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Neural Darwinism and consciousness

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Abstract

Neural Darwinism (ND) is a large scale selectionist theory of brain development and function that has been hypothesized to relate to consciousness. According to ND, consciousness is entailed by reentrant interactions among neuronal populations in the thalamocortical system (the 'dynamic core'). These interactions, which permit high-order discriminations among possible core states, confer selective advantages on organisms possessing them by linking current perceptual events to a past history of value-dependent learning. Here, we assess the consistency of ND with 16 widely recognized properties of consciousness, both physiological (for example, consciousness is associated with widespread, relatively fast, low amplitude interactions in the thalamocortical system), and phenomenal (for example, consciousness involves the existence of a private flow of events available only to the experiencing subject). While no theory accounts fully for all of these properties at present, we find that ND and its recent extensions fare well.
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Keywords: Dynamic core; Edelman; Neural Darwinism; Thalamocortical system; Complexity; Degeneracy; Reentry

1. Introduction

Neural Darwinism (ND),[1] a large scale theory of brain function, was proposed initially in 1978 (Edelman, 1978), and has since been developed extensively and hypothesized to relate to

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[1] Neural Darwinism is here used as shorthand for Edelman's Theory of Neuronal Group Selection (TNGS). Primary references for this theory are (Edelman, 1978, 1987, 1989, 1993).

Table 1
Sixteen widely recognized properties of consciousness that are used to assess the adequacy of Neural Darwinism as a theory of consciousness

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 1. Range of conscious contents
 2. Widespread brain effects
 3. Informative conscious contents
 4. Rapid adaptivity and fleetingness
 5. Internal consistency
 6. Limited capacity and seriality
 7. Sensory binding
 8. Self attribution
 9. Accurate reportability
10. Subjectivity
11. Focus-fringe structure
12. Consciousness facilitates learning
13. Stability of conscious contents
14. Allocentricity
15. Consciousness is useful for voluntary decision making
16. Involvement of the thalamocortical core

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consciousness (Edelman, 1987, 1989, 1993, 2003, 2004; Edelman & Tononi, 2000; Tononi & Edelman, 1998). Here we attempt a thorough analysis of the degree to which that claim has been sustained, and what gaps remain. Our strategy will be to emphasize empirical results and to deliberately sidestep philosophical debates. We will assess the consistency of ND with more than a dozen widely recognized properties of consciousness (see Table 1); however, we do not attempt a comparative analysis of competing theories. Scientific studies of the brain basis of consciousness are now quite common, and of good quality (Baars, Banks, & Newman, 2003). It therefore seems timely to review the evidence that any theory, such as ND, must account for.

1.1. Consciousness and the brain

Physiologically, three fundamental facts stand out about consciousness. First, there is the finding, dating back to Hans Berger in 1929 (Berger, 1929), that waking consciousness is associated with low-amplitude, irregular EEG activity in the 20–70 Hz range. Conversely, unconscious states like deep sleep, coma, general anesthesia, and epileptic states of absence show a predominance of slow-wave, high-amplitude and more regular voltages at less than 4 Hz (Baars, Ramsoy, & Laureys, 2003).[2]

The second fundamental fact is that consciousness seems to be distinctively associated with the thalamus and cortex. Damage to the brainstem or thalamus can abolish the *state* of consciousness, while damage to sensory cortex appears to delete *specific conscious features* such as color vision, visual motion, conscious experiences of objects and faces, and the like. No other brain structures show these distinctive effects when damaged.

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[2] More recent work has shown that cortical gamma activity may co-occur with classical deep sleep activity, in synchronized bursts during the peaks of the slow waves (Steriade, McCormick, & Sejnowski, 1993). Nevertheless, there is still a striking association of consciousness with continuous gamma, and unconscious states with intermittent gamma bursts at slower than 4 Hz intervals.

The third basic finding is more recent. It is that consciousness is distinctively associated with widespread brain activation related to the conscious content. Perhaps two dozen experiments show that sensory input supporting consciousness spreads from sensory cortex to parietal, prefrontal, and medial-temporal cortex, while closely matched input that does not reach consciousness activates mainly local sensory regions (Baars, 2002). Further, the widespread activity appears to involve more globally coordinated activity (Cosmelli et al., 2004; Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Russell, & Edelman, 1998c). Similar findings show that novel tasks, which tend to be conscious and reportable, recruit wide regions of cortex, while the same tasks do not when they are practiced, automatic and unconscious. And finally, there is evidence that loss of consciousness due to sleep, coma, or general anesthesia disrupts widespread coordinated activity among cortical regions (John et al., 2001).

In sum, it is widely believed that *consciousness involves widespread*, *relatively fast*, *low amplitude interactions in the thalamocortical core of the brain*, *driven by current tasks and conditions.* Any theoretical framework should take these facts into account.

1.2. Neural Darwinism

ND is a biological perspective on brain processes with roots in evolutionary theory and immunology that stresses the importance of large and varied populations. It suggests that brain development and dynamics are *selectionist* in nature, not *instructionist*, in contrast to computers, which carry out explicit symbolic instructions. Selectionist processes have four features:

1. A set of elements are characterized by *diversity*, such as individual members of a species, antibodies in the immune system, or populations of neurons in the brain.
2. These elements can reproduce or *amplify*.
3. A process of *selection* operates on the products of diversity. For example, differential reproductive success serves to select some offspring and not others. In the immune system, successful antigen-antibody matches lead to selective clonal amplification of cells containing matched antibodies.
4. Finally, inherent in such systems is *degeneracy*, the ability of structurally different combinations of elements to perform the same function (Edelman & Gally, 2001).

These features make selectionist systems highly adaptive, as reflected in biological evolution. Indeed, evolution has produced somatic systems which themselves possess adaptive selectional properties, such as the immune system and (according to ND) the brain.

Key to any selectionist theory is identification of appropriate unit(s) of selection. In biological evolution the individual, the gene, and the social group have all been proposed as selectional units. In the immune system the likely candidates are lymphocytic cells displaying the antibodies, and ND suggests that in the brain the 'neuronal group' serves as the fundamental unit of selection. Within ND, a neuronal group refers to a collection of cells of a variety of types (for example, excitatory and inhibitory), ranging in number from hundreds to thousands, that are more closely connected in their intrinsic circuitry than they are externally, and whose mutual dynamic interactions may be enhanced by changes in synaptic efficacy (Edelman, 1987; Izhikevich, Gally, & Edelman, 2004).
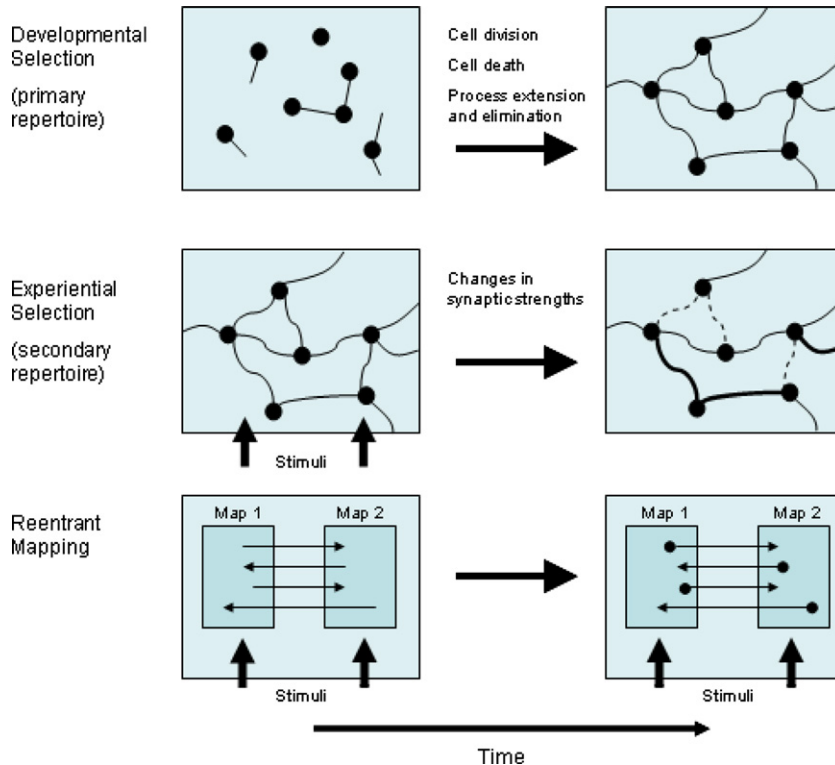
Fig. 1. The three main tenets of ND (adapted from Edelman (1987)). Developmental selection yields a diverse set of neural circuits by cell death, cell division, and process extension and elimination. Experiential selection leads to changes in synaptic strengths favoring some pathways over others. Reentrant connections enable spatiotemporal coordination of neural activity (black dots indicate strengthened synapses).

ND places particular emphasis on degeneracy, which provides multiple alternative pathways for any function (Edelman & Gally, 2001; Tononi, Sporns, & Edelman, 1999). Such flexibility is conspicuously missing in instructionist systems like computers, as shown by the great difficulty encountered in building artificial systems that simulate biological capacities. Edelman and colleagues argue that degeneracy follows inherently from selectionist systems, rather than being especially built in, as in the multiple redundant computers that run the space shuttle.[3]

In the brain, selectionism applies both to neural development and to moment-to-moment functioning. Edelman postulates two overlapping phases of developmental and experiential variation and selection. The first is the formation during development of a *primary repertoire* of many neuronal groups by cell division, migration, selective cell death, and the growth of axons and dendrites. This primary repertoire of neurons is 'epigenetically' constructed through a combination

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[3] Edelman and Gally cite two dozen examples of biological degeneracy, from multilayered gene networks and multiple proteins that carry out overlapping functions, to the brain's ability to shift functions after brain damage (Edelman & Gally, 2001).

of genetic and environmental influences, and generates a high level of diversity in the nascent nervous system (see Fig. 1).

The second, experiential, phase involves the dynamic formation from this primary repertoire of a *secondary repertoire* of functional neuronal groups, by the strengthening and weakening of synapses through experience and behavior. This phase involves the selective amplification of functional connectivities among the neurons produced in the first phase, with which it overlaps. In this manner, an enormous diversity of anatomical and functional circuits is produced.

Both phases show a high degree of degeneracy as a result of variation and selection. Evidence for degeneracy in the nervous system is plentiful: a given neuronal function can be shaped by many different neural signaling pathways, and many different neural networks can generate equivalent motor outputs, as shown by the remarkable capacity of the brain to recover from major damage as new populations of neurons take over lost functions (Edelman & Gally, 2001; Tononi et al., 1999).

Brain plasticity and flexibility is evident not just in the case of gross brain damage, but in experience-dependent development, learning and adaptation to novel environmental conditions, and changes in cortical neuronal feature assignment due to selective attention and habituation (Buonomano & Merzenich, 1998). For example, the cellular responses of specific sensory finger maps in monkeys change when a given finger is tapped to the point of habituation (Mersenich & Jenkins, 1995). Some theorists refer to degeneracy to explain individual variation in brain activity even for the same cognitive task (Price & Friston, 2002).

Selection in the brain is constrained by *value*, which reflects the salience of an event and can be positive or negative. Value is analogous to selective pressure in evolution. In the brain it is reflected by pleasure, pain, and emotional salience networks mediated by diffuse ascending neural systems. These include the noradrenergic nucleus, the serotonergic raphé nucleus, and the dopaminergic, cholinergic and histaminergic nuclei (Edelman & Tononi, 2000; Friston, Tononi, Reeke, Sporns, & Edelman, 1994; Schultz, 2000). Value-guided selective attention also shapes brain dynamics, for example by enhancing or suppressing neural activity related to an attended stimulus at the expense of an ignored background (Chen, Seth, Gally, & Edelman, 2003; Fries, Reynolds, Rorie, & Desimone, 2001; Steinmetz et al., 2000).

The application of ND to neuronal function requires one more key concept, namely *reentry*: the recursive exchange of signals among neural areas across massively parallel reciprocal connections.[4] Reentry enables the spatiotemporal coordination of activity in different regions of the brain, and is the critical third tenet of ND in addition to developmental and experiential selection (see Fig. 1). In simulation studies, reentry has been shown to lead to perceptual categorization, simple types of learning, and motor control (Seth, McKinstry, Edelman, & Krichmar, 2004; Tononi, Sporns, & Edelman, 1992). Reentry is a distinctively neurobiological aspect of ND, without direct parallel in evolutionary theory or immunology. As we shall discuss, it is the key element in extending ND to account for consciousness.

A number of biologically-inspired automata with simulated brains, known as the 'Darwin' series of 'brain-based devices', have tested these ideas in practice. A brain-based device has (i) an embodied morphology including sensors and motors, (ii) a neural simulation incorporating fea-

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[4] Reentry is to be distinguished from cybernetic feedback, which involves reducing or amplifying an error signal across a single set of lines. Edelman maintains that feedback is an instructionist, computer-like operation.

tures of mammalian neuroanatomy and neurophysiology that allow comparison with empirical data, and (iii) a value system that responds to salient events in the environment and modulates plasticity in the simulated nervous system. Darwin automata have demonstrated simple perceptual categorization, invariant object recognition, and multimodal conditioned behavior. Recent incarnations of Darwin possess several sensory maps, each consisting of tens or hundreds of simulated neuronal groups.[5] These areas are connected by long range reentrant projections. These models have demonstrated the importance of self-motion in perceptual categorization and the role of reentry in enabling the various features of a visual object to be 'bound' together into a single percept (Almassy, Edelman, & Sporns, 1998; Edelman et al., 1992; Krichmar & Edelman, 2002; Seth et al., 2004; Seth, Mckinstry, Edelman, & Krichmar (2004)).[6]

2. Selectionism and consciousness

How can such a selectionist perspective cast light on consciousness? Consciousness may be shaped by major aspects of brain dynamics and neural development, as suggested by experiential learning in the selective development of visual neurons in infancy (Burkhalter, Bernardo, & Charles, 1993). Some researchers associate consciousness with binding of separate perceptual features into unitary objects and events. The Darwin series of selectionist machines demonstrates binding capacity in a simple form, as well as crossmodal and sensorimotor integration. Perceptual categories are also plausibly associated with consciousness, since human consciousness is most detailed for the perceptual world; selectionist theory has been concerned with perceptual categorization from the beginning. Also, as we discuss below, the association of consciousness with globally coordinated activity in the thalamocortical core is addressed by recent extensions of ND. We can see already that the complexity of this activity is consistent with the diversity inherent in repertoires of neuronal groups generated by variation and selection.

2.1. Specific theoretical claims

A series of efforts have been made to extend ND to consciousness. These include three books: *The Remembered Present* (Edelman, 1989), *A Universe of Consciousness* (Edelman & Tononi,

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[5] Although a given Darwin's neural system is implemented using computers, this is consistent with the claim that neural systems are fundamentally different from computers. It is simply the case that computers are very good tools for modeling complex systems; they are also used to model the weather, for example, without anyone believing that the weather is like a computer. Indeed, computers are routinely used to simulate selectionist processes, for example in evolutionary algorithm optimisation (Mitchell, 1997), and in unsupervised learning in neural networks (Hinton & Sejnowski, 1999).

[6] Edelman expresses the importance of self-motion via the concept of a *global mapping*, which is a relation between the movement of an organism, its changing sensory input, and the covariation of cortical activity with activities of various subcortical structures involved in the temporal sequencing of perception and action, such as the basal ganglia, hippocampus, and certain brain stem nuclei and parts of the cerebellum (Edelman, 1987; Edelman & Tononi, 2000). Self-motion induces correlated activity in various sensory sheets of the brain, and these correlations, which form classification couples (or *n*-tuples), and which are mediated by reentrant connections, enable degenerate perceptual categories to be derived from an initially unlabelled world.

2000), and *Wider than the Sky: The Phenomenal Gift of Consciousness* (Edelman, 2004); and a number of papers (notably (Edelman, 2003; Tononi & Edelman, 1998)). Two major themes occupy these works. The first is an association of primary (sensory) consciousness with reentrant interactions between perceptual categorization and memory, where primary consciousness refers to the presence of a multimodal scene of perceptual and motor events (James' "specious present", or Edelman's "remembered present"). The second is an attempt to associate consciousness with neural activity in the thalamocortical core, where activity in the core corresponds to the discrimination of sensorimotor signals in a high dimensional space, yielding adaptive behavior (Edelman, 2003; Tononi & Edelman, 1998).

The first theme, presented in Edelman (1989), is summarized as follows (Edelman & Tononi, 2000, p. 102): "We propose that primary consciousness emerged in evolution when, through the appearance of new circuits mediating reentry, posterior areas of the brain that are involved in perceptual categorization were dynamically linked to anterior areas that are responsible for a value-based memory. With such means in place, an animal would be able to build a remembered present—a scene that adaptively links immediate or imagined contingencies to that animal's previous history of value driven behavior". Primary consciousness, by this view, provides an animal with increased discriminatory selectivity, flexibility, and planning capacity when responding to complex environments, as compared to its preconscious ancestors (see Fig. 2).
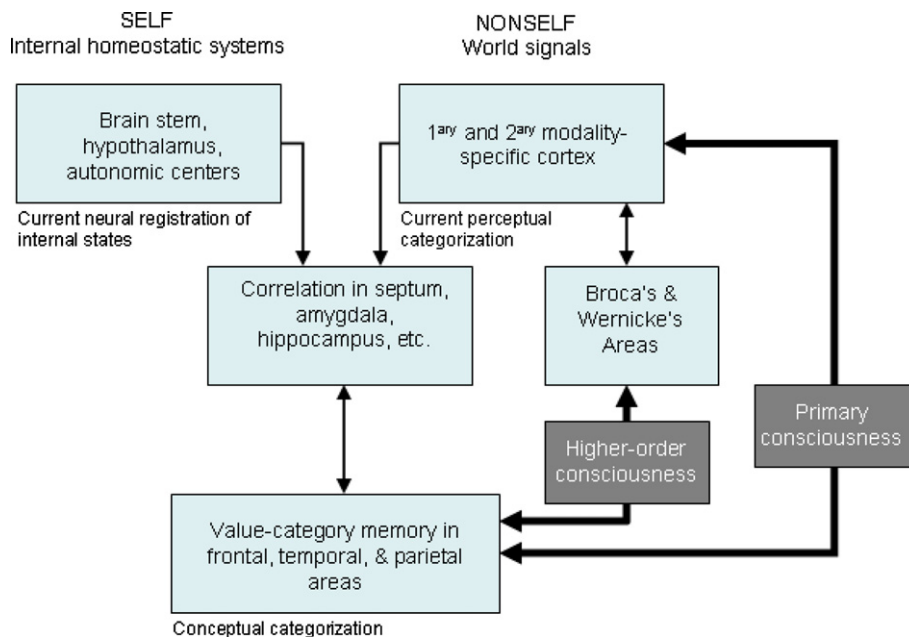

Fig. 2. Mechanisms of primary (sensory) consciousness and higher-order consciousness (adapted from Fig. 9.1 and Fig. 15.1 in Edelman and Tononi (2000)). Signals related to value and signals from the world are correlated and produce value-category memories. These memories are linked by reentry to current perceptual categorization, resulting in primary consciousness. Higher-order consciousness depends on further reentry between value-category memory and current categorization via areas involved in language production and comprehension.

Edelman and Tononi take up the second theme by observing that consciousness is at once highly differentiated (each conscious event is one among an astronomical number of possible conscious events) and highly integrated (each conscious event is experienced as a unity). The sight of a red square, for example, is both a unified experience—we see the redness and the squareness 'all at once'—and a unique event: Even a simple red square is experienced against a constantly varying and enormously diverse background of stimuli of all kinds—visual, auditory, olfactory, kinesthetic, and somatosensory, among others.

According to these views, the thalamocortical system presents a very special kind of neuroanatomy with high interconnectivity, well suited to balancing the integration and differentiation characterizing consciousness. Importantly, these properties are not shown by other major brain structures such as the cerebellum, which in many mammals has a similar number of neurons to the thalamocortical system.

To make their case, Edelman and colleagues introduce several novel quantitative concepts which rest upon the statistical foundations of information theory (Shannon & Weaver, 1949), and which extend the basic idea of spatially correlated oscillatory activity (Tononi, McIntosh, Russell, & Edelman, 1998b; Tononi, Sporns, & Edelman, 1994; Tononi et al., 1999) (see also (Seth & Edelman, 2004b; Sporns, Tononi, & Edelman, 2000)). They define a *Functional Cluster* as a subset of a neural system with dynamics 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). A term called *Integration* captures the overall statistical dependence of elements in a system (or subset); the higher the integration, the more tightly yoked the activity of the elements are to each other. Most importantly, *Complexity* reflects the extent to which the dynamics of a system are both differentiated, such that small subsets of the system behave more-or-less independently, and integrated, such that large subsets tend to behave coherently. As we discuss later (see Section 3.3; *Informativeness*), a complex system of this kind is one with many heterogeneous parts that can act quasi-independently but that can also interact with each other to form larger ensembles that yield global functions (Edelman, 2003).

All of these definitions depend on being able to measure the *entropy* (the overall statistical independence) of a system and the *mutual information* between its various partitions, for which standard formulae exist (Papoulis & Pillai, 2002).[7]

The application of these concepts to consciousness comes together in the 'dynamic core' hypothesis, which has two parts (Edelman & Tononi, 2000, p.144),:

1. A group of neurons can contribute directly to conscious experience only if it is part of a distributed functional cluster, that, through reentrant interactions in the thalamocortical system, achieves high integration in hundreds of milliseconds.
2. To sustain conscious experience, it is essential that this functional cluster be highly differentiated, as indicated by high values of complexity.

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[7] Mutual information expresses the statistical dependence between two systems, or between two partitions of a single system, by the degree to which the entropy of one is accounted for by the entropy of the other.

Edelman and Tononi stress that neurally complex states can only be sustained by highly reentrant neural networks like those in the thalamocortical core. Moreover, only certain dynamical states of such networks are highly complex—others, such as those prevalent in slow wave sleep and general anaesthesia, are significantly less complex and perhaps for that reason unconscious.[8] In slow wave sleep, for example, cortical activity is characterized by a pattern of high frequency 'bursts' and globally synchronized 'pauses' (Steriade et al., 1993), corresponding to an enormous reduction in the repertoire of available neural states and hence low complexity, as compared to the waking state.

While direct evidence for dynamic cores in real brains is still lacking, the hypothesis is consistent with the evidence that we have reviewed so far, and in particular, with the association of consciousness with widespread, spatially correlated activity in the thalamocortical core during waking and dreams. Moreover, it has been known for some time that strokes involving the intralaminar nuclei of the thalamus can result in persistent vegetative states with total loss of consciousness (Kinney, Korein, Panigrahy, Dikkes, & Goode, 1994).

The two themes are united in the extended theory by a general claim and by other more specific conceptual bridges. The general claim is that the neural systems underlying consciousness arose in evolution as a result of their ability to integrate a large number of sensory inputs and motor outputs occurring in parallel, allowing the discrimination of sensorimotor signals in a high dimensional space. The concept of reentry provides a more specific link: The complex reentrant interactions sustained by the core are supposed to be precisely those which link current perceptual categorization to a value-category memory in the generation of the remembered present (Edelman, 2004). Also, the complexity of the dynamic core is consistent with the enormously diverse repertoire of neuronal groups generated as a result of developmental and experiential variation and selection. Finally, degeneracy plays a fundamental role in both themes, in the former as an inevitable concomitant of selectionist neural processes, and in the latter as providing a dynamical continuity and associativity among transiently stable core states.

A challenge for future research is to extend the quantitative description of these connections. For example, it would be useful to model explicitly the connection between degeneracy and complexity in the context of selection and behavior. This would constitute a step towards a demonstration that only highly degenerate selectional processes can generate sufficient diversity to support a reentrant dynamic core with the requisite complexity for consciousness.

We now consider 16 further properties of consciousness that command a wide consensus (see Table 1), and we gauge their compatibility with Neural Darwinism.[9]

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[8] Theories with elements similar to the dynamic core hypothesis have become increasingly widespread. In a recent paper, Crick and Koch proposed the existence of 'coalitions' of neurons which constitute neural correlates for consciousness (Crick & Koch, 2003; Koch, 2004). John has suggested that consciousness is the result of the conversion of dispersed elements of negative entropy into a global negatively entropic brain state, specifically proposing that consciousness is a property of ''electrical resonance in a critical mass of coherently coupled brain cells'' (John, 2001). Freeman has argued that perceptual events associate with the coalescence of a 'macroscopic pool' of mesoscopic 'wave packets' of neural activity that themselves are induced by destabilization of sensory cortex. While these accounts differ in their neurophysiological and mathematical specificity, they all share the common feature of the formation of a macroscopic brain state involving both specific sensory and non-specific contextual information (Freeman, 2003).

[9] Edelman and Tononi (2000, chap. 12) pursues a similar strategy; a similar but non-identical list of properties of consciousness is given in (Edelman, 2003) (see Table 3).

3. The adequacy of ND in accounting for widely recognized properties of consciousness

3.1. Range of conscious contents

One of the obvious properties of consciousness is its extraordinary range of contents—perception, imagery, emotional feelings, inner speech, abstract concepts and action-related ideas (see Table 3).

The broad range of conscious contents suggests that consciousness involves multiple brain regions. Sensory cortex clearly contributes to conscious perceptual events, and recent studies show frontal activation in non-sensory conscious events such as mental effort and the tip-of-the-tongue experience (Maril, Wagner, & Schacter, 2001; Sheinberg & Logothetis, 1997). An integrative view of consciousness must incorporate interactions among many brain regions, and additional structures—such as the hippocampus—involved in conscious recall, conscious control of motor skills,

Table 2
Adequacy of ND in accounting for properties of consciousness

Well accounted for	Moderately accounted for	Further development needed
Involvement of the thalam ocortical core	Widespread brain effects	Allocentricity
Range of conscious contents	Limited capacity and seriality	Focus-fringe structure
Informative conscious contents	Self attribution	Stability of conscious contents
Rapid adaptivity and fleetingness	Subjectivity	Consciousness facilitates learning
Internal consistency	Consciousness is useful for voluntary decision making	
Sensory binding	Accurate reportability	

Allocations in this table are necessarily subjective and somewhat arbitrary. However the aim is to provide guidelines for further research rather than a final pronouncement on the theoretical reach of ND.

Table 3
Edelman lists a similar but non-identical set of properties of consciousness (Edelman (2003))

General
1. Conscious states are internally consistent, integrated, and constructed by the brain
2. They can be enormously diverse and differentiated
3. They are temporally ordered, serial, and changeable
4. They reflect binding of diverse modalities
5. They have constructive properties including gestalt, closure, and phenomena of filling in

Informational
1. They show intentionality with wide-ranging contents
2. They have widespread access and associativity
3. They have center periphery, surround, and fringe aspects
4. They are subject to attentional modulation, from focal to diffuse

Subjective
1. They reflect subjective feelings, qualia, phenomenality, mood, pleasure, and unpleasure.
2. They are concerned with situatedness and placement in the world
3. They give rise to feelings of familiarity or its lack

and the like. A reentrant dynamic core mobilizing thalamocortical connectivities to construct a conscious scene (or a remembered present) could in principle address such a wide range of brain activities.

Edelman and colleagues have argued that only certain kinds of neuroanatomical connectivity patterns can support a dynamic core (see *Specific Theoretical Claims*, above). While this may account for the exclusion of certain subcortical areas from dynamic core activity (for example basal ganglia, cerebellum), it does not explain why certain *cortical* areas are less involved in consciousness than others. For example, the dorsal visual stream is generally believed not to support conscious contents directly, though it constantly interacts with ventral regions that appear to provide the distinctive perceptual features of conscious objects and events (Goodale & Milner, 1992). Thus dorsal functions like egocentric spatial frameworks are themselves unconscious, yet they are necessary for normal conscious contents. In right parietal neglect, when a critical part of the dorsal anatomy is lost, the left side of visual space collapses. However, the specific features of conscious objects—color, motion, retinal location—are apparently dependent on the ventral stream (Bartels & Zeki, 2000; Ungerleider & Haxby, 1994). At present it is not clear that ND can explain this difference.

Another question is why cortical areas which are neuroanatomically similar can contribute to conscious events in very different ways; the content of a visual experience is very different from a taste of food, or the sound of a bell. Edelman and Tononi (2000) suggest that the content of any conscious event is not simply a consequence of activity in the relevant cortical area. The sensation of redness does not come from activity in the visual cortex alone, although such activity may be required. Rather, a sensation of redness is determined by the state of the entire dynamic core. More formally, any conscious event can be associated with a single point in an N-dimensional space, where N represents the number of neuronal groups that are part of the dynamic core at any time (these authors suggest that N can range from 10^3 to 10^7). A sensation of redness is therefore entailed by a very high dimensional discrimination - not simply a discrimination amongst possible colors, but among a vastly larger number of possible dynamic core states.

According to the extended theory, the diversity of conscious contents arises from the ways in which different neuronal groups influence the N-dimensional space. Although a large proportion of the mammalian cortex is surprisingly uniform in its histology, input to different cortical areas varies greatly. For example, visual input is very different in its statistical structure from proprioceptive input. Neuronal groups sensitive to color may therefore organize the space in a different way to those sensitive to proprioception. Each sensory modality will therefore influence the state of a dynamic core in a unique manner, and this may explain why the content of a conscious event dominated by vision is reliably different from one dominated by a sound, a touch, or a taste.

3.2. Widespread brain effects

Baars (2002) cites several bodies of evidence indicating that the neuronal substrates of conscious events have widespread brain effects outside of the focus of current conscious contents, as indicated by phenomena like implicit learning, episodic memory, biofeedback, and the like. Recently, the direct brain evidence for this point has grown markedly.

Conscious events are associated with widespread brain effects, both within and beyond the focus of current conscious contents. A number of recent studies show widespread activation peaks in parietal, prefrontal and other regions for conscious perceptual input, as compared to unconscious inputs which remain localized to sensory cortex (Dehaene et al., 2001). Recent implanted electrode studies in epileptic subjects confirm this hypothesis for medial-temporal regions, which closely track conscious visual events (Kreiman, Fried, & Koch, 2002).

Such widespread effects are consistent with the idea that reentrant loops connect current perceptual categorization to a value-category memory, since such looping necessarily involves widespread thalamocortical regions. They are also consistent with the dynamic core hypothesis. Individual conscious events are associated with brain states having high complexity, and complex states involve a balance between integration and differentiation that requires contributions from many brain regions. The reentrant neural substrate of a dynamic core is necessarily distributed.

The dynamic core may also enjoy privileged access to brain structures outside the thalamocortical system, such as the hippocampus and basal ganglia. For example, the hippocampus is implicated in the transfer of conscious contents into episodic long-term memory and thus may interact closely with the dynamic core. Similarly, the basal ganglia support automatic skill components, which are initially conscious and cortical. Functional imaging studies of practice effects show a decrease in cortical activation as a repeated event becomes automatic, along with an increase in basal ganglia activation (Haier et al., 1992; Stephan et al., 2002). This again suggests that conscious events, with detailed cortical representation, can mobilize brain regions that do not directly support conscious contents, but which constantly interact with them.

Edelman and Tononi (2000) introduce the terms 'ports in' and 'ports out' to denote neuronal groups that interface between the dynamic core and, respectively, sensory input and motor output. They stress that interactions via these ports cannot themselves form part of the core since they are almost exclusively one-way. For example, thalamocortical projections via the basal ganglia are usually multisynaptic and feedforward (Graybiel, 1995a). Recent empirical and computational studies (Gurney, Prescott, & Redgrave, 2001a; Gurney, Prescott, & Redgrave, 2001b) suggest that this kind of anatomy is more suited to the minimization of interaction between parallel neural processes than the generation of highly interactive, complex dynamics.

Computer simulations have shown that highly complex network dynamics are well suited to the distribution of input throughout a network, inasmuch as the input acts by amplifying the intrinsic dynamics of complex networks (Tononi, Sporns, & Edelman, 1996). Additional simulations have shown that complex dynamics are able to reproduce the same output from many different subpartitions of the network, which is a key aspect of degeneracy (Tononi et al., 1999). While these simulations deal with network input and network output separately, high complexity has also been found for networks that adaptively couple input to output when controlling the behavior of a simulated agent (Seth & Edelman, 2004a). Thus both empirical evidence and computational modeling indicate that the characteristics of a reentrant dynamic core can lead to the widespread brain effects and adaptive flexibility associated with consciousness.

3.3. 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 (Stephan et al., 2002). Studies of attentional selection also show a preference for more informative stimuli.

Informally, consciousness is associated with informative events, those which are surprising or require a novel response. In the face of novel conditions or tasks, more brain resources must be recruited. Although Edelman and colleagues follow this intuition, their concept of informativeness is more specific: ''At any given time we experience a particular conscious state selected out of billions of possible states, each of which can lead to a specific behavioral consequence. The occurrence of a particular conscious state is therefore highly informative in the specific sense that information is the reduction of uncertainty among a number of alternatives'' (Edelman & Tononi, 2000, p.125).

Information in this formal sense is associated with Shannon's concept of informational entropy (Shannon & Weaver, 1949); indeed entropy is often interpreted as a measurement of the information content of a system, the number of 'yes/no' questions needed to know its state. High entropy signifies high uncertainty about the state of a system, and the greater this uncertainty, the greater the information revealed by the system being in one particular state and not another. Because Shannon information was originally developed in the context of communication theory, many of its applications involve 'external observers', 'channels,', and 'codes'. However, in a functional cluster, such as a dynamic core, it is more natural to think in terms of Bateson's definition of information as 'a difference that makes a difference' (Bateson, 1979). Since the elements of a functional cluster interact much more with each other than with elements outside the cluster, its information content can be understood as the extent to which changes in the state of any of its subsets make a difference to the state of the rest of the cluster.

Information content in this sense can be associated with a complexity measure. As we remarked in the Introduction, a 'complex' system expresses a balance between dynamical integration and dynamical segregation (see Fig. 3). Specifically, the complexity measure of a system is calculated as the average mutual information between each subset of a system and the rest of the system for all possible bipartitions of the system (Tononi et al., 1994). This value will be high if each of its subsets can take on many different states and if these states make a difference to the rest of the system. In other words, complexity measures the amount of information under the constraint that this information is partially available to all parts of the system; it is therefore sensitive to the scaling properties of the distribution of information over different subsets of a system.[10] The dynamic core hypothesis states that conscious events are supported by functional clusters of high complexity. This is therefore a very specific sense in which consciousness is informative, and may explain why—informally—consciousness is preferentially associated with novel events and actions.

3.4. The rapidly adaptive and fleeting nature of conscious events

Consciousness is remarkable for its present-centeredness (Edelman, 1989; James, 1890). Immediate experience of the sensory world may last about the length of sensory memory, a few seconds, and our fleeting cognitive present, though somewhat longer, is surely less than half a minute. In

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[10] A related measure, based on 'effective information', aims to capture the amount of information integrated by a neural system (Tononi & Sporns, 2003). Effective information is a measure of all causal interactions between two parts of a system.
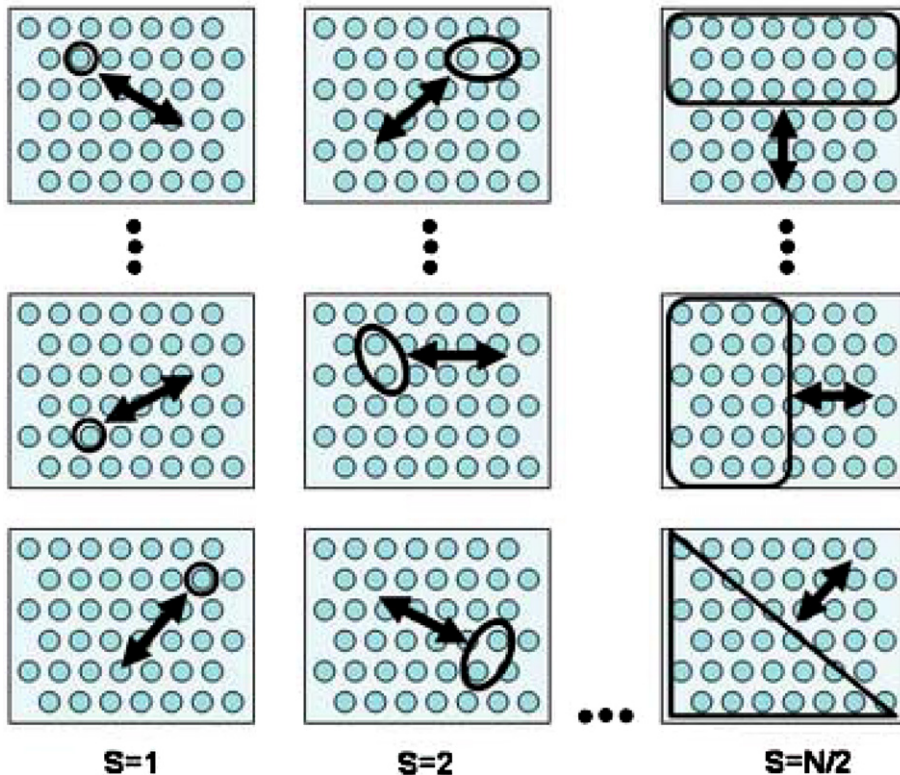
Fig. 3. Neural complexity as the ensemble average mutual information between subsets of a given size and their complement, summed over all subset sizes (adapted from Fig. 2 in Tononi et al. (1998a)). Small circles represent neuronal elements and bold arrows indicate mutual information between subsets and the remainder of the system. Shown in the figure are a selection of subsets of size 1 ($S = 1$), size 2 ($S = 2$), and size $N/2$ for system size N ($S = N/2$). A neurally complex system is one in which small subsets of the system show high statistical independence, but large subsets show low statistical independence. In other words, such 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.

contrast, vast bodies of knowledge are encoded in long-term memory. They are uniformly unconscious. The fleetingness and rapid adaptivity of consciousness require explanation.

For conscious events 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 constantly evolving into subsequent events. To understand this, it is worth returning to the concept of the reentrant dynamic core as embedded in an N-dimensional space, with dimensions defined by all N diverse neuronal groups comprising the core. Think of the topology of this space as an 'attractor landscape' consisting of high-dimensional hills and valleys. A simple example is a landscape consisting of a single attractor, a deep pit in an otherwise flat plain. A dynamic core 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.

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 suggests that brain dynamics can be described in this way (Freeman, 2000). It is possible that some brain dysfunctions can be understood as disruptions of metastability, for example the recurrent and intrusive delusional representations common in schizophrenia have been suggested to result from 'parasitic attractors' in brain dynamics (Hoffman & McGlashan, 2001).

3.5. 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. The literature on dual input tasks shows without exception that of two mutually inconsistent stimuli presented simultaneously, only one becomes conscious (Baars, 1988).

According to the dynamic core hypothesis, conscious events must be internally consistent because each event is defined as an integrated state of the entire dynamic core. As Edelman and Tononi say, "Since a dynamic core is a unified whole, mutual interactions among its constituent neural elements will bring about certain global states of the core that automatically preclude the simultaneous occurrence of certain other global states at any given time" (Edelman & Tononi, 2000, p.147).

It may be possible, however, that under some circumstances the dynamic core can split to form two or more sub-cores. In these cases the consistency constraint would apply to each sub-core separately, but not to the brain state as a whole.

Certain clinical conditions may manifest a split core. Severe epilepsy is sometimes treated by surgically severing the corpus callosum, the major fiber tract connecting the two cerebral hemispheres. While post-operative patients may appear entirely normal in many circumstances, careful tests suggest divided consciousness, for example incongruities between verbal report (usually mediated by the left hemisphere) and the actions of the left hand (usually mediated by the right hemisphere); see, for example (Sperry, 1968). Other conditions that may reflect the splitting of a dynamic core include dissociative disorders, fugue states, and conversion hysteria. It is possible that future experiments may be able to directly visualize split cores by, for example, measuring the distribution of coherent brain activity in subjects in hypnotic dissociative states (Hilgard, 1977).

3.6. 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 (Cowan, 2001; Miller, 1956), and the limits of

selective attention (Pashler, 1999). While consciousness is not to 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. The serial nature of consciousness 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.

Limited capacity and seriality are closely connected to internal consistency. If conscious events are associated with global states of the dynamic core, such that only one such event can prevail at any one time, it follows that *global* states of the core appear serially. Of course, if 'split-cores' are possible then these constraints would apply to each sub-core separately, and not to the brain state as a whole.

What remains to be explained is how the limited capacity of consciousness is related to the limits of other aspects of the brain such as selective attention and working memory. Some researchers adopt a computational stance and suggest that working memory limits are part of optimized heuristics for searching 'lists' of items (Dirlam, 1972; MacGregor, 1987). Others tend towards explanations in terms of neurophysiological constraints. The extended theory, for example, suggests that "capacity limitation . . . may be due to the specific properties of temporal summation mechanisms and to the precision and speed of synchronization needed among neurons to constitute the dynamic core" (Edelman & Tononi, 2000, p. 151). Further clarification of this connection is clearly needed.

3.7. Sensory binding

Binding is one of the most studied topics related to consciousness (Crick, 1984; Crick & Koch, 1990; Edelman, 1993; Singer & Gray, 1995; Treisman, 1998) 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. One classic question is how these functionally segregated regions coordinate their activities in order to generate the gestalts of ordinary conscious perception.

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, Gore, & Marois, 2002) and (ii) binding through the selective synchronization of dynamically formed neuronal groups (Edelman, 1993; Gray, 1999; Singer, 1999). The appeal to attentional mechanisms often focuses on parietal or frontal areas, the operations of which are distant from early stages of sensory processing (Posner & Dehaene, 1994; Posner, Walker, Friedrich, & Rafal, 1984). 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 (Shafritz et al., 2002; Treisman, 1998). Advocates of neural synchrony, by contrast, suggest that sensory binding is an automatic, dynamic, and pre-attentive process. In this view, of which ND is an example, combinations of features relating to visual objects are bound by the dynamic synchronization of corresponding neuronal groups in different cortical areas. According to Edelman, reentry imposes correlations on the interactions of neuronal groups such that synchronously active circuits across widely distributed brain regions are selectively favored (Edelman, 2003).

Theories based on neural synchrony remain controversial. Although they are supported by neurophysiological recordings of synchronous activity in macaque monkey and cat brains (Fries et al., 2001; Gray & Singer, 1989; Steinmetz et al., 2000), a recent study found that neural synchrony did not correlate with the coherence of a moving stimulus (Thiele & Stoner, 2003). It has also been argued, based on recordings from macaque prefrontal cortex, that synchronous activity may be a property of local rather than global circuits (Constantinidis & Goldman-Rakic, 2002).

Theoretical objections to binding by synchrony have also been raised. Treisman has suggested 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). Shadlen and Movshon (1999) also note the lack of specific brain mechanisms designed to 'interpret' the synchrony 'code'.

Recent experiments with Darwin automata—following on a computer simulation (Tononi et al., 1992)—have addressed some of these theoretical concerns by demonstrating the successful categorization of multiple visual objects by the dynamic synchronization of neuronal groups in a brain-based device (Seth et al., 2004). These experiments demonstrate the critical role of reentry in sensory binding—eliminating reentrant connections in the model prevented synchronization among simulated neuronal groups, which in turn disrupted the perceptual categorization of the system.

An important feature of this model is that neural synchrony supports successful categorization by enabling the coherent interaction of local and global processes. Locally, sensory stimuli are processed by specialized visual areas. Activity in these areas gives rise via reentry to a global dynamic characterized by the formation of synchronously active neuronal circuits. This global dynamic in turn constrains the activity of the local elements themselves—for example, neuronal units in early visual areas are more likely to form part of neuronal circuits associated with 'target' objects than with 'distracter' objects. Binding is achieved by the interaction of these processes, neither 'bottom-up' or 'top–down' directions of information flow are by themselves sufficient (Seth et al., 2004).

While ND has shown that reentrant connectivity and dynamic synchronization provide a sufficient mechanism for solving the binding problem, the role of attentional mechanisms is not yet fully explained. For example, there is abundant evidence for disruptions of conscious scene perception following parietal impairment (Brighina et al., 2002). A common interpretation of this effect is that parietal lesions impair the ability to pay attention to certain regions of visual space—a patient with visual hemineglect may appear unable to perceive stimuli on their left. Accounting for this evidence within a framework based on neural synchrony is a challenge for future versions of ND.

3.8. Self attribution

Conscious experiences are always attributed to an experiencing self, the ''observing self'' as James called it (James, 1890). Self functions appear to be associated with several levels of the brain, prominently orbitofrontal cortex in human beings.

Until now we have focused on primary consciousness, the contents of which relate to entities in the world. Ideas of the self in consciousness usually relate to a higher-order consciousness, whose contents relate to the contents of primary consciousness, or to other mental events. Higher-order

consciousness, according to Edelman and Tononi, presupposes the existence of primary consciousness and "is accompanied by a sense of self and the ability in the waking state to explicitly construct past and future scenes" (Edelman & Tononi, 2000, p.102). Higher-order consciousness can construct a narrative by which organisms can escape the remembered present.

A basic notion of the self also makes an appearance in primary consciousness. A running theme in ND is that primary consciousness arises from interactions between current sensory input and a value-based memory. This is described in *The Remembered Present* as an interaction between non-self (i.e. sensory input) and self (value, autonomic, and memory systems). ND is not unique in this respect. More recently, Damasio has suggested that consciousness happens when the brain represents the ways in which views of the environment and of the body change each other, a mapping of coupled maps (Damasio, 2000).

The self as an interpreter of conscious content is very likely not limited to humans. The limbic system may support some version of this function for other mammals. Even lower in the brainstem, there exist appetitive systems like the hypothalamus, emotional-attachment areas such as the periaqueductal gray, and body maps as in the mesencephalic reticular formation. All these arguably involve ancestral aspects of self that may also participate in a human sense of identity.

Higher-order consciousness, by contrast, "flourishes in humans" (Damasio, 2000, p. 102). Edelman has suggested that it requires semantic capability, and for the most developed forms of the narrative self, a linguistic capability. He proposes 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 (see Fig. 2). 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 past and future. Many adaptive advantages would follow: "Relationships that promise positive rewards can be fostered, resentments can be nourished, and plots can be laid." (Edelman & Tononi, 2000, p. 195).

With the possible exception of absorbed and meditative states, in which one is focused exclusively on a sensory source of information, 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.

3.9. Accurate reportability

It is not at all obvious why conscious contents are reportable by a wide range of voluntary responses. Yet it appears to be fundamental, since our standard operational index of consciousness is based on it.

If someone yells 'Ouch! That hurts!' after striking a finger with a hammer, we infer that they feel pain. Accurate, verifiable report is so widely accepted as an operational criterion for consciousness, and as a means of communicating conscious content between individuals, that we risk forgetting that it must still be accounted for.

ND offers some intriguing hints about the sources of reportability. For instance, there is the fact that conscious events evoke widespread brain activity anterior to sensory cortex (see Section 3.2: *Widespread Brain Effects*). It is likely that such widespread activity—mediated by reentry—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).

One can speculate further. A dynamic core consists of both local dynamics (differentiation) and a global state (integration), which are in continual interaction. In Section 3.3; *Informativeness*, this was expressed as the idea that the information content of a dynamic core comes from its state making a difference to the core itself. It is possible that this property of the dynamic core underlies the reportability of conscious events; a distinction can only be reported to an external party if it first is distinguishable to the reporting system itself. Another way of saying this invokes the concept of the self as an interpreter of conscious input. As we remarked above, the most basic form of self in ND is defined by an interaction between current sensory and bodily input and a value-based memory. Explicit report, however, is facilitated by the linguistic capability implicated in the emergence of a higher-order self, which for conscious humans is the normal state of affairs.

Reliance on verbal report as evidence for consciousness may bias against the attribution of consciousness to non-human animals. However, some 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). Following lesions to half of V1, monkeys remain able to make above-chance discriminations in the occluded visual field (choosing between different colors, for example). But they are not able reliably to distinguish 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).[11]

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.

3.10. 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.

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

The peculiar position of attempting an objective, scientific description of subjective conscious events 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; Rowlands, 2001). 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).

Edelman suggests that this reflects a misunderstanding of science, saying: "A scientific theory cannot presume to replicate the experience that it describes or explains . . . to experience the discriminations of an individual, it is necessary to be that individual" (Edelman, 2003). In other words, coming up with a scientific theory that explicitly solved the 'hard problem' would be like developing a theory of hurricanes that was actually windy.

Still, subjectivity must be accounted for. The aspect of *privacy* may be the most tractable. According to the extended theory, conscious events are supported by reentrant dynamic cores, and dynamic cores are supported by particular physical brains; i.e. they are the property of a *phenotype*. Thus, conscious events are inextricably attached to individual brains 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 self or a 'higher-order' narrative self, see Section 3.8: *Self attribution*). 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 orbitofrontal cortex, the limbic system and brainstem value systems (Baars, 2002).

The qualitative feel of conscious events is less easily explained. Why should sensation accompany the complex discriminations enacted by a dynamic core, but not the discrimination of light from dark by a photodiode? Edelman and Tononi suggest that the answer lies in the complexity (in the technical sense) of the discrimination. A sensation of redness does not correspond to a discrimination among a small number of colors; rather, it is entailed by the state of the entire dynamic core. The qualitative feel of a conscious event is a consequence of the vast amount of information disclosed by the core by being in one state out of very many possible states.

The relationship of 'entailment' appears to be critical to the conception of qualia in ND. For Edelman (2003, 2004), qualia *are* high-dimensional discriminations *that are entailed by* neural activity in the core. They differ because their underlying neural systems differ. Qualia are entailed by this distinctive form of neural activity in the same way that the structure of hemoglobin entails a certain spectroscopic response: One is not caused by the other, rather, one is an inevitable property of the other. This concept implies that neural systems underlying consciousness were selected in evolution to carry out discriminations in a high dimensional space of possible inputs, yielding adaptive advantage.

3.11. Focus-fringe structure

While consciousness tends to be thought of as a focal, clearly articulated set of contents, 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 focal consciousness.

Yet people show remarkable accuracy in fringe judgments like feelings of knowing or intuition (Bowers, Regehr, Balthazard, & Parker, 1990). In this respect these events differ from truly unconscious knowledge, like long term memory or automatic motor skills.

Recently, Baars (2003) has proposed that fringe consciousness may be selectively associated with prefrontal areas of cortex, which have few direct projections to posterior sensory cortical areas. In the first brain imaging study of a canonical fringe experience, dominant activation in prefrontal cortex and cingulate gyrus was found in the ''tip of the tongue'' state (Maril et al., 2001). Baars' proposal may be cast in terms of ND by the suggestion that fringe events may be associated with connections to a dynamic core that consist primarily of neuronal groups in prefrontal cortex, supported by prefrontal-thalamic reentrant loops or cingulate-thalamic loops.

Self-functions are frequently experienced as vague and fringe-like as well. This is consistent with the idea, described in Section 3.8: *Self attribution*, 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.

3.12. Consciousness facilitates learning

The possibility of unconscious learning has been debated for decades, but there appears to be only very limited evidence for long term learning of unconscious input. In contrast, the evidence for learning of conscious episodes 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 initial learning of novel motor and cognitive skills also requires conscious effort.

ND offers several related accounts of procedural or perceptual ('skill') learning. At present, ND has less to contribute to accounts of episodic memory formation, which in humans is closely associated with the operations of the hippocampus (Squire, 1992). While in recent work (Edelman, 2003) it has been suggested that the hippocampus may play a role in the early development of consciousness, further development of this suggestion is required.

Perceptual categorization itself can be a form of learning. As we remarked in the introduction, a basic theme of ND is that current perceptual categorization interacts with a value-based memory of previous perceptual categories, and that it is this interaction that evokes (primary) consciousness.

The association of consciousness with motor and cognitive skill learning is better understood in terms of the relations between the thalamocortical system and other closely related structures such as the basal ganglia. The extended theory describes a two stage process. In the first, learning involves the progressive functional isolation of neuronal circuits involved in carrying out novel motor or cognitive acts. Initial widespread cortical activity is progressively replaced by relatively localized circuits depending largely on basal ganglia. This transfer is catalyzed by the activity of value systems. In support of this idea is evidence that plasticity in basal ganglia can be modulated by dopamine (Reynolds & Wickens, 2000).

The second stage involves the linkage of actions together into novel sequences. Again this involves a shift from cortex to basal ganglia and probably cerebellum. Cortex is initially responsible for the formation of sequences of motor and cognitive acts, but once established, they can be expressed via the long multi-synaptic loops through the basal ganglia. There are now several functional imaging studies which support these claims (Haier et al., 1992).

The differential involvement of cortex and basal ganglia during learning and the expression of learnt behavior has been well established for some years (Graybiel, 1995a, 1995b). ND contributes an understanding of why consciousness is preferentially associated with learning. The involvement of cortex in learning may derive from properties of the reentrant dynamic core. Novel acts and sequences may benefit from the flexible, adaptive, and associative dynamics that complex neural states provide. These states, according to the core hypothesis, support consciousness. In contrast, the expression of learnt behavior is unlikely to require the same kind of adaptive flexibility. Rather, a learnt behavior should be expressed with minimal interference from other neural processes. As we have already discussed, the anatomy of the basal ganglia is well suited for this purpose, and the resulting neural dynamics are not likely to be complex. Therefore, the expression of many learnt behaviors may often not require consciousness.

3.13. Stability of conscious contents relative to sensory input

Conscious contents are impressively stable, given the variability of input that is dealt with. Perceptually, the confounding influence of eye, head, and body motion is often excluded from conscious experience (Merker, in press). Even abstract 'fringe' conscious contents such as beliefs, concepts, and the motivational self are remarkably stable over years.

The stability of conscious experience is striking given the continually varying sensory activity resulting from multiple sensor arrays (eyes, mechanoreceptors, ears) mounted on body parts which continually move in many different ways. The complex orchestrations of muscle movements required for action are also largely excluded from consciousness.

Conscious beliefs and concepts are also stable over time. Indeed, fundamental beliefs often last an entire adult lifetime. The same general point has been found true for conscious thoughts and inner speech, using thought-monitoring studies (Singer, 1993). It appears that endogenous conscious contents, like thoughts and images, are quite recurrent for most people.

In terms of ND, the very act of perceptual categorization embodies a stable dynamic, since a category is by definition more stable than the sensory input that gives rise to it. The intrinsic dynamics of the core may also be associated with the stability of conscious experience. In Section 3.3: *Informativeness*, we remarked that a property of the dynamic core is that it is *metastable*, that is, it consists of a series of self-limiting recurrent patterns. It may be that metastable states can only be sustained if the high input and output variability caused by sensor and muscle movements is filtered out, or at least reduced, before entry to the core. Such variability may preclude the global integration that is characteristic of a complex state of the core.

Why should consciousness be associated with stability? Merker proposes that consciousness is the phylogenetic outcome of neural processes that ensure stability in order to ensure effective decision making (Merker, in press). By stripping away the confounding effects of self-motion, decision mechanisms with access to conscious events are more able to cope with the continual problem of what to do next.

3.14. 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 show allocentric mapping, in which representations of object position are stable with respect to observer position.

It seems that conscious events are, generally speaking, allocentrically represented—they have "otherness." But of course the otherness of perceived conscious objects in the world 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. This requires explanation.

There are several reasons why consciousness might be preferentially associated with allocentric representations. First, allocentricity coincides with stability. A viewer-independent world is likely more stable than a world which constantly shifts with the perspective of the observer. The association between stability and consciousness has already been explored (Section 3.13: *Stability of conscious contents relative to the world*).

Conscious allocentricity may 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 reaching and grasping, seems to be much less so. Object recognition is likely to benefit from a stable, allocentrically represented 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. However, as we remarked above, neural accounts of how ventral and dorsal activity contribute differentially to consciousness are still lacking (see Section 3.1: *A wide range of conscious contents*).

ND is consistent with these various proposals, especially in its emphasis on primary consciousness as a result of interactions between external (allocentric) relations (perceptual categorization) and internal (egocentric) relations (a value category memory).

3.15. Consciousness is useful for voluntary decision making

Consciousness is obviously useful for knowing the world around us, and for knowing our own internal processes. Conscious sensations of pain, pleasure, appetites and emotions refer to endogenous events. Conscious sensory perception and abstract ideas typically involve knowing the outer world. While there are many kinds of unconscious knowledge, conscious knowing may be distinctively useful for executive decision making and planning.

The knowing function of consciousness may seem obvious. It is what philosophers often refer to as 'intentionality', the property that conscious states have of being 'about' something (Brentano, 1924–1928). But there is also massive evidence for unconscious kinds of knowledge and unconscious states of intentionality. 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.

This is not to say that conscious and unconscious states are equivalent with respect to knowing. Many unconscious processes do not exhibit intentionality, for example spinal reflexes. But a large proportion of conscious events, with minor exceptions such as visual after-images and the like, seem to involve knowing of some kind. Why might this be? A very general possibility, which is consistent with ND, follows from the idea that conscious events are high-dimensional and highly informative discriminations. Simply in virtue of being informative, such events must necessarily be 'about' something. Edelman argues that because states of the dynamic core necessarily involve correlations of perceptual categories with value-category memories, the conscious experiences that arise are by their very nature intentional (Edelman, 2003). Indeed, because conscious discriminations are always referenced to the body, they may necessarily involve a knowing of the world and body together (see Section 3.8: *Self attribution*).

What distinguishes conscious intentionality from unconscious intentionality? Here it useful to recall some properties of consciousness which we have already discussed. As well as being informative, conscious events are rapidly adaptive, internally consistent, reportable, referenced to a self, stable, and allocentrically represented. Furthermore, learning appears to require consciousness. Together, these properties suggest that conscious intentionality is particularly suited to dealing with novelty, and relatedly, to facilitating executive decision-making processes in circumstances in which the automatic reactions of an organism may not suffice.

3.16. Involvement of the thalamocortical system

As mentioned in the introduction to this article, it is widely believed that consciousness involves widespread, relatively fast, low amplitude interactions in the thalamocortical system of the brain, driven by current tasks and conditions.

By now it should be obvious that extended ND is well aligned with this feature inasmuch as it proposes that dynamic cores can only be supported by thalamocortical neuroanatomy. The concept of neural complexity suggests how brains may balance integration and differentiation in the thalamocortical system by moving through a continuous series of globally consistent metastable states (Tononi & Edelman, 1998). According to ND, these reentrant interactions link current perceptual categorization with a value-category memory to generate a conscious scene.

The property of complexity may account for why not all spatially correlated and widespread oscillations in the brain are associated with consciousness. It may be that highly variable runs of relatively fast, broad range oscillations are distinctively appropriate for balancing differentiation and integration within the core. Other brain oscillations, for example the delta-range oscillations prevalent in slow-wave sleep, while certainly spatially correlated and widespread, may be biased too far in favor of integration to support complex and hence conscious states.

4. Summary and conclusions

According to ND, the neural systems underlying consciousness arose to enable high-order discriminations in a multidimensional space of signals, and conscious qualia *are* those discriminations (Edelman, 2003, 2004). Although we have focused largely on the dynamic core aspect of the extended theory, this concept is intimately tied to the selectional aspects of ND via a combi-

nation of neuronal diversity, reentry, and degeneracy. Future research directed towards explicit and quantitative modeling of these links is likely to be valuable.

In this article we have explored ND in light of a number of widely recognized properties of consciousness. While at present no theory accounts completely for all of these properties, ND and its recent extensions fare well. Table 2 provides a summary, allocating each of the 16 properties into one of three lists: well accounted for, moderately accounted for, and those for which further research would be most likely to be fruitful.

Acknowledgments

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