whether it aids voluntary decision making (#17).

The testability of the remaining properties is less evident. Some may seem difficult to test, but with sufficient ingenuity can in fact be tested. For example, good evidence for conscious seriality (#8) comes from paradigms such as binocular rivalry, in which human subjects report perceptual alterations despite stable sensory input. Application of this paradigm to non-human animals requires a sufficiently reliable means of behavioral report (Leopold et al. 2003; Cowey & Stoerig 1995). Given such means, neural activity following sensory input can be separated from neural activity that follows a (putatively) conscious percept. Similar approaches can be applied to internal consistency (#7) and perhaps also to stability of conscious contents (#15).

Even so, there are some properties which do not seem currently testable. Most prominently, subjectivity (#12) is not something that seems testable in a given experiment. Rather, subjectivity is a defining property of consciousness to which empirical results may be related. In this case, the best to hope for is to indirectly infer subjectivity from a sufficiently well validated report in conjunction with a battery of consistent brain evidence. This point stresses an important distinction foreshadowed in the foregoing discussion: A good scientific theory requires both *criteria* for deciding the admissibility and relevance of empirical data, as well as clearly defined *properties* to which these data should relate. It is often testability itself that distinguishes between criteria and properties, moreover, as a theory matures, properties can migrate to criteria (for example, informativeness (#5) becomes testable when framed in the quantitative language of information theory) and *vice versa* (accurate reportability (#11), the standard operational criterion for consciousness, is also a property of consciousness requiring explanation).

Along with subjectivity, the wide range of conscious contents (#4), self attribution (#10), focus-fringe structure (#13), and allocentricity (#16) are most likely to remain as properties; they

---

<sup>4</sup> Of course, even this step becomes difficult for non-mammals and especially invertebrates. First steps in this directions are discussed in (Edelman et al. this volume).



do not describe phenomena that are either present or not present in currently available empirical data. In these cases we may ask that empirical data should provide explanatory leverage to drive the maturation of theory to the point at which these properties do in fact become explicitly testable.

Finally, we note that the present list should be treated as provisional. Neural theories of consciousness are young, and their further development may lead not only to migrations between properties and criteria, but also to a repopulation of the list itself.

### *Conclusions*

Contrary to widespread belief, the question of animal consciousness is not unapproachable. Human consciousness depends on well-established properties of the thalamocortical complex, a structure that is shared with other mammals. While a great deal remains to be discovered, there are at least 17 properties that can also be tested, with varying degrees of precision, in other species.

### *Acknowledgments*

This work was supported by The Neuroscience Institute and the Neuroscience Research Foundation, which are gratefully acknowledged. We thank Drs. Gerald M. Edelman and Bjorn Merker for constructive comments.

- Baars, B. J. 1988 *A cognitive theory of consciousness*. New York, NY: Cambridge University Press.
- Baars, B. J. 2002 The conscious access hypothesis: origins and recent evidence. *Trends Cogn Sci* **6**, 47-52.
- Baars, B. J. in press How brain reveals mind: Neuroimaging supports the fundamental role of conscious experience. *Journal of Consciousness Studies*.
- Baars, B. J., Banks, W. P. & Newman, J. (ed.) 2003 *Essential sources in the scientific study of consciousness*. Cambridge, MA: MIT Press.
- Baars, B. J., Ramsay, T. & Laureys, S. in press Brain, conscious experience, and the observing self. *Trends Neurosci*.
- Berger, H. 1929 Ueber das Elektroencephalogramm des Menschen. *Archiv fuer Psychiatrie und Nervenkrankheiten, Berlin* **87**, 527-570.
- Block, N. & Stalnaker, R. 1999 Dualism, conceptual analysis, and the explanatory gap. *Philosophical Review* **108**, 1-46.
- Bowers, K. S., Regehr, G., Balthazard, C. G. & Parker, K. 1990 Intuition in the context of discovery. *Cognitive Psychology* **22**, 72-100.
- Brentano, F. 1924-28 *Psychologie vom empirischen standpunkt*. Leipzig: Meiner.
- Bressler, S. L. & Kelso, J. A. 2001 Cortical coordination dynamics and cognition. *Trends Cogn Sci* **5**, 26-36.
- Brewer, A. A., Press, W. A., Logothetis, N. K. & Wandell, B. A. 2002 Visual areas in macaque cortex measured using functional magnetic resonance imaging. *J Neurosci* **22**, 10416-26.
- Chalmers, D. J. 1995 The puzzle of conscious experience. *Sci Am* **273**, 80-6.
- Chun, M. M. & Marois, R. 2002 The dark side of visual attention. *Curr Opin Neurobiol* **12**, 184-9.
- Clark, R. E., Manns, J. R. & Squire, L. R. 2002 Classical conditioning, awareness, and brain systems. *Trends Cogn Sci* **6**, 524-531.
- Cowan, N. 2001 The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences* **24**, 87-114.
- Cowey, A. & Stoerig, P. 1995 Blindsight in monkeys. *Nature* **373**, 247-9.
- Crick, F. 1984 Function of the thalamic reticular complex: the searchlight hypothesis. *Proc Natl Acad Sci U S A* **81**, 4586-90.

- Crick, F. & Koch, C. 1990 Some reflections on visual awareness. *Cold Spring Harb Symp Quant Biol* **55**, 953-62.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B. & Riviere, D. 2001 Cerebral mechanisms of word masking and unconscious repetition priming. *Nat Neurosci* **4**, 752-8.
- Denton, D., Shade, R., Zamarippa, F., Egan, G., Blair-West, J., McKinley, M., Lancaster, J. & Fox, P. 1999 Neuroimaging of genesis and satiation of thirst and an interoceptor-driven theory of origins of primary consciousness. *Proc Natl Acad Sci U S A* **96**, 5304-9.
- Edelman, D. B., Baars, B. J. & Seth, A. K. this volume Identifying the hallmarks of consciousness in non-mammalian species. *Consciousness and Cognition*.
- Edelman, G. M. 1989 *The remembered present*. New York, NY: Basic Books.
- Edelman, G. M. 1993 Neural Darwinism: selection and reentrant signaling in higher brain function. *Neuron* **10**, 115-25.
- Edelman, G. M. 2003 Naturalizing consciousness: a theoretical framework. *Proc Natl Acad Sci U S A* **100**, 5520-4.
- Edelman, G. M. 2004 *Wider than the sky: The phenomenal gift of consciousness*: Yale University Press.
- Edelman, G. M. & Tononi, G. 2000 *A universe of consciousness: How matter becomes imagination*. New York, NY: Basic Books.
- Freeman, W. J. 2000 Mesoscopic neurodynamics: from neuron to brain. *J Physiol Paris* **94**, 303-22.
- Freeman, W. J. & Rogers, L. J. 2003 A neurobiological theory of meaning in perception part V: Multicortical patterns of phase modulation in gamma EEG. *International Journal of Bifurcation and Chaos* **13**, 2867-2887.
- Freeman, W. J. & Skarda, C. A. 1985 Spatial EEG patterns, non-linear dynamics and perception: the neo-Sherringtonian view. *Brain Res* **357**, 147-75.
- Fries, P., Reynolds, J. H., Rorie, A. E. & Desimone, R. 2001 Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291**, 1560-3.
- Friston, K. J. 1997 Transients, metastability, and neuronal dynamics. *Neuroimage* **5**, 164-71.
- Fuster, J. M. 1999 Synopsis of function and dysfunction of the frontal lobe. *Acta Psychiatr Scand Suppl* **395**, 51-7.
- Gazzaniga, M. S., Bogen, J. E. & Sperry, R. W. 1965 Observations on visual perception after disconnection of the cerebral hemispheres in man. *Brain* **88**, 221-36.
- Glassman, R. B., Garvey, K. J., Elkins, K. M., Kasal, K. L. & Couillard, N. L. 1994 Spatial working memory score of humans in a large radial maze, similar to published score of rats, implies capacity close to the magical number 7 +/- 2. *Brain Res Bull* **34**, 151-9.
- Gray, C. M. 1999 The temporal correlation hypothesis of visual feature integration: still alive and well. *Neuron* **24**, 31-47.
- Gray, C. M. & Singer, W. 1989 Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc Natl Acad Sci U S A* **86**, 1698-702.
- Graybiel, A. M. 1995 Building action repertoires: memory and learning functions of the basal ganglia. *Curr Opin Neurobiol* **5**, 733-41.
- Griffin, D. R. 2001 *Animal minds: Beyond cognition to consciousness*. Chicago: University of Chicago Press.
- Griffin, D. R. & Speck, G. B. 2004 New evidence of animal consciousness. *Anim Cogn* **7**, 5-18.
- Hampton, R. R. 2001 Rhesus monkeys know when they remember. *Proc Natl Acad Sci U S A* **98**, 5359-62.
- Hendry, S. H., Huntsman, M. M., Vinuela, A., Mohler, H., de Blas, A. L. & Jones, E. G. 1994 GABAA receptor subunit immunoreactivity in primate visual cortex: distribution in macaques and humans and regulation by visual input in adulthood. *J Neurosci* **14**, 2383-401.
- Herman, L. M., Kuczaj, S. A., 2nd & Holder, M. D. 1993 Responses to anomalous gestural sequences by a language-trained dolphin: evidence for processing of semantic relations and syntactic information. *J Exp Psychol Gen* **122**, 184-94.
- Herman, L. M., Morrel-Samuels, P. & Pack, A. A. 1990 Bottlenosed dolphin and human recognition of veridical and degraded video displays of an artificial gestural language. *J Exp Psychol Gen* **119**, 215-30.
- Hilgard, E. R. 1977 *Divided Consciousness*: John Wiley and Sons.
- James, W. 1890 *The principles of psychology*. New York: Henry Holt.

- Jueptner, M., Stephan, K. M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. & Passingham, R. E. 1997 Anatomy of motor learning. I. Frontal cortex and attention to action. *J Neurophysiol* **77**, 1313-24.
- Leopold, D. A. & Logothetis, N. K. 1996 Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* **379**, 549-53.
- Leopold, D. A., Maier, A. & Logothetis, N. K. 2003 Measuring subjective visual perception in the nonhuman primate. *Journal of Consciousness Studies* **10**, 115-130.
- Levine, J. 1983 Materialism and qualia: The explanatory gap. *Pacific Philosophical Quarterly* **64**, 354-361.
- Logothetis, N. K. 2003 MR imaging in the non-human primate: studies of function and of dynamic connectivity. *Curr Opin Neurobiol* **13**, 630-42.
- Louie, K. & Wilson, M. A. 2001 Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep. *Neuron* **29**, 145-56.
- Manabe, K., Kawashima, T. & Staddon, J. E. 1995 Differential vocalization in budgerigars: towards an experimental analysis of naming. *J Exp Anal Behav* **63**, 111-26.
- Mangan, B. 1993 Taking phenomenology seriously: The fringe and its implications for cognitive research. *Conscious Cogn* **2**, 89-108.
- Maril, A., Wagner, A. D. & Schacter, D. L. 2001 On the tip of the tongue: an event-related fMRI study of semantic retrieval failure and cognitive conflict. *Neuron* **31**, 653-60.
- Marino, L. 2002 Convergence of complex cognitive abilities in cetaceans and primates. *Brain Behav Evol* **59**, 21-32.
- Merikle, P. M., Smilek, D. & Eastwood, J. D. 2001 Perception without awareness: perspectives from cognitive psychology. *Cognition* **79**, 115-34.
- Merker, B. (in press) The liabilities of mobility: A selection pressure for the transition to consciousness in animal evolution. *Conscious Cogn*.
- Miller, G. A. 1956 The magical number seven, plus or minus two: Some limits on our capacity for processing information. *The Psychological Review* **63**, 81-97.
- Milner, A. D. & Goodale, M. A. 1995 *The Visual Brain in Action*. Oxford: Oxford University Press.
- Nagel, T. 1974 What is it like to be a bat? *Philosophical Review* **83**, 435-50.
- Pashler, H. E. 1997 *The psychology of attention*. Cambridge, MA: MIT Press.
- Pashler, H. E. 1999 *The psychology of attention*. Cambridge, MA: MIT Press: Bradford books.
- Pepperberg, I. M. & Shive, H. R. 2001 Simultaneous development of vocal and physical object combinations by a Grey parrot (*Psittacus erithacus*): bottle caps, lids, and labels. *J Comp Psychol* **115**, 376-84.
- Pepperberg, I. M. & Wilcox, S. E. 2000 Evidence for a form of mutual exclusivity during label acquisition by grey parrots (*Psittacus erithacus*)? *J Comp Psychol* **114**, 219-31.
- Plourde, G. & Sperry, R. W. 1984 Left hemisphere involvement in left spatial neglect from right-sided lesions. *Brain* **107 ( Pt 1)**, 95-106.
- Preuss, T. M. & Coleman, G. Q. 2002 Human-specific organization of primary visual cortex: alternating compartments of dense Cat-301 and calbindin immunoreactivity in layer 4A. *Cereb Cortex* **12**, 671-91.
- Preuss, T. M., Qi, H. & Kaas, J. H. 1999 Distinctive compartmental organization of human primary visual cortex. *Proc Natl Acad Sci U S A* **96**, 11601-6.
- Raichle, M. E. 1998 The neural correlates of consciousness: an analysis of cognitive skill learning. *Philos Trans R Soc Lond B Biol Sci* **353**, 1889-901.
- Ranganath, C., Cohen, M. X., Dam, C. & D'Esposito, M. 2004 Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *J Neurosci* **24**, 3917-25.
- Rayport, S. G. & Kandel, E. R. 1986 Development of plastic mechanisms related to learning at identified chemical synaptic connections in *Aplysia*. *Neuroscience* **17**, 283-94.
- Richards, D. G., Wolz, J. P. & Herman, L. M. 1984 Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *J Comp Psychol* **98**, 10-28.
- Savage-Rumbaugh, E. S. 1990 Language acquisition in a nonhuman species: implications for the innateness debate. *Dev Psychobiol* **23**, 599-620.
- Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L. & Rumbaugh, D. M. 1993 Language comprehension in ape and child. *Monogr Soc Res Child Dev* **58**, 1-222.
- Seth, A. K., Edelman, D. B. & Baars, B. J. in press Let's not forget about sensory consciousness. *Behavioral and Brain Sciences*.

- Seth, A. K. & Edelman, G. M. 2004 Environment and behavior influence the complexity of evolved neural networks. *Adaptive Behavior* **12**, 5-20.
- Seth, A. K., McKintstry, J. L., Edelman, G. M. & Krichmar, J. L. 2004 Visual binding through reentrant connectivity and dynamic synchronization in a brain-based device. *Cerebral Cortex*.
- Shadlen, M. N. & Movshon, J. A. 1999 Synchrony unbound: a critical evaluation of the temporal binding hypothesis. *Neuron* **24**, 67-77.
- Shafritz, K. M., Gore, J. C. & Marois, R. 2002 The role of the parietal cortex in feature binding. *Proc Natl Acad Sci USA* **99**, 10917-10922.
- Sheinberg, D. L. & Logothetis, N. K. 1997 The role of temporal cortical areas in perceptual organization. *Proc Natl Acad Sci U S A* **94**, 3408-13.
- Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M. & Pettigrew, J. D. 1996 The echidna *Tachyglossus aculeatus* combines REM and non-REM aspects in a single sleep state: implications for the evolution of sleep. *J Neurosci* **16**, 3500-6.
- Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M., Shalita, T. & Pettigrew, J. D. 1999 Sleep in the platypus. *Neuroscience* **91**, 391-400.
- Singer, J. E. 1993 Experimental studies of the flow of ongoing thought. In *Experimental and theoretical studies of consciousness* (ed. J. Marsh). London: Wiley Interscience.
- Singer, W. 1999 Neuronal synchrony: a versatile code for the definition of relations? *Neuron* **24**, 49-65.
- Singer, W. & Gray, C. M. 1995 Visual feature integration and the temporal correlation hypothesis. *Annu Rev Neurosci* **18**, 555-86.
- Smith, J. D., Shields, W. E. & Washburn, D. A. 2003 The comparative psychology of uncertainty monitoring and metacognition. *Behav Brain Sci* **26**, 317-39; discussion 340-73.
- Spitzer, H., Desimone, R. & Moran, J. 1988 Increased attention enhances both behavioral and neuronal performance. *Science* **240**, 338-40.
- Srinivasan, R., Russell, D. P., Edelman, G. M. & Tononi, G. 1999 Increased synchronization of magnetic responses during conscious perception. *Journal of Neuroscience* **19**, 5435-48.
- Standing, L. 1973 Learning 10,000 pictures. *Q J Exp Psychol* **25**, 207-22.
- Steinmetz, P. N., Roy, A., Fitzgerald, P. J., Hsiao, S. S., Johnson, K. O. & Niebur, E. 2000 Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature* **404**, 187-90.
- Stephan, K. M., Thaut, M. H., Wunderlich, G., Schicks, W., Tian, B., Tellmann, L., Schmitz, T., Herzog, H., McIntosh, G. C., Seitz, R. J. & Homberg, V. 2002 Conscious and subconscious sensorimotor synchronization--prefrontal cortex and the influence of awareness. *Neuroimage* **15**, 345-52.
- Steriade, M., McCormick, D. A. & Sejnowski, T. J. 1993 Thalamocortical oscillations in the sleeping and aroused brain. *Science* **262**, 679-85.
- Stoerig, P. & Cowey, A. 1997 Blindsight in man and monkey. *Brain* **120 ( Pt 3)**, 535-59.
- Thiele, A. & Stoner, G. 2003 Neuronal synchrony does not correlate with motion coherence in cortical area MT. *Nature* **421**, 366-70.
- Tomaiuolo, F., Ptito, M., Marzi, C. A., Paus, T. & Ptito, A. 1997 Blindsight in hemispherectomized patients as revealed by spatial summation across the vertical meridian. *Brain* **120 ( Pt 5)**, 795-803.
- Tononi, G. & Edelman, G. M. 1998 Consciousness and complexity. *Science* **282**, 1846-51.
- Tononi, G., Edelman, G. M. & Sporns, O. 1998a Complexity and coherency: Integrating information in the brain. *Trends Cogn Sci* **2**, 474-484.
- Tononi, G., McIntosh, A. R., Russell, D. P. & Edelman, G. M. 1998b Functional clustering: identifying strongly interactive brain regions in neuroimaging data. *Neuroimage* **7**, 133-49.
- Tononi, G., Sporns, O. & Edelman, G. M. 1992 Reentry and the problem of integrating multiple cortical areas: simulation of dynamic integration in the visual system. *Cereb Cortex* **2**, 310-35.
- Tononi, G., Sporns, O. & Edelman, G. M. 1994 A measure for brain complexity: relating functional segregation and integration in the nervous system. *Proc Natl Acad Sci U S A* **91**, 5033-7.
- Tononi, G., Srinivasan, R., Russell, D. P. & Edelman, G. M. 1998c Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc Natl Acad Sci U S A* **95**, 3198-203.
- Tootell, R. B., Tsao, D. & Vanduffel, W. 2003 Neuroimaging weighs in: humans meet macaques in "primate" visual cortex. *J Neurosci* **23**, 3981-9.
- Treisman, A. 1998 Feature binding, attention and object perception. *Philos Trans R Soc Lond B Biol Sci* **353**, 1295-306.

- Tsuda, I. 2001 Toward an interpretation of dynamic neural activity in terms of chaotic dynamical systems. *Behav Brain Sci* **24**, 793-810; discussion 810-48.
- Ungerleider, L. G. & Haxby, J. V. 1994 'What' and 'where' in the human brain. *Curr Opin Neurobiol* **4**, 157-65.
- Walters, E. T., Carew, T. J. & Kandel, E. R. 1981 Associative Learning in Aplysia: evidence for conditioned fear in an invertebrate. *Science* **211**, 504-6.
- Weiskrantz, L. 1998 *Blindsight: A case study and implications*. Oxford: Oxford University Press.
- Widner, R. L., Jr. & Smith, S. M. 1996 Feeling-of-knowing judgments from the subject's perspective. *Am J Psychol* **109**, 373-87.