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Criteria for consciousness in humans and other mammals

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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.

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1. 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

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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 (Brewer, Press, Logothetis, & Wandell, 2002; Hendry et al., 1994; Tootell, Tsao, & Vanduffel, 2003, but see Preuss & Coleman, 2002; Preuss, Qi, & Kaas, 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 (Griffin & Speck, 2004; Herman, Kuczaj, & Holder, 1993; Herman, Morrel-Samuels, & Pack, 1990; Manabe, Kawashima, & Staddon, 1995; Marino, 2002; Pepperberg & Shive, 2001; Pepperberg & Wilcox, 2000; Richards, Wolz, & Herman, 1984; Savage-Rumbaugh, 1990; Savage-Rumbaugh et al., 1993). For a recent review, see Griffin and 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 (Merikle, Smilek, & Eastwood, 2001; Milner & Goodale, 1995). 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

Table 1

Basic brain facts (1–3), and 14 other widely recognized properties of consciousness

1. *EEG signature.* Irregular, low-amplitude, and fast electrical activity in the brain ranging from 12 to 70 Hz. 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 4 Hz.
2. *Cortex and thalamus.* 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. *Widespread brain activity.* 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 *outside* the focus of current conscious contents, as indicated by implicit learning, episodic memory, biofeedback training of autonomic and motor function, and the like.
4. *Wide range.* 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. *Informativeness.* 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. *The rapidly adaptive and fleeting nature of conscious scenes.* 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. *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 moment. In general, of two mutually inconsistent stimuli presented simultaneously, only one can become conscious.
8. *Limited capacity and seriality.* 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. *Sensory binding.* 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 functionally segregated regions coordinate their activities in order to generate the *gestalts* of ordinary conscious perception.
10. *Self-attribution.* 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. *Accurate reportability.* 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. *Subjectivity.* 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. *Focus-fringe structure.* 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. *Facilitation of learning.* 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. *Stability of contents.* 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.

(continued on next page)

Table 1 (continued)

- | | |
|-----|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 16. | <i>Allocentricity.</i> 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. | <i>Conscious knowing and decision making.</i> 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. |

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, 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).¹ 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, Baars, & Seth, this volume).

2. Consciousness and the brain

Physiologically, three basic facts stand out about consciousness.

2.1. 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 4 Hz (Baars, Ramsoy, & Laureys, in press). Virtually, all mammals studied thus far exhibit the range of neural activity patterns diagnostic of both conscious states.²

¹ '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.

² 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 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, Manger, Nienhuis, Fahringer, & Pettigrew, 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).

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

96 2.2. *Involvement of the thalamocortical system*

97 In mammals, consciousness seems to be specifically associated with the thalamus and cortex
98 (Baars, Banks, & Newman, 2003). Regions such as the hippocampal system and cerebellum can
99 be damaged without a loss of consciousness per se. Indeed, in cases like Rasmussen encephal-
100 itis, an entire hemisphere can be surgically removed without a loss of consciousness (although
101 a form of blindsight can occur after surgery for this condition; see Tomaiuolo, Ptito, Marzi,
102 Paus, & Ptito, 1997). Damage to the brainstem, including the thalamus, can abolish the state
103 of consciousness; but a very local lesion in sensory cortex may delete only specific conscious
104 features such as color vision, visual motion, conscious experiences of visual objects and faces,
105 and the like. Such cortical damage does not disrupt the state of consciousness, but changes its
106 contents.

107 To a first approximation, the lower brainstem is involved in maintaining the state of conscious-
108 ness, while the cortex (interacting with thalamus) sustains conscious contents. No other brain re-
109 gions have been shown to possess these properties.

110 2.3. *Widespread brain activity*

111 Recently, it has become apparent that conscious scenes are distinctively associated with wide-
112 spread brain activation (Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Rus-
113 sell, & Edelman, 1998c). Perhaps two dozen experiments to date show that conscious sensory
114 input evokes brain activity that spreads from sensory cortex to parietal, prefrontal, and medial-
115 temporal regions; closely matched unconscious input activates mainly sensory areas locally (Deh-
116 aene et al., 2001). Similar findings show that novel tasks, which tend to be conscious and report-
117 able, recruit widespread regions of cortex; these tasks become much more limited in cortical
118 representation as they become routine, automatic and unconscious (Baars, 2002).

119 2.3.1. *Basic properties of consciousness*

120 Together, these first three properties indicate that *consciousness involves widespread, relatively*
121 *fast, low-amplitude interactions in the thalamocortical core of the brain, driven by current tasks*
122 *and conditions*. Unconscious states are markedly different and much less responsive to sensory in-
123 put or endogenous activity. These properties are directly testable and constitute necessary criteria
124 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.

2.4. *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, Wagner, & Schacter, 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.

2.5. *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 (Edelman, 2003; Tononi & Edelman, 1998). 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, McIntosh, Russell, & Edelman, 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, Sporns, & Edelman, 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 Fig. 1). By definition, a complex dynamic core is also highly informative.

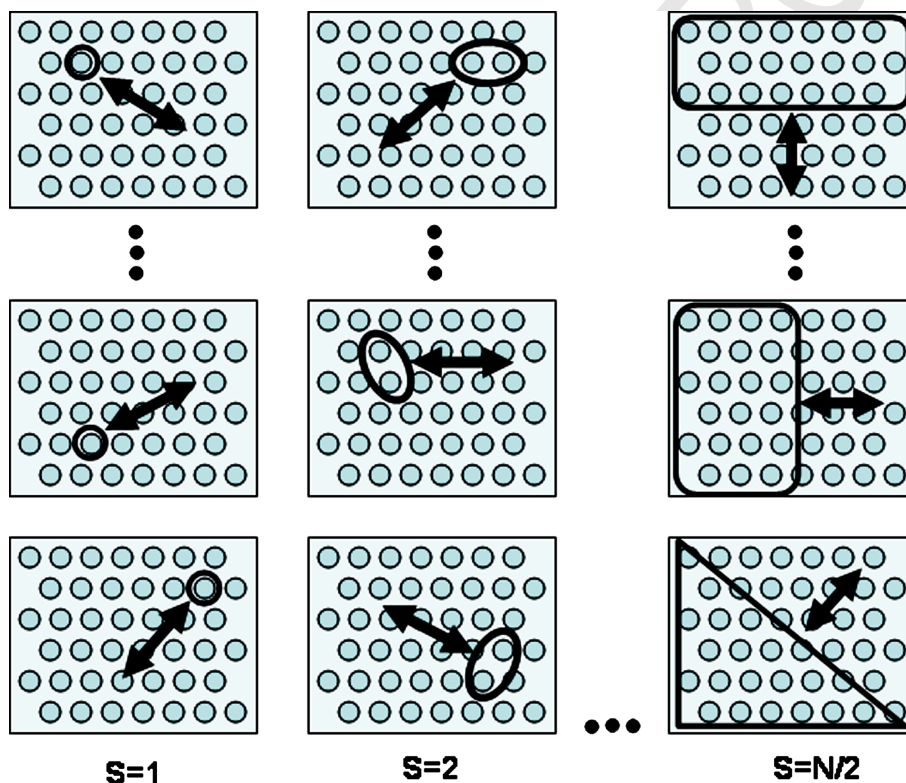


Fig. 1. Neural complexity, after Fig. 2 in Tononi et al. (1998a). The figure shows an idealized neural system composed of N neuronal elements (small circles) divided into subsets of size 1 ($S = 1$), size 2 ($S = 2$), and size $N/2$ ($S = N/2$). Bold arrows indicate mutual information between subsets 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.

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

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

187 2.6. *The rapidly adaptive and fleeting nature of conscious scenes*

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

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

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

213 Evidence from cortical electroencephalographic (EEG) recordings from humans, cats, and
214 rabbits suggests that brain dynamics can be described in this way (Freeman, 2000; Freeman
215 & Rogers, 2003; Tsuda, 2001). Almost 30 years ago, metastable EEG patterns in the rabbit
216 olfactory bulb were found to correspond to odor stimuli (Freeman & Skarda, 1985), and recent
217 studies have extended these findings to larger regions of mammalian cortex (Freeman & Rogers,
218 2003).

219 2.7. *Internal consistency*

220 Consciousness is marked by a consistency constraint. For example, while multiple meanings
221 of most words are active for a brief time after presentation, only one becomes conscious at any
222 given moment. The literature on dual input tasks shows without exception that of two mutu-
223 ally inconsistent stimuli presented simultaneously, only one becomes conscious (Baars, 1988).
224 This fact has been known for many years for selective listening, binocular rivalry, and ambig-
225 uous words and figures. Binocular rivalry in particular has become a popular topic for animal
226 studies: Landmark work by Leopold and Logothetis (1996) and Sheinberg and Logothetis
227 (1997) used single-unit recordings in awake-behaving monkeys to distinguish neurons in the
228 primate visual system that correlated with the stimulus from those that correlated with the
229 percept.

230 In certain clinical conditions, it is possible that the consistency constraint may no longer
231 apply to the brain state as a whole. Severe epilepsy is sometimes treated by surgically severing
232 the corpus callosum, the major fiber tract connecting the two cerebral hemispheres. Although
233 post-operative patients may appear entirely normal in many circumstances, careful tests show
234 incongruities between verbal report—usually mediated by the left hemisphere—and the actions
235 of the left hand—usually mediated by the right hemisphere (Gazzaniga, Bogen, & Sperry,
236 1965, but see Plourde & Sperry, 1984). Other conditions that may involve functional discon-
237 nection within the brain include dissociative disorders, fugue states, and conversion hysteria. It
238 is possible that future experiments will allow direct visualization of such phenomena by, for
239 example, measuring the distribution of coherent brain activity in subjects in hypnotic dissocia-
240 tive states (Hilgard, 1977); it may turn out that such states are accompanied by ‘split’ dynamic
241 cores.

242 2.8. *Limited capacity and seriality*

243 Several aspects of the brain have surprisingly limited capacity, such as the famous “seven plus
244 or minus two” limit of rehearsable working memory (Cowan, 2001; Miller, 1956), and the limits
245 of selective attention (Pashler, 1997). These limits have also been studied in non-human animals.
246 For example, Glassman, Garvey, Elkins, Kasal, and Couillard (1994) showed that humans and
247 rats have similar working memory limits when tested in comparable radial maze situations, and
248 Spitzer, Desimone, and Moran (1988) correlated task difficulty in a visual discrimination task
249 with attentional modulation of neuronal activity in macaque monkeys (see also Chun & Marois,
250 2002).

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

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

260 2.9. *Sensory binding*

261 Binding is one of the most striking properties of consciousness. It is certainly among the most
262 assiduously studied of topics in consciousness research (Crick, 1984; Crick & Koch, 1990; Edelman,
263 1993; Singer & Gray, 1995; Treisman, 1998). The visual brain is functionally segregated such that dif-
264 ferent cortical areas are specialized to respond to different visual features such as shape, color, and
265 object motion. Yet consciousness of a visual scene has the property that these distinct aspects are
266 bound together in a unified percept. Binding also appears to occur with more abstract conscious con-
267 tents, such as the meaning of a phrase or even a paragraph, in which consistent discourse reference
268 occurs, such as using the word “it” to refer to a previous noun (called deixis in linguistics). In both
269 cases, a key question persists: How do functionally segregated regions and brain events coordinate
270 their activities in order to generate the gestalts of ordinary conscious perception and cognition.

271 Most proposed solutions to the binding problem fall into one of two general classes: (i) binding
272 through the influence of attentional processes, executive mechanisms, or superordinate maps
273 (Shadlen & Movshon, 1999; Shafritz, Gore, & Marois, 2002) and (ii) binding through the selective
274 synchronization of dynamically formed neuronal groups (Edelman, 1993; Gray, 1999; Singer,
275 1999). The former often focuses on parietal or frontal areas, the operations of which are spatially
276 and temporally distant from early stages of sensory processing. It has been suggested that these
277 areas implement an executive mechanism, such as a spotlight of attention, that is able to combine
278 visual features at specific locations in space (Shafritz et al., 2002; Treisman, 1998). Advocates of
279 neural synchrony, by contrast, suggest that sensory binding is an automatic, dynamic, and pre-at-
280 tentive process: combinations of features relating to visual objects are bound by the dynamic syn-
281 chronization of corresponding neuronal groups in different cortical areas.

282 Theories based on neural synchrony have received empirical support from neurophysiological
283 recordings that show synchronous activity among neurons in mammalian brains (Fries, Reynolds,
284 Rorie, & Desimone, 2001; Gray & Singer, 1989; Steinmetz et al., 2000, but see Thiele & Stoner,
285 2003). That this evidence derives from non-human mammals strongly suggests that sensory bind-
286 ing via neural synchrony may be a mechanism shared by many species.

287 Synchrony-based theories have also been strongly criticized. For example, Treisman suggests
288 that although synchrony may allow the brain to ‘hold on’ to a solution to the binding problem,
289 it does not explain how such solutions are arrived at (Treisman (1998)). The lack of specific brain
290 mechanisms for reading a synchrony-based ‘code’ has also been noted (Shadlen & Movshon,
291 1999). Recently, theoretical models have addressed some of these concerns by demonstrating
292 the successful categorization of multiple visual objects by the dynamic synchronization of neuro-
293 nal groups (Seth, McKinsty, Edelman, & Krichmar, 2004; Tononi, Sporns, & Edelman, 1992). In
294 these models, synchronously active neural circuits form which correspond to distinct objects in the
295 environment. The emergence and stability of these circuits depended on the presence of wide-
296 spread reentrant connectivity among neural areas (Seth et al., 2004).

297 2.10. *Self-attribution*

298 Conscious experiences are always attributed to an experiencing self, the “observing self” to
299 which James referred (James, 1890). Self-functions appear to be associated with several brain re-
300 gions, 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, 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, Shields, & Washburn, 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, Edelman, & Baars, 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.

2.11. Accurate reportability

Accurate report 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).³

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.

2.12. 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 con-

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

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.

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, 2003; Edelman, 2004; Tononi & Edelman, 1998); according to Edelman and Tononi, *qualia are* these high-order discriminations.

2.13. *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., Bowers, Regehr, Balthazard, & Parker, 1990; Widner & Smith, 1996). 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.

424 2.14. *Consciousness facilitates learning*

425 The possibility of unconscious learning has been debated for decades. Indeed, conditioning
426 studies of a (putatively) non-conscious invertebrate, the sea snail *aplysia* have become the bench-
427 mark for many researchers seeking to define the fundamental molecular and physiological prop-
428 erties of learning (Rayport & Kandel, 1986; Walters, Carew, & Kandel, 1981). Nevertheless, there
429 appears to be only very limited evidence for long term learning of unconscious input (Clark,
430 Manns, & Squire, 2002). In contrast, the evidence for learning of conscious episodes, even without
431 any intention to learn, is overwhelming. The capacity of conscious visual memory is enormous
432 (Standing, 1973). Even implicit learning requires conscious attention to the stimuli from which
433 regularities are (unconsciously) inferred, and the learning of novel motor and cognitive skills also
434 requires conscious effort.

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

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

450 Learned behavior based on conscious experience differs from the acquisition of episodic mem-
451 ories, which represent, or reconstruct, past conscious scenes (the moment of standing—or fall-
452 ing—from the surfboard). The acquisition and retrieval of episodic memories appears to
453 require the interplay of the hippocampal complex and the neocortex (Ranganath, Cohen, Dam,
454 & D'Esposito, 2004).

455 2.15. *Stability of conscious contents relative to sensory input*

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

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

470 2.16. *Allocentricity of the objects of experience in an egocentric framework*

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

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

486 Conscious allocentricity may also be related to the distinction between ventral and dorsal
487 visual pathways (Ungerleider & Haxby, 1994). The ventral pathway, which has to do with ob-
488 ject recognition, is closely associated with consciousness, but the dorsal pathway, which has to
489 do with egocentric and allocentric maps, reaching and grasping, seems to be much less so. Ob-
490 ject recognition is likely to benefit from a stable, allocentrically represented (and hence con-
491 scious) visual world, whereas reaching and grasping are viewer-dependent operations which
492 are more likely to require sensitivity to the details of the position, posture, and motion of
493 the reacher. Strikingly, beyond the fact that perceptual feature fields are mainly found in the
494 ventral stream, neural analyses of differences in consciousness between ventral and dorsal activ-
495 ity are still lacking.

496 2.17. *Conscious knowing is useful for voluntary decision-making*

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

501 The knowing function of consciousness may seem obvious. But there is also overwhelming evi-
502 dence for unconscious kinds of knowledge and unconscious intentional states. Implicit learning,
503 implicit cognition, unconscious moods, overpracticed skills, spared implicit functions after brain
504 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).

3. 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).⁴ 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 (Cowey & Stoerig, 1995; Leopold, Maier, & Logothetis, 2003). 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

⁴ 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).

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 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.

4. 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.

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