The Transition to Experiencing: I. Limited Learning and Limited Experiencing

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Abstract

This is the first of two papers in which we propose an evolutionary route for the transition from sensory processing to unlimited experiencing, or basic consciousness. We argue that although an evolutionary analysis does not provide a formal definition and set of sufficient conditions for consciousness, it can identify crucial factors and suggest what evolutionary changes enabled the transition. We believe that the raw material from which feelings were molded by natural selection was a global sensory state that we call *overall sensation*, which is a by-product of the incessant activity of the highly interconnected nervous systems that characterize all neural animals. We argue that global sensory states generated *limited experiencing* once they became coupled to the simplest kinds of nervous-system-mediated learning, a coupling that occurred in the most ancient taxa of neural animals, which were similar to present-day cnidarians and ctenophores. In such animals, limited experiencing involves a small number of persistent global sensory states. These sensory states, however, do not have a function and do not act as motivational states. As we argue in the next paper, with the evolution of associative learning they evolved into systems that gave animals basic consciousness.

Keywords

cnidaria, evolutionary transition, limited experiencing, memory, nerve net, overall sensation, selective stabilization

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Explaining basic consciousness, the ability to experience, is regarded as one of the most difficult problems in biology. We approach this problem by focusing on the evolutionary transition from animals that cannot yet be said to have experiences and feelings to those that can. Our basic argument is that private, first-person experiences/feelings, which are diverse, unitary, subjective, and intentional, can be studied through the third-person perspective on memory and learning. This is because we see feelings and learning as different facets of the same integrated set of mechanisms. The evolution of learning can therefore give us the clues about the nature of the evolutionary transition that led to consciousness. Hence, we concentrate on the transition that led to the first and simplest animals that can be said to have experiences rather than mere sensations (see Box 1 for definitions of terms as used in this article).

Most modern neurobiologists and biologically oriented philosophers who are interested in the nature of consciousness define and study it by considering the nervous systems (brains) of vertebrates, especially primates and humans, which are highly evolved organisms. Crick (1994), Damasio (1999), Edelman and Tononi (2000), Crick and Koch (2003), and Koch (2004), for example, have provided crucial insights into the nature of consciousness by using this strategy. They showed that what they call “primary” or “core” consciousness in humans and other vertebrates depends on several complex interacting brain regions and processes, and therefore assumed that consciousness can be attributed only to the vertebrate taxa that manifest them. However, while accepting that their insights are of great importance, we think that it is misleading to base a general analysis of consciousness on such evolutionarily derived structures and processes. The parts, processes, and couplings in evolved brains are so highly modified and specialized that they may lead to erroneous conclusions about their necessity for consciousness in general. It is like defining the necessary conditions for circulating blood around the body by asserting that a four-chambered heart is needed: although it is true that a heart of this structure is necessary for circulating blood in a mammal, there are many organisms with differently constructed hearts. The necessity for a four-chambered heart is a highly derived feature of a blood-circulating system. This analogy is, of course, too simple, since the function of the heart—circulating blood around the body—is very obvious. In the case of consciousness, it is not clear what its original function was. So, to account for consciousness, we need to find the conditions for its evolution by natural selection—the function that requires the minimal, indispensable characteristics of consciousness for its operation. We therefore address only the simplest kind of consciousness, which we define, like Merker (2007), as *those processes that make experience itself possible.* We will not discuss the evolution of the sophisticated consciousness found in vertebrates, so we will not address topics such as episodic memory, voluntary motor control, self-awareness, theory of mind, and second-order mental states, where frameworks such as the global workspace of Baars (1997) and Dehaene and Naccache (2001) may be required. In fact, we shall not go beyond the feelings and experiences of the simplest invertebrates with the ability to learn through the formation of associations.

In this article we suggest that the evolution of learning and the evolution of consciousness were intertwined, and discuss the building blocks that were necessary for basic consciousness to evolve. In doing so, we point to the “gray area” where the attribution of experiences and feelings to animals is still ambiguous and uncertain. In the companion paper we suggest that open-ended associative learning, as it is realized in evolved neural organisms, involves the ability to detect, discriminate, and categorize sensory inputs and motor effects according to an internal value system based on overall, whole-organism sensory states, which we refer to as feelings. The internal value systems in animals are very different from those we install in learning robots: advanced robots, built according to neuro-anatomical and physiological principles (brain-based devices), can learn by association, and their learning is guided by internal value systems that modulate changes in the strength of associations (Krichmar and Edelman 2002; Edelman 2006), yet these value systems do not seem to involve feelings and experiences. So how did animal learning come to involve feelings? How did the value systems that enable learning evolve in animals, and what does it mean to say that they are based on feelings?

The first scientist to give a systematic evolutionary account of feeling was Jean Baptiste Lamarck (*Philosophie Zoologique* 1809, book III). He believed that activity in the interconnected nervous system of simple invertebrates led to a general feeling of existence, which he called “inner feeling,” and that this was the basis for the further evolution of the nervous system and of animal cognition. Damasio’s (1999: 154) “proto-self,” defined as “a coherent collection of neural patterns which map, moment by moment, the state of the physical structure of the organism in its many dimensions,” seems to be somewhat similar to Lamarck’s “inner feeling,” although Damasio restricts proto-self to vertebrates. The proto-self is a precondition for what Damasio describes as “background feelings,” which are feelings that are associated mainly with internally generated overall (neural and hormonal) states. Prominent background feelings are: fatigue/energy-excitement, wellness/sickness, tension/relaxation, surging/dragging, stability/instability, balance/imbalance, harmony/discord (Damasio 1999: 283). Damasio’s background feelings are thus “inner feelings” with an intrinsic value attached—feelings that can stimulate reinforcing or modifying adaptive motor behaviors.

Denton (2006), like Lamarck and Damasio, also focuses on internal states. He suggests that the first feelings are those related to the maintenance of homeostatic systems such as salt, gas, and water balance, tissue integrity, and reproduction. He calls feelings such as thirst, hunger, suffocation, the sexual urge, craving for salt, and so forth, "primordial emotions," and believes that they are the first type of emotions/feelings an animal may be said to have. These emotions, he argues, are initiated by receptors located deep within the body (interoceptors). Most of the receptors signal that survival is threatened, and are felt as "imperious states of arousal and compelling intentions to act" (Denton 2006: 7).

Although we recognize the importance of internal receptors for the evolution of feelings, we think that receptors both within the body (interoceptors) and at its surface (exteroceptors) have been important for the evolution of consciousness. We suggest that the "inner feeling" and, later, background feelings and primordial emotions were formed and evolved in animals that had to integrate multiple sensory inputs and coordinate complex motor outputs as they learnt.

The Leap to Experiencing, Limited and Unlimited

The transition from sensory processing to feelings and experiences is a qualitative one, which, like most qualitative transitions, is difficult to capture and fully characterize. Most people agree that there is some level of organization *below* which it does not make any sense to ascribe experience to the animal (or object) concerned, although at what point this level is crossed and feelings or affect can be attributed to an entity is a matter of debate. Lamarck, like all biologists before and after him, had to make a conceptual leap when trying to characterize the transition from sensory processing to experience. He believed that the most basic experiencing involves integrated, global, whole-organism sensations, which form an "inner feeling," a kind of existential buzz. Although Lamarck's jump from the sum total of sensations that reverberate throughout an animal with an integrated nervous system to an "inner feeling" cannot be justified on formal-logical grounds, it fits with the general intuition that there is an intimate connection between sensations and feelings: sensation, that is, the processing of sensory inputs, which is usually involved in the triggering and control of action, can occur without feelings (as in robots and plants), but feelings cannot occur without some such sensory processing.

A high level of interconnectedness is certainly a property of all present-day animals with neurons: no animal has isolated, noninterconnected neurons. Cnidarians (e.g., jellyfish) and ctenophores (e.g., sea gooseberries), which are ancient extant groups of animals with a nervous system (Conway Morris 2000; Chen et al. 2002), have a nerve net: a diffuse, highly interconnected system of neurons. Stimulation of any sensory neuron initiates activity that spreads across the nerve net, activating various interneurons and motor neurons. The external and internal sensory inputs that trigger this widespread activity cause a chain reaction, because the motor actions that result from them activate new sensors whose activity also ripples through the whole system. The signaling that is involved enables rapid and systemic communication, as seen, for example, in the coordinated movements of a jellyfish (Mackie and Meech 1995a, 1995b, 2000).

The aspect of the activity of interconnected nerve nets we want to highlight is an epiphenomenon: it is a by-product, a side effect, of the two-way signaling in a nerve net. The unavoidable consequence of all the sensations that result from the incessant and persistent neural stimulation of the animal's external and internal sensors is a global by-product of neural activity we call "overall sensation." We suggest, by way of metaphor, that it is a kind of "white-noise sensation"—a weak, completely functionless, and meaningless side-effect of an interconnected sensory-motor system, which is dynamically processing electrical and chemical signals triggered by sensors, communicated to effectors, sent back to sensors again, and so on. This neural system is also interacting with all the other integrating signaling networks in the animal, such as the hormonal network. We would like to stress that the sensory-motor interconnectedness of the nerve net is very functional and is, we suspect, under strong selection, *but the by-product—the white noise of the overall sensory state—is initially functionless*. An "overall sensation" is not yet a feeling or an experience, but we suggest that it is the raw material for the first types of experiencing. We maintain that when overall sensations became linked with some simple nonassociative learning, the first limited, and as yet nonfunctional types of experiencing appeared.

How can one justify the assumption that overall sensation constitutes an inner feeling, the beginning of experiencing? We see the problem and its resolution as similar to those presented by the attempt to define life. Although an evolutionary analysis does not provide a formal definition and set of sufficient conditions for consciousness, it can identify crucial factors and suggest what evolutionary changes enabled it. In *The Major Transitions in Evolution* (1995), John Maynard Smith and Eörs Szathmáry discussed the transition from chemistry to biology. They recognized the futility of seeking a sufficient set of criteria of life, yet thought that some criteria—having heredity and being able to evolve by natural selection—are crucial because *they have led, and must almost inevitably lead to life*. They therefore suggested a distinction between limited and unlimited heredity. Some systems may display heredity and even hereditary variation, but the number of possible variants in the system is small, and therefore evolutionary change is extremely limited. Although systems with limited heredity are not fully living, they belong to the gray area between the nonliving and the living phases, and are on the evolutionary route to life if they evolve further to have a theoretically vast, almost unlimited, number of hereditary variations. We suggest that a similar distinction between limited and unlimited experiencing may be useful when thinking about the origin of consciousness.

"Limited experiencing" occurs when an animal has several types of "overall sensations" that follow body changes triggered by sensory stimulation, and when such "overall sensations" become integrated and persist. The overall sensations underlying the bodily changes are the result of an interconnected and constantly active nervous system that permeates the whole organism. Each overall sensation has a different pattern of global activity. An animal with such sensory states has inner feelings, but these are not motivational states. Experiencing is limited both because it is based on a limited learning ability, which can only modulate preexisting reflexes, and because the inner feelings do not yet have a function, so evolution based on them is limited. A system can be defined as one with "*un*limited experiencing" when a theoretically very large number of whole-organism sensory states can be generated, and when these states can be given a value and function as motivational states. An animal with such a system can be said to experience and feel: it can be said to have affective states and basic consciousness. At the behavioral level, the difference between an animal with basic consciousness and unlimited experiencing, and one with limited experiencing is that the former can adapt flexibly, by creating a (theoretically) large number of new associations and new adaptive behaviors, based on partial cues related to its idiosyncratic, individual, ontogenetic learning history. An animal with limited experiencing has fixed behaviors, and only a limited repertoire of adaptive new behaviors.

Lamarck pointed out some of the important characteristics of a system endowed with basic consciousness: sensors and effectors interacting through incessant neural signaling. To these we must add several others: open-ended plasticity, memory mechanisms, and an internal value system that sorts sensations and activities according to their fitness-enhancing or fitness-reducing effects. These characteristics are still *not sufficient* for basic consciousness, but we believe that an animal that has them—an animal with "limited experiencing" (and limited learning)—can be thought of on the evolutionary road to mentality. Since our starting point is learning, we first consider learning as an aspect of adaptive plasticity.

Adaptive Plasticity, Learning, and Value Systems

Living organisms have adaptive, plastic responses: they respond to the ongoing changes in their environment either by altering their development, physiology, morphology, or behavior, or by actively ignoring or neutralizing the changes impinging on them. This enables them to react to changing conditions in a manner that promotes fitness (West-Eberhard 2003).

Adaptive plasticity not only allows the organism to respond differently to different situations. It also underlies their ability to compensate for multiple "noisy" inputs and produce a *uniform* adaptive response: different inputs can become linked to new or preexisting developmental trajectories that all lead to a single adaptive end state. Hence, the same adult phenotype (a red eye in the fruit fly *Drosophila*) may develop in genetically and developmentally dissimilar individuals. Most variations, genetic as well as environmentally induced, are actively compensated for (actively "canalized") by the developmental system. Canalization, the evolved processes that lead to a stable and uniform end result despite genetic and environmental noise (Waddington 1942), is therefore the result of an underlying plasticity.

There are different types of plastic adaptive responses: they can be reversible or irreversible, active or passive, continuous or discontinuous. From our point of view, the important distinction is that between fixed-pattern and open-ended types of plasticity. Fixed-pattern behavioral plasticity is seen when there are several preexisting developmental trajectories leading to different responses, depending on the stimulus (or combination of stimuli) received by the sensors. The response therefore depends on environmental conditions, but the organism responds to each of a predetermined set of stimuli with a predetermined response. Different stimuli may share the same receptor, and pathways may share common elements, but each signal transduction pathway is specific and predetermined. A new stimulus cannot lead to an adaptive response if an appropriate trajectory is not already in place.

Open-ended plasticity occurs when organisms respond to new stimuli by constructing *new* adaptive developmental paths or trajectories. Exploration and selective stabilization are among the most important mechanisms underlying open-ended plasticity. They can lead either to extensive plasticity at the output level or to strong canalization and the masking of "noise." Exploration and selective stabilization mechanisms occur at the cellular, physiological, behavioral, and social levels, and are all based on a similar principle—*the generation of a large set of local variations from which only a small subset is eventually stabilized and manifested*. Which particular output is realized depends on the initial conditions and the number of possible points around which development can be stably organized. Following convention, these points are called "attractors," since they are the set of properties toward which the system tends to proceed, regardless of the conditions from which it started. Biological attractors are dynamically stabilized end states that are often *functional*: the mechanisms that enable them to be reached evolved by natural selection and promote the organism's fitness. Such attractors can therefore be said to have "values," because by reaching them, the organism actively maintains and enhances a fitness-promoting state or avoids fitness-decreasing conditions.

There are many examples of exploration and selective stabilization processes in biology (Gerhart and Kirschner 1997; Plotkin 1997; West-Eberhard 2003; Kirschner and Gerhart 2005). We shall describe only a few of them. The best-known example is, of course, natural selection.

In the nervous system, there is selective stabilization of neuronal cell number, of synaptic connections during development and learning, and of connections between neuronal regions. Nerve cells are overproduced and most of them die. They commit suicide unless they are stabilized by survival factors during development: only axons whose tips accidentally hit a region with "survival factors" remain alive (Levi-Montalcini et al. 1996; Buss et al. 2006). Hence, the number of nerve cells is pruned through competition for "survival factors," and the location of these growth factors determines where neurons will connect. The synapses in surviving neurons are also overproduced, and most are pruned: connections that have the highest functional efficacy persist according to Hebb's rule: "neurons that fire together wire together." There are many other factors that guide the formation of stable synapses, which are determined by both the presynaptic growth cone and the postsynaptic target cell [reviewed by Munno et al. (2003)]. The net result is that only certain synaptic connections among the many initially possible are stabilized. This is the basis of Changeux et al.'s (1973) model for a developmentally evolving neural network. Edelman (1987) went further and suggested that stabilization of some of the multiple connections formed among different *regions* of the nervous system contributed to the final pattern of connectivity (through persistent reentrant activity).

Selective stabilization can also occur at the behavioral level. Foraging in army ants is based on exploration. Ants move in random directions, chemically marking outgoing and returning paths while doing so. A path that is productive (leads to food) is used more frequently than others and hence is more heavily marked, leading to further use, and so on. The persistence of the more frequently used path is therefore an example of selective stabilization (Deneubourg et al. 1989). Trial-and-error associative learning is another well-known example of selective stabilization; stabilization occurs through negative or positive reinforcement of behavior (Skinner 1981; Plotkin 1997).

Learning, both in individuals and in systems, is a rather special case of plasticity. It is special because it requires more than adaptive, open-ended, responses to stimuli. *Learning requires*, in addition, *that responses to particular stimuli are remembered and can be recalled.* A generally accepted definition of learning is: "A relatively permanent change in behavior potential as a result of experience" (Abramson 1994: 2). Following this and many similar definitions, we shall say that an organism has learnt (in the most general sense possible) when:

1. an input (an external sensory stimulus or the organism's own behavior) leads to a reaction that has one or more functional effects;
2. the input–effect relation is memorized, that is, some physical traces of the reaction persist;
3. this memorized relation can be recalled upon exposure to the same type of input conditions: the effect (the functional reaction or behavior) appears more readily or with less exposure to the input.

This is a very general definition of learning. It applies to different types of learning, including some reactions in plants, unicellular organisms, and sophisticated machines like robots. Protozoa, for example, can be said to learn when the magnitude of the reaction to a stimulus decreases when it is applied continuously (Wood 1988a, 1988b). Plants, too, exhibit something that can be defined as learning in the general sense, for example, the habituation of mimosa to repeated touching (Abramson 1994; Abramson et al. 2002). Learning can even occur in a system that is a part of an organism—the immune response in vertebrates is a plastic adaptive strategy that conforms to the definition of learning. There is no good, replicable evidence, however, that nonneural organisms can learn a *new association* between stimuli or between stimuli and responses (Abramson 1994; Hinkle and Wood 1994). Learning in nonneural organisms seems to be extremely limited: the nature of the stimulus and the response to it are predetermined by previous evolutionary history.

Some of the molecular machinery that enables learning in protozoa and plants (e.g., ion channels and second messengers) is the same as that seen in animals with a nervous system, but in spite of the biochemical similarities, learning by neural animals is fundamentally different. It occurs in an interconnected system of cells specialized for communication. Neurons are always part of a neural *system*—at its simplest, a diffuse nerve net—which depends on the structural and functional properties of the neuron: its elongated fibers, which allow it to link spatially remote cells, and the chemical and electrical signals propagated via these fibers. Together, these features enable precise and rapid communication between specific cells. Neurons presumably arose through selection for communication between different but distinct parts of a moving organism. Once this mediating-communicating cell type had evolved, and the number of such cells within an organism grew, neurons inevitably interacted with each other to form a neural net. The neural network structure allowed specific types of learning and memory, which are observed in the simplest extant neural animals, the cnidarians and the ctenophores.

The Building Blocks of Limited Experiencing

Extant cnidarians and ctenophores have many derived characters, and are taxonomically distinct from other phyla, but we assume that the neural structure of the simplest cnidarians is indicative of the features that were present in the early neuronal animals that eventually evolved into animals with more complex nervous systems and behaviors. We suggest that limited experiencing was in place very early on in animal evolution, and that its biological building blocks can be identified in cnidarians and ctenophores. These include (1) an interconnected nervous system, which is associated with the global sensory state that we call "overall sensation"; (2) simple memory and learning mechanisms (habituation and sensitization) that can modify reflex behavior; (3) a neural organization that enables sensory and motor coordination and integration of information coming from multiple sources; (4) *transient* selective stabilization of *newly formed* neural connections; and (5) some centralization of the nervous system, which may have led to an extension of limited experiencing.

The Interconnected Nerve Net

Cnidarians have clearly defined neurons with many interconnections, but they have no segmental ganglia or brains, and their nervous systems are organized as nets. Nevertheless, they have many of the features of the complex nervous systems of higher animals, including sodium-dependent action potentials (Spafford et al. 1998), neuron interactions through chemical and electrical synapses (Anderson 2004), and neuronal integration (Mackie and Meech 1995a, 1995b, 2000). The conduction of electrical impulses in some nerve cells of cnidarians is, however, nonpolar, that is, the action potential can travel in either direction, whereas in bilateral metazoans most nerve impulses are propagated in one direction only, and two-way signaling is achieved through reciprocal anatomical connections. Although there is differentiation in the nerve net, which in some cnidarians is quite sophisticated (Anderson 2004), many types of cnidarian neurons are multifunctional (Koizumi 2002). Whether or not the net is differentiated, it is always interconnected. Cnidarians therefore inevitably have "overall sensation," the kind of overall sensory buzz we discussed earlier. However, as we argue below, some "overall sensations" in cnidarians become distinct when persistent stimuli activate a particular local reflex circuit, or when, through selective stabilization, new neural states persist. The persistent activation of a local circuit adds a specific "sensory signature" to the white noise.

Simple Learning and Memory: Habituation and Sensitization

In the simplest neural organisms, the terms "learning" and "memory" are applied to habituation and sensitization. Cnidarians possess specific neural reflex circuits, for example those associated with withdrawal upon tissue injury and those associated with detection of a food source. These reflex circuits enable animals to respond to salient environmental cues, and to somewhat modify their behavior when the same types of environmental cues reoccur. The attractor states in this case are those end states that the animal reaches as a result of its modulated and unmodulated reflex responses. "Value systems," which were set by past natural selection, are the reflex-related neural structures and processes that enable the animal to learn, that is, to modify its behavior and reach the attractor state.

Cnidarians can modulate reflex behavior through habituation and sensitization, which means that they have memory mechanisms that involve the strengthening of synaptic connections in part of their neural network. Because intracellular recording from cnidarians is difficult, the ionic and molecular bases for habituation and sensitization have not been worked out in detail. However, electrophysiological and behavioral studies of their responses to tactile stimuli, chemical stimuli, and light have revealed many manifestations of habituation and sensitization (Lawn 1975; Logan 1975; Logan and Beck 1977, 1978; Johnson and Wuensch 1994; Kass-Simon and Scappaticci 2002). Habituation and sensitization therefore seem to have evolved early, with or before the origin of the cnidarians.

Habituation can be defined as a decrease in the magnitude of a behavioral response to an iterative stimulus (Eisenstein et al. 2001); it enables the organism to *ignore* irrelevant stimuli, thereby minimizing energy waste. The simplest type of sensitization, reflex potentiation, is the mirror image of habituation: it involves an increase in the magnitude of a behavioral response to a stimulus or the lowering of the response threshold upon repeated stimulations of the same type. Sensitization, however, can take more complex forms, and a specific unlearnt ("innate") response can be affected by the general excitatory state of the animal, and by the state of other reflex pathways, which can modify the response pattern (Razran 1971; Dyal and Corning 1973).

The evolution of the ability to learn through habituation and sensitization presumably involved selection among animals that varied in their ability to repeat or sustain particular reflex responses. The ability to modulate reflex responses had several potential advantages (Razran 1971; Dyal and Corning 1973; Abramson 1994: 107); for example, when the benefits of continuing an action were outweighed by the cost in terms of energy, animals that became less responsive to continued stimulation were favored, so selection led to habituation. Conversely, sensitization would have resulted from multigenerational selection in situations in which it was beneficial to respond to continued stimulation with more of the same activity. In both habituation and sensitization, the type of input and the type of response are predetermined (by past selection).

The plasticity given by habituation and simple sensitization (through reflex potentiation) is of the fixed-pattern type. What changes, and what is learnt and remembered, is the extent of the response (smaller in habituation, larger in sensitization). The organism does not organize new relations, only modulates preexisting, previously selected, ones.

The basis of many forms of memory in all animals is thought to be changes in synaptic efficiency, and anatomical or structural changes in synaptic connections. The anatomical and molecular mechanisms underlying habituation and sensitization have been worked out for several invertebrates (Rose and Rankin 2001; Steidl et al. 2003; Hawkins et al. 2006). Short-term habituation and sensitization are accompanied by recruitment of presynaptic (and perhaps also postsynaptic) molecules to new sites, but they do not require protein synthesis; they require only covalent changes in preexisting proteins and changes in preexisting connections. In short-term sensitization of the *Aplysia* gill withdrawal reflex, for example, the modulatory transmitter serotonin, released from facilitating interneurons that connect to the sensory neuron, triggers a cascade ending in the activation of a kinase. This activation leads to short-term facilitation: to an increase in the synaptic strength of the connection between the sensory and motor neuron (Klein et al. 1982; Kandel 2001). In short-term habituation of the same withdrawal reflex, synaptic depression occurs, that is, a weakening of synaptic strength between the sensory and motor neurons (Castellucci et al. 1970; Byrne 1982).

Long-term sensitization and habituation, which occur in cnidarians as well as more complex animals, involve protein and RNA synthesis. The memory mechanisms underlying them involve growth of new synaptic connections (Bailey et al. 1996) and require the persistence of structural changes at the synapse (Hawkins et al. 2006). Si et al. (2003) have suggested a molecular model for self-sustaining changes at the synapse, based on prion-like proteins. DNA methylation and histone acetylation are also known to be involved in long-term memory (Levenson and Sweatt 2005).

There are two facets to the evolved mechanisms of memory. First, and most obviously, "memory traces" endure in the absence of the initiating sensory stimuli. Second, when the neural network is activated by incoming stimuli, the activity lasts longer. This latter aspect of persistence is similar to what William James (1890) called the "specious present," Humphrey (1992) called the "extended present," and Edelman and Tononi (2000) called the "remembered present." Edelman and Tononi believe that its emergence occurred in the stem group that split into birds and mammals, and depended on the evolution of massive reentrant connections between multimodal cortical areas. The "remembered present" lasts long enough for neural activity to resonate throughout the whole animal. Humphrey suggests that the "extended present" is based on self-reactivating positive feedback loops in the sensory part of the brains of birds and mammals. We agree that the persistence of activity, the "extended present," is crucial for both limited and unlimited experiencing, but suggest that it emerged very early on in metazoan evolution. The memory mechanisms that we have described in the simple nervous systems of cnidarians open up the possibility for present-extending sensory activity patterns as these animals respond to stimuli in their environment.

Sensory and Motor Coordination

Although the learning capacity of cnidarians is limited, behavioral and physiological studies have shown that they are capable of considerable behavioral modifications (Ross 1965; Rushforth 1973). The interconnected nerve net of present-day cnidarians presumably evolved through selection for the coordination of motor responses in ancestral animals with few reflex pathways, and only chance connections between them. Initially, interconnectivity probably enabled only simple integration of sensory inputs of the same type coming from different parts of the animal. Today's cnidarians can respond to various types of stimuli, including those produced by internal processes (e.g., in the coelenteron), and motor activity may be initiated spontaneously by neural pacemaker systems that lead to rhythmic movements. It is through the interconnectedness of the nerve net that the different neural pathways interact to produce the coordinated responses seen, for example in the swimming, escaping, and feeding behaviors of jellyfish.

Animals live in a "noisy" sensory world. As their total cell number and the number and types of their sensors increase, their world becomes more difficult to manage and the decision as to how to act—to which stimuli to respond, which can be ignored, and when—becomes crucial. Habituation solves part of this problem, since stimuli that lead to habituation require no action and can be ignored. Similarly, sensitization marks certain stimuli as salient. However, these mechanisms are insufficient because it may be necessary for the animal to *decide* how to act when two or more simultaneous stimuli occur. It is therefore necessary for it to be able to integrate or choose among stimuli, and to coordinate motor responses both in space and time.

Although habituation and simple sensitization are modulations of preexisting reflex pathways, they can be the basis of guidelines for action in complex situations because these processes can themselves be modulated (Razran 1971; Dyal and Corning 1973; Grau and Joynes 2005). For example, a noxious stimulus may lead to a *general* sensitized state, and thusly increase the *specific* response to a particular sensitizing stimulus. Another possibility is that an additional trajectory from sensor to effector is anatomically closely linked to the reflex response pathway, and therefore costimulation of the additional sensory-motor path with the primary path later leads to an enhanced response to either input. At the behavioral level, different types of sensitization, both associative (affected by an additional stimulus paired with the original one) and nonassociative, have been described (Dyal and Corning 1973). Modulation of habituation is also possible: habituation can be stopped when a different stimulus is presented to the animal and causes a waned response (dishabituation). Habituation is also much slower when the normally habituating stimulus is paired with a different stimulus, a situation referred to as "protection from habituation." All of these modulations reflect simple ways of combining and integrating stimuli and responses. Several studies of cnidarians suggest that these animals are able to modulate reflex actions, because combinations of stimuli sometimes change their response patterns [reviewed in Rushforth (1973)].

Selection for integration and coordination was probably possible because the receptors of different neurons can respond to the same neuromodulators (hormones and neurotransmitters). Neuromodulators can activate or inhibit synapses in a network either by acting on the synaptic connections of specific cells or by acting more globally as circulating hormones. The effect is to reversibly alter the functioning of the neural circuit without changing its hard-wiring. Typically, the concerted action of neuromodulators affecting several interacting pathways changes the threshold of behavioral responses (Birmingham and Tauck 2003). In invertebrates, including cnidarians and flatworms, many neurotransmitters have been shown to act as hormones that control behavior (Welsh and King 1970; Takahashi et al. 1997). A change in conditions such as the appearance of food, a mate, or a predator can lead to the discharge of certain types of hormones and neurotransmitters from groups of neurons that richly interact with the rest of the nervous system, alerting the animal to the salient event. The choice of responses may initially be based on the relative dominance of different reflex paths (e.g., "when simultaneous signals are equal in strength, respond to predator signal rather than to food signal"), on differences in the strength of the induced neural activity ("great food deficiency overcomes small danger signal"), and so on. The problem of how animals decide "what to do next" when in a multi-faceted environment with conflicting stimulations (action selection) has been addressed by many biologists and cognitive scientists, taking various approaches to tackle it. Lorenz (1950) suggested a hydraulic model, Tinbergen (1950) took a hierarchical approach, and McFarland (1985) used a drive model; the problem has been defined and reviewed by Tyrell (1992) and Prescott et al. (2007).

Continued selection for coordinated neural responses and more information-integration probably favored increased anatomical centralization (Tononi 2004). This enabled greater integration of sensory inputs and motor responses, and the sophistication of the way in which different neurons and neural pathways share receptors for the same neuromodulators. Edelman (1987) suggests that reentry—ongoing, recursive interchange of parallel signals between reciprocally connected areas of the nervous system—synchronizes the activity of neuronal groups, binding them into circuits that allow a coherent, integrated, and coordinated output.

Transient Selective Stabilization of New Connections

When complex organisms with many sensors and effectors encounter variable conditions, their responses to a stimulus or set of stimuli cannot be uniform and stereotyped. For example, in order to approach a food source, movements have to be consistently directed toward it. Semirandom movements would be an inefficient way of reaching food, and fixed reflexes would also be inappropriate, because the location of the food source is different at different times and movement toward it requires use of different muscles and neural trajectories. There would be an obvious advantage in any mechanism that resulted in consistent movement toward food wherever it is detected. In a neural organism, such behavior will depend on exploration and selective stabilization mechanisms within the nervous system.

Changeux et al. (1973) and Edelman (1987) suggested that a primary repertoire of extensive and more or less randomly generated neural connections is formed during development, and some of these are then stabilized through activity. Following this suggestion, we propose that exploration and selective stabilization mechanisms in the nervous systems first evolved through natural selection for (1) the capacity to transiently reinforce the activity of the neural circuits underlying any new pattern of motor activities that promotes the repeated stimulation of sensors (e.g., food sensors) that indicate favorable (e.g., food-plentiful) conditions, and (2) the capacity to transiently inhibit activities that lead to reduced stimulation of such sensors. Similarly, there was natural selection for (1) the capacity to transiently reinforce and stabilize new motor activities that *prevented* the repeated stimulation of receptors (e.g., mechanoreceptors) that were triggered in fitness-reducing conditions (e.g., where a withdrawal response is appropriate) and (2) the capacity to inhibit motor activities that led to repeated stimulation of these receptors. Neural mechanisms of stabilized excitation and inhibition built on the existing reflex pathways embedded within the randomly generated neural connections formed developmentally. However, by recruiting additional, interconnected, *newly used* parts of the nerve net, they went beyond the reflex pathways (Figure 1a).

We believe that selection of the capacity to transiently stabilize newly utilized sensory-motor pathways had additional consequences. The nature of the interconnected nerve net is such that there is communication between the neural pathways of simultaneously activated sensors. We suggest that sensory pathways that are persistently and concurrently activated along with a preexisting reflex path are stabilized because the shared

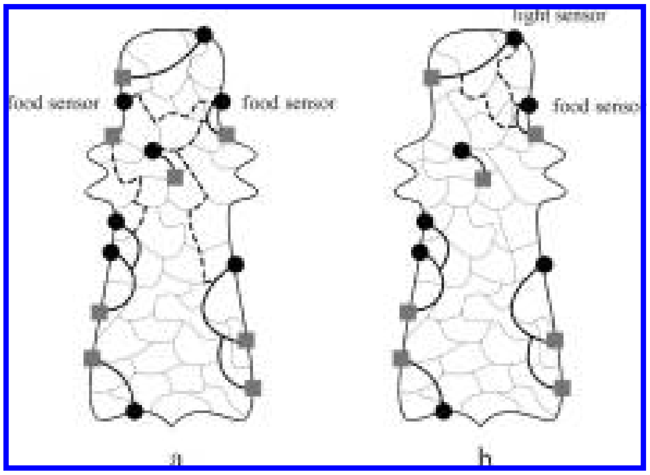

Figure 1.
Selective stabilization. Heavy continuous lines denote the constant and stable neural connections that produce local reflexes and can be modulated by short, intermediate and long-term habituation and sensitization; thin continuous lines denote the numerous neural connections formed during development; broken lines denote newly stabilized pathways. Stabilization of these pathways is short term and depends on the continuous presence of the stimulus. Circles denote sensors; squares denote effectors. 1a: Selective stabilization of motor pathways: activated pathways connecting sensors and effectors are stabilized when they are effective. For simplicity, exploratory activities involving motor pathways that were activated but not selected are not shown; nor are stabilized inhibitory pathways. Note that the new stabilized trajectories do not involve new anatomical connections. 1b: Selective stabilization of neural connections between coactivated sensors: concurrent activation of light and food sensors leads to strengthening, and therefore stabilization of the connecting pathways between them. The result is sensory binding.

parts of the pathway contribute to the ease of mutual activation or inhibition (Figure 1b). A side effect of the selection for the stabilization of coactivated sensory connections was therefore the binding of sensory stimuli: multiple aspects of an object (e.g., size, taste) had a unitary, integrated impact, and could be processed as aspects of a single sensory unit. Binding was enormously advantageous because it led to the ability to distinguish between sources of complex (combined) stimuli. And when new mechanisms allowed memorization of new input associations, it also enabled the animal to anticipate the effects of the associated stimuli. Since binding enhanced the ability to discriminate, we suggest that selection for its further stabilization and reliability was strong and ongoing.

If our argument is correct, the ability of organisms like cnidarians to stabilize new sensory and motor connections resulted in a new type of stimulus-dependent behavior: a degree of open-ended plasticity had evolved. This can be seen as the evolution of the mechanisms underlying Hebb's law, but *without long-term stabilization* of the repeatedly activated *new connections*. The neural, activity-dependent stabilization underlying behavioral reinforcement in these taxa is still transient, depending on the continued presence of the triggering stimulus. In other words, the selectively stabilized, new neural connections do not carry any long-term traces of their activated states. The animal cannot build on and benefit from past encounters; it has to reinvent the wheel (the new adaptive response) time and time again.

Neural Centralization

Selective stabilization is likely to have been more significant and potent in animals with a centralized nervous system. By bringing sensors closely together and minimizing signal dissipation due to distance, neural centralization enhances the formation of persistent new connections. There is some centralization of the nerve net in cnidarians such as cubozoans, where four clusters of neurons underlie the four clusters of eyes, and in hydra, where "nerve rings" are found around the hypostome (gastric opening). In the jellyfish *Aglantha*, different swimming modes are controlled by a rich circuitry involving several distinct nerve rings, and its motor behavior, which is controlled by these nerve rings, shows it is a well-coordinated animal with proto-centralization (Mackie 2002).

Although the degree of neural centralization differs among species, and little is known about the mechanisms by which they modulate habituation and sensitization, we believe that all of the building blocks for the construction of limited experiencing are in place in cnidarians. First, they have several distinct types of overall sensations associated with different reflex trajectories. Second, they have simple short- and long-term memory mechanisms that modulate reflex paths through habituation and sensitization. These allow changes in the sensory states that accompany these stimulations to persist and reverberate throughout the organism, and can themselves be modulated. Third, cnidarians have distinct and persistent overall sensory states that result from the selective stabilization of new connections. However, the stabilized end states depend on the continuous presence of the stimulating conditions, and the new connections that are established cannot be maintained, so they cannot be remembered and cannot become attractors. They accompany the stabilization process, but have no function. Although an animal with this kind of nervous system can accomplish a great deal, it does not yet have the behavioral and sensory flexibility that characterizes animals with unlimited (open-ended) learning by association.

Summary and Discussion

We have taken an evolutionary approach to the study of experiencing and the simplest type of consciousness. Although such an approach cannot reveal universally necessary and sufficient criteria for experiencing, it can point to the actual and contingent evolutionary paths that eventually led to animals with the ability to experience. We believe that the first stage in the evolution of experiencing, which we called "limited experiencing," appeared with the evolution of the memory mechanisms that enabled simple types of learning in neural organisms. Like

Box 1: Definition of Terms (words in bold are defined elsewhere in the list)

Affective systems: The systems that lead to the production of **feeling**.
Attractor: The set of physical properties which the system tends to reach (the state it tends eventually to settle in), regardless of the conditions from which it started.
Basic consciousness: Having **unlimited experiencing**.
Canalization: Evolved processes leading to a stable and uniform developmental end result, compensating for and masking genetic and environmental noise. These evolved mechanisms are **plasticity** mechanisms.
Exploration and selective stabilization: The generation of a large set of local variations from which only a small subset is eventually stabilized. Selective stabilization occurs when the system reaches an **attractor**.
Feeling: The private aspect of a particular, integrated, present extending, **overall sensation** that motivates and guides the actions of an animal. We suggested that animals without a flexible ability to learn by association do not yet have feelings in this full sense, since their overall sensations do not yet act as motivational states.
Inner feeling: The feeling of existence that animals with **overall sensation** have. Lamarck suggested that psychological processes evolved from the inner feeling.
Limited experiencing: Persistent global sensory states that are linked to preselected values. These states are associated with a fixed number of preselected neural response trajectories, are functionless, and have limited evolutionary potential.
Limited learning: The ability to learn through habituation, sensitization and their simple modulations. No flexible associative learning is possible.
Motivation: A state of the organism that is the outcome of an activated **reward system** leading to action.
Overall sensation: The global state resulting from the ongoing sensory stimulation and processing in an interconnected nerve net.
Plasticity: "the ability of an organism to react to an internal or external environmental input with a change in form, state, movement, or rate of activity" (West-Eberhard 2003: 33).
Reinforcement: The **selective stabilization** of a behavioral response, usually through the operation of a **value system** that defines and leads to an **attractor**. The likelihood that the response will recur in a situation like that in which the reinforcing condition originally occurred is increased.
Reinforcer: A stimulus that follows some behavior and increases the probability that the behavior will occur.
Reward system: A **value system** based on **feelings**.
Selective stabilization: See **exploration and selective stabilization**.
Sensing: The detection and relaying of signals received by a **sensor**. Processing of sensory inputs does not require any feelings.
Sensor: A biological or man-made device, such as a cellular receptor or a photoelectric cell, that detects and relays a signal or a stimulus.
Somatic selection: **Selective stabilization** that occurs within the organism during development, dynamic self-maintenance, and learning. Includes, but is not confined to, selection among somatic cells.
Unlimited experiencing: Having overall sensory states that are linked to flexible learning mechanisms and to dynamic and flexible **value systems**. These can act as motivational states and have a great evolutionary potential.
Unlimited learning: The unconstrained ability to learn by association new relations between inputs and outputs, forming new connections. Although the actual learning an animal may display during its life may be highly constrained, many flexible responses are theoretically possible.
Value system: The features and processes underlying **selective stabilization** mechanisms that allow the system to reach a particular type of **attractor**. In the nervous system, value systems are neural structures that are necessary for an organism to modify its behavior according to the salience of an environmental cue (Krichmar and Edelman 2002: 818).

many evolutionary innovations, experiencing originated as a by-product of the organization and activity of the system. The first, limited experiencing was the outcome of integrated activity in a neural network of an integrated multicellular organism with many internal and external sensors and effectors, and the memory mechanisms that enabled simple learning.

We called the unselected side effect of the activity of an interconnected, incessantly active, and dynamic neural net "overall sensation." The temporal persistence of sensory states during neural processing that occurred as the animal responded to changes in its environment (the extension of the present) was the result of the memory mechanisms that enabled the animal to learn through habituation and sensitization (and their modulation). The inevitable combination of changed overall sensations with memory-based, present-extending persistence meant that some "overall sensations" had specific enduring sensory signatures, which reverberated through the animal and were associated with phylogenetically selected values—the preselected relations between reflex systems (that give one reflex path dominance over another) and the mechanisms that modulate reflex responses. In addition, the ability to stabilize associations that lasted as long as the stimulating conditions persisted also imparted specific sensory signatures on the white noise of overall sensation. The effect of both types of sensory signature was that the animal had "limited experiencing": global, yet distinct, sensory states that were persistent enough to impart a certain tone on the indistinct buzz of ongoing neural activity. These neural states, however, were not functional and were evolutionarily limited. Because new associations were not remembered, new sensory states could not function as motivational states.

We have pointed to several aspects of neural organization and activity that are important in the construction of limited experiencing: neural interconnectedness and ongoing activity, memory mechanisms allowing simple types of learning, integration and coordination mechanisms enabling modulations of learning, and exploration and selective stabilization mechanisms. Several predictions follow from our argument:

1. Even in nonneural organisms like plants and protists, modulations of simple habituation and sensitization may be found if there is close physical proximity and linkage between different signal transduction pathways.
2. In organisms with a nerve net, the extent and type of limited experiencing will vary among taxa according to the degree and nature of their neural centralization. We expect that studies comparing the ability of members of different taxa of cnidarians and ctenophores to modulate habituation and sensitization (the ability for dishabituation, pseudoconditioning, and so on) will point to neural centralization as a major factor affecting the modulations of nonassociative learning. Ross (1965) reported that the movement of the sea anemone *Stomphia*, which reacts to an extract of a particular starfish by swimming toward it, can be inhibited if the extract stimulus is preceded by a tactile prodding stimulus that leads to contraction. This inhibitory effect seems, however, unique, since other stimuli do not elicit any conditioned response in the sea anemone. The inhibitory effect may be the consequence of the anatomical proximity of the associated neural paths.
3. A specialized ability to learn by association (through classical and instrumental conditioning) in the visual domain may be found in the cubozoans, a taxon of jellyfish without a brain but with wonderfully complex multiple eyes underlain by well-integrated clusters of neurons (Piatigorsky and Kozmik 2004; Nilsson et al. 2005).

As we argue in the companion paper, the next steps in the evolution of experiencing were associated with cephalization and new memory mechanisms that led to flexible associative learning. Cephalization was a crucial element in the evolution of learning by association because sensory-motor paths were brought into proximity in a restricted area enabling further integration. A related and necessary factor for the emergence of open-ended associative learning was the evolution of persistently stabilized new connections. These enabled the construction of flexible internal reward systems: value systems based on feelings.

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