

Naturalizing consciousness: A theoretical framework

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Consciousness has a number of apparently disparate properties, some of which seem to be highly complex and even inaccessible to outside observation. To place these properties within a biological framework requires a theory based on a set of evolutionary and developmental principles. This paper describes such a theory, which aims to provide a unifying account of conscious phenomena.

Since Descartes' dualistic proposal (1), consciousness has been considered by many to be outside the reach of physics (2), or to require strange physics (3), or even to be beyond human analysis (4). Over the last decade, however, there has been a heightened interest in attacking the problem of consciousness through scientific investigation (5). To succeed, such a program must take account of what is special about consciousness while rejecting any extraphysical assumptions. It must then construct a theory to account for the properties of consciousness and provide a framework for the design and interpretation of experiments. My aim in this paper is to consider these two main issues. To do so in a brief compass, I shall summarize a number of key conclusions, referring to the available literature for more extended accounts.

Properties and Constraints

Scientific understanding of consciousness in neural terms requires the acceptance of a number of constraints. Any account of consciousness must reject extraphysical tenets such as dualism, and thus be physically based as well as evolutionarily sound. Consciousness is not a thing but rather, as William James pointed out (6), a process that emerges from interactions of the brain, the body, and the environment. As shown in Table 1, it is a multidimensional process with a rich variety of properties. Of the properties listed in Table 1, several stand out as particular challenges to any theoretical effort. (i) The contrast between the diversity and changeability of conscious states and the unitary appearance to the conscious individual of each conscious state. This unity requires the binding together of diverse sensory modalities that show constructive features such as those seen in Gestalt phenomena. (ii) The property of intentionality. This term refers to the fact that consciousness is generally, but not always, about objects or events. At the same time, consciousness is modulated by attention and has wide access to memory and imagery. (iii) Subjective feelings or qualia; the experiencing, for example, of the redness of red, the warmth of warmth. This is put pointedly by Nagel's phrase: "What is it like to be a bat?" or, as he implies, any other conscious being (7).

Can we construct a neural framework to account for such a wide range of properties? I believe that present advances in neuroscience permit us to do so, provided that we take into account some constraints based on experimental observations. These suggest that consciousness is not a property of a single brain location or neuronal type, but rather is the result of dynamic interactions among widely distributed groups of neurons. A major system that is essential for conscious activity is the thalamocortical system. The integrative dynamics of conscious experience suggest that the thalamocortical system behaves as a functional cluster; that is, it interacts mainly with itself (8). Nevertheless, it also interacts with other brain systems. For example, interactions between the basal ganglia and the thalamocortical system are likely to influence the modulation of

Table 1. Features of conscious states

General
1. Conscious states are unitary, 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.

consciousness by attention as well as the development of automaticity through learning. The threshold of activity in these neural structures is governed by diffuse ascending value systems, such as the mesencephalic reticular activating system interacting with the intralaminar nuclei of the thalamus, as well as noradrenergic, serotonergic, cholinergic, and dopaminergic nuclei.

The thalamus governs levels of the conscious state, altering thresholds of cortical activity by means of input from the intralaminar nuclei. In addition, brainstem influences on the thalamus play a central role in altering the conscious state during sleep (9). In a particular state, the content of consciousness depends on the activity of various cortical areas. A classic example is provided by gross lesions to area V1, resulting in blindness (10). Although these various functions differ for cortex and thalamus, it is their mutual interaction that is critical to understanding the properties of consciousness.

Function, Qualia, and Privacy

For what did the neural substrates of consciousness evolve? I shall consider the selective advantages of neural changes during evolution that allowed this remarkable process to arise. I argue that the evolutionary emergence of consciousness depended on the natural selection of neural systems that gave rise to consciousness, but not on selection for consciousness itself. Given the properties listed in Table 1 and certain temporal features of conscious responses, a very likely adaptive function of neural systems underlying consciousness is their ability to integrate a very large number of sensory inputs and motor responses occurring in parallel. These neural systems connect perception with memory or imagery and thus relate complex sensory input to past learning responses and to future needs. The capacity to distinguish among very large numbers of inputs, while integrat-

Abbreviation: TNGS, theory of neuronal group selection.

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ing them in ways related to the past history of an individual, provides an adaptive advantage not possessed by animals without such systems. The hippocampus, which coevolves with the cerebral cortex and interacts with it to yield so-called episodic memory, may be critical in the development of this capacity.

It has been suggested that, in any attempt to connect neural activities to the phenomenal or subjective experience of qualia, there is an explanatory gap and that this constitutes the so-called hard problem (11). The framework position I have taken here is that consciousness consists of qualia, by which I mean not just isolated submodalities of red, warm, etc., but also complex scenes, memories, images, emotions; indeed, the entire rich panoply of subjective experience. If, as I have suggested, the neural systems underlying consciousness arose to enable high-order discriminations in a multidimensional space of signals (8), qualia are those discriminations. Differences in qualia correlate with differences in the neural structure and dynamics that underlie them. Thus, for example, olfactory neurons and their circuits differ from retinal neurons and circuits, and such differences seem sufficient to account for differences in their respective qualia. These reflections apply as well to complex scenes, and I have stressed that it is the distinctions among the entire set of experienced qualia that allow the specific defining property of each quale to appear (8).

To expect that a theoretical explanation of consciousness can itself provide an observer with the experience of “the redness of red” is to ignore just those phenotypic properties and life history that enable an individual animal to know what it is like to be such an animal. A scientific theory cannot presume to replicate the experience that it describes or explains; a theory to account for a hurricane is not a hurricane. A third-person description by a theorist of the qualia associated with wine tasting can, for example, take detailed account of the reported personal experiences of that theorist and his human subjects. It cannot, however, directly convey or induce qualia by description; to experience the discriminations of an individual, it is necessary to be that individual.

Even if we must accept this inherent limitation imposed by privacy, the understanding that qualia are higher-order discriminations that are entailed by the activity of neural systems underlying consciousness provides a considerable clarification. It allows us to pay attention to the hard enough problem, which is to formulate a global theory that provides neural bases for the general and special features of consciousness.

A Theoretical Basis

Given the complex distributed nature of the neural processes underlying consciousness, which integrate many signals in short time periods, a proposed mechanism for consciousness must be in accord with a global theory of brain action that is itself consistent with the features listed in Table 1. I have put forth arguments elsewhere (12) that a theory based on the notion that the brain is a computer or an instructional system is not tenable. Instead, I have indicated that the brain is a selectional system, one in which large numbers of variant circuits are generated epigenetically, following which particular variants are selected over others during experience (12–14). Such repertoires of variant circuits are degenerate, i.e., structurally different circuit variants within this selectional system can carry out the same function or produce the same output. Subsequent to their incorporation into anatomical repertoires during development, circuit variants that match novel signals are differentially selected through changes in synaptic efficacy. Differential amplification of selected synaptic populations in groups of neurons increases the likelihood that, in the future, adaptive responses of these groups will occur following exposure to similar signals.

Inasmuch as this theory of neuronal group selection (TNGS) abandons the basic computational notions of logic and a clock,

a means for spatiotemporal coordination must be put in place. This is provided by a process called reentry, the operation of which is central to the emergence of consciousness. Reentry is an ongoing process of recursive signaling among neuronal groups taking place across massively parallel reciprocal fibers that link mapped regions such as those found in the cortex. Reentry is a selectional process occurring in parallel; it differs from feedback, which is instructional and involves an error function that is serially transmitted over a single pathway. As a result of the correlations that reentry imposes on the interactions of competing neuronal groups, synchronously active circuits across widely distributed brain areas are selectively favored. This provides a solution to the so-called binding problem: how do functionally segregated areas of the brain correlate their activities in the absence of an executive program or superordinate map? Binding of the activity of functionally segregated cortical areas for each sensory modality is essential for perceptual categorization, the selective discrimination of different objects or events for adaptive purposes.

According to the TNGS, selectional events in the brain are necessarily constrained by the activity of diffuse ascending value systems. The activity of these systems affects the selectional process by modulating or altering synaptic thresholds. These systems, which include the locus coeruleus, the raphe nucleus, and the cholinergic, dopaminergic, and histaminergic nuclei, are necessary to bias selective events and thereby favor certain species-specific behaviors during evolution. Value systems also affect systems of learning and memory (15). The dynamic synaptic changes in individual neuronal groups that are based on past perceptual categorizations are positively and negatively influenced by limbic and brainstem value systems. The synaptic alterations that occur contribute collectively to a system I have called a value-category memory (15). This system, based largely on the activity of frontal, parietal, and temporal cortices, is critical to the emergence of consciousness.

The tenets of the TNGS or neural Darwinism are central in two main ways to the framework proposed here for consciousness. First, by its nature, a selectional neural system has huge diversity, a property that is a necessary basis for the differentiated complexity of conscious brain events (16). Second, as mentioned earlier, reentry provides the critical means by which the activities of distributed multiple brain areas are linked, bound, and then dynamically altered in time during perceptual categorization. Both diversity and reentry are necessary to account for the fundamental properties of conscious experience.

A Mechanism for Consciousness

We may now turn to a mechanism for consciousness based on the tenets of the TNGS. It is useful first to distinguish primary from higher-order consciousness. Animals with primary consciousness can integrate perceptual and motor events together with memory to construct a multimodal scene in the present; more specifically, in James’ “specious present” or in what I have called the remembered present (15). Different signals contributing to components of that scene may or may not be causally connected, but they can be related to the value systems and past learning of the individual conscious animal. On this basis, the animal may alter its behavior in an adaptive fashion. Such an animal with primary consciousness has no explicit narrative capability (although it has long-term memory), and, at best, it can only plan to deal with the immediate scene in the remembered present. Nonetheless, it has an advantage over an animal lacking such an ability to plan.

Higher-order consciousness emerges later in evolution and is seen in animals with semantic capabilities such as chimpanzees. It is present in its richest form in the human species, which is unique in possessing true language made up of syntax and semantics. Higher-order consciousness allows its possessors to go beyond the

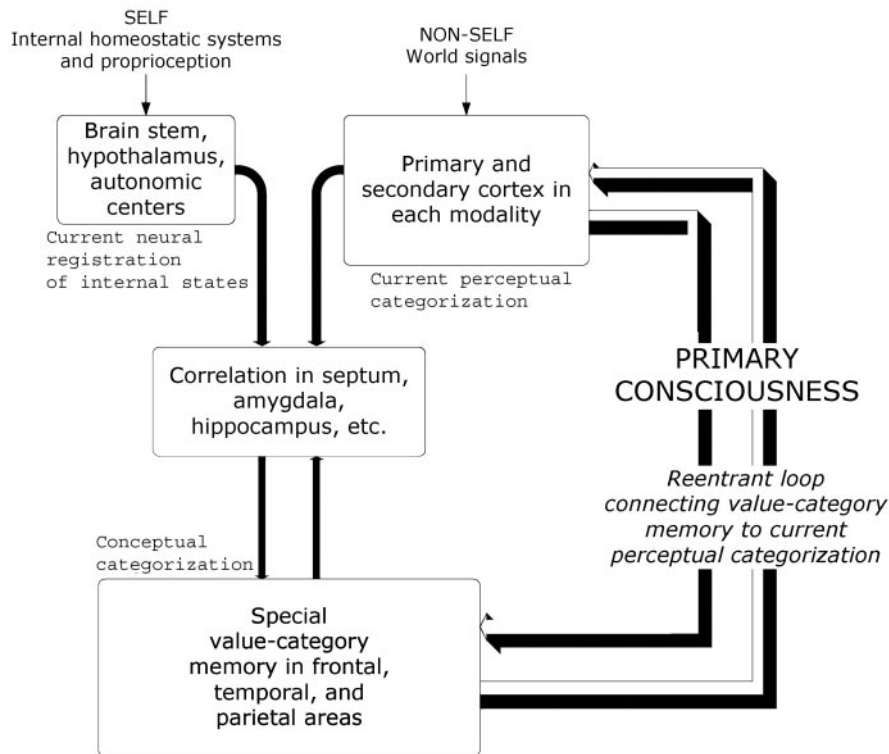


Fig. 1. Reentrant pathways leading to primary consciousness. Two main kinds of signals are critical: those from self, constituting value systems and regulatory elements of the brain and body, and those from nonself, signals from the world that are transformed through global mappings. Signals related to value and categorized signals from the outside world are correlated and lead to memory, which is capable of conceptual categorization. This value-category memory is linked by reentrant paths (heavy lines) to the current perceptual categorization of world signals. This reentrant linkage is the critical evolutionary development that results in primary consciousness. When it occurs across many modalities (sight, touch, and so forth), primary consciousness can connect objects and events through the memory of previous value-laden experiences. The activity of the underlying reentrant neural systems results in the ability to carry out high-level discriminations. This ability enhances survival value.

limits of the remembered present of primary consciousness. An individual's past history, future plans, and consciousness of being conscious all become accessible. Given the constitutive role of linguistic tokens, the temporal dependence of consciousness on present inputs is no longer limiting. Nevertheless, the neural activity underlying primary consciousness must still be present in animals with higher-order consciousness.

With these distinctions in hand, we may consider how the neural mechanisms underlying primary consciousness arose and were maintained during evolution. The proposal is as follows. At some time around the divergence of reptiles into mammals and then into birds, the embryological development of large numbers of new reciprocal connections allowed rich reentrant activity to take place between the more posterior brain systems carrying out perceptual categorization and the more frontally located systems responsible for value-category memory (Fig. 1). This reentrant activity provided the neural basis for integration of a scene with all of its entailed qualia. The ability of an animal so equipped to discriminatively relate a present complex scene to its own unique previous history of learning conferred an adaptive evolutionary advantage. At much later evolutionary epochs, further reentrant circuits appeared that linked semantic and linguistic performance to categorical and conceptual memory systems. This development enabled the emergence of higher-order consciousness.

The Reentrant Dynamic Core

How can the postulated reentrant activity account for both the unitary nature of consciousness as well as its complexity and changeability? As was mentioned in considering the TNGS, a brain working by selection necessarily must be highly complex to

maintain sufficiently large repertoires of diverse circuits as well as massive reentrant circuitry. A recent analysis of complexity in biological networks (16) reveals just the properties required to account for the unitary yet differentiated nature of consciousness. That analysis suggests that a complex system is one with many heterogeneous, smaller regions that can act quasi-independently but that also can interact with each other to form larger ensembles and thereby yield integrated functions. The thalamocortical system, whose activity is mainly responsible for the contents of consciousness, is just such a complex system. It contains distributed functionally segregated parts that interact over relatively long distances to yield new integrated functions.

Dynamic reentrant interactions across cortical circuits driven by signals from the body and the environment, but chiefly by the brain itself, allow binding combinations to occur. Because these integrative interactions occur among degenerate repertoires, they allow synchronous linking and binding to take place among widely distributed brain areas. The critical reentrant events within an integrated circuit of this system are metastable and, in time periods of 500 ms or less, give way to a new set of integrated circuits. This process occurs in an ongoing manner over successive time periods within the thalamocortical system, which, as a functional cluster, interacts mainly with itself. This functional cluster has been called the reentrant dynamic core (8) to emphasize its central properties as a complex system capable of yielding differentiated yet unitary states. In a recent paper, Crick and Koch (17) essentially agree with this formulation; their coalitions correspond roughly to core states.

The activity of the dynamic core entails the phenomenal appearance of a unitary scene, one made up of the higher-order

discriminations that we call qualia. Core activities integrating large amounts of information in a short time are necessarily affected by new signals in small intervals of time. Whereas the core interacts mainly with itself, it is not totally cut off from the nonconscious activities of the rest of the brain. Indeed, at the same time that certain cortical circuits contribute to the core activity underlying consciousness, these and other cortical circuits interact with basal ganglia and thalamic nuclei. At the next moment, neuronal groups that previously were not in the core are incorporated into it; others leave the core. The modulation of conscious states by attention is likely to occur via input to the cortex from the basal ganglion loops as well as from the gating of core responses through the activity of the reticular nucleus of the thalamus. During behavior dedicated to learning, core activity influences the development of automatic motor sequences by sending signals to and receiving signals from the basal ganglia. In this way, depending on context, neural areas underlying conscious and nonconscious activities can interact to enhance attention or develop automaticity.

Because the reentrant interactions of the core necessarily involve correlations of perceptual categories and concepts with value-category memory, the conscious experiences that arise are by their very nature largely intentional. A ubiquitous set of inputs to the dynamic core is continually received from bodily and brain systems concerned with motor behavior and homeostatic control. These inputs to the core are not only among the earliest but are also among the most persistent, and they provide a fundamental basis for subjectivity or the self-referential aspects of consciousness.

Subjectivity and Causality

Recognizing that conscious experience is a first person affair, how can we account for subjectivity? The incessant activity of the dynamic core, which leads to a succession of integrated discriminatory states, entails a rich set of phenomenal experiences. But who or what experiences these higher-order discriminations, these qualia? A reasonable suggestion emerges from the facts of embodiment. The brain and body exchange signals from the earliest times of neuronal development, and together they interact with the world. Self-referential signals come from motor systems and their sensory components, such as muscle spindles, which are all active from embryonic times onward. Even at these early times, the sources of an individual's action can be distinguished by the brain as separate from the signals arising from motion that is induced by external means. All of these interactions are strongly influenced by the various diffuse ascending value systems. The components of these value systems continually help regulate the synaptic thresholds affecting memory, and they contribute in an ongoing manner to perceptual categorizations. Other homeostatic systems in the brainstem and periaqueductal gray (18, 19) also contribute to these events that distinguish self from nonself (see Fig. 1).

In animals with primary consciousness, the self that emerges and serves as a reference is not self-conscious. Only with the flowering of higher-order consciousness and linguistic capabilities does a self arise that is nameable to itself. Consciousness of consciousness becomes possible via the linguistic tokens that are meaningfully exchanged during speech acts in a community. Episodic memory, which requires the activity of the hippocampus, contributes to the sense of continuity experienced by such a self. In humans, the play between the fundamental bodily based self of primary consciousness and the self-conscious agent of higher-order consciousness provides a higher ground for the development of rich subjectivity. Nevertheless, the temptation to appeal to a witness, to a homuncular self, must be resisted; as James pointed out, "the thoughts themselves are the thinker" (20).

Much of behavior is caused by neural activity in brain systems that do not contribute to consciousness. What can we say about

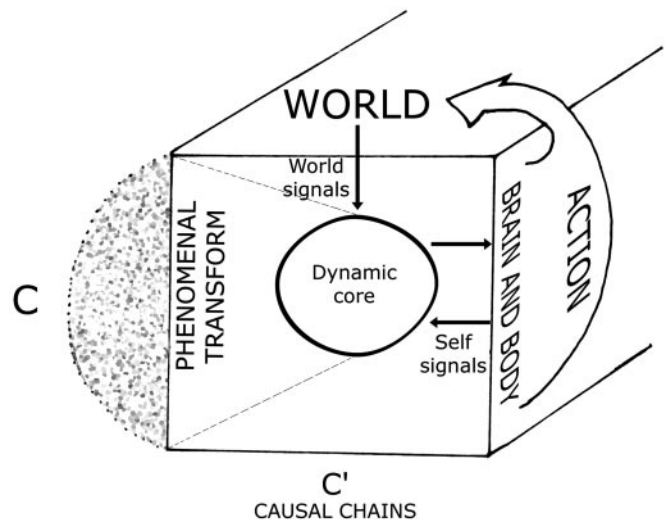


Fig. 2. Causal chains in the world, body, and brain affect the reentrant dynamic core. Core activities (C') in turn affect further neural events and actions. Core processes confer the ability to make high-order distinctions. The entailed qualia (C) consist of those distinctions. The shaded area labeled "phenomenal transform" has no causal efficacy but consistently reflects the C' states, which are causal. The boundary of the dynamic core in the figure should not be interpreted too strictly, because in real brains it fluctuates in time.

the causes of behavior in conscious agents? In considering the facts of human agency, a key issue concerns the relation between consciousness and causation. In line with common sense impressions, many authors have suggested that consciousness itself is causal. But consciousness accompanies particular brain events and is not a material entity. Instead, it is a process that is entailed by those material events. Those events are part of the physical world, and that world is causally closed; only matter energy can be causal.

A scientific view that assumes that consciousness arises from reentrant interactions among neural populations must therefore conclude that it is the neural activity of the dynamic core that is causal. If we call that activity C' and the qualia it entails C , then it is C' that is the cause of our actions and further C' events (Fig. 2). Some philosophers have recoiled from this view, considering it as simply another version of epiphenomenalism or even dualism. There is, however, no need to conclude that C is therefore meaningless and unnecessary; C states are informational even if not causal. C states are the discriminations entailed by causal transactions among C' states. Because C' and C are coherent, in certain contexts it is useful to talk of C as standing for C' ; at higher levels of description, it is convenient to talk as if C is causal as long as no confusion results about the true causes that arise in the neural system. Of course, as time goes on and improved neurophysiological methods and brain-imaging techniques are developed, more detailed analyses of core events will become possible for a third person observer. Even at such a time, however, the reports of a first person subject will be necessary, and necessarily they will be in C language. When we speak to each other, our speech is drawn from C' , as is all our activity, but it is in C terms that we carry out our exchanges.

Experimental Approaches

A literature is beginning to emerge that is concerned with neural correlates of consciousness (5). Neuropsychological analysis of responses to binocular rivalry in monkeys (21) and MEG experiments on similar phenomena in humans (22) has begun to distinguish neural events that are correlated with input signals

from events that are correlated with conscious percepts of a responding animal. Experiments in the visual domain have successfully distinguished cortical responses when a subject becomes aware of an object from those responses occurring when a subject is unaware of that object. Such discriminations occur in a conscious waking subject. As revealing as these findings are, we must also understand the neural events that distinguish nonconscious activities from those concerned with various levels and states of conscious awareness. This will require methods for measuring changes in the dynamic core as individuals emerge from deep anesthesia or from deep sleep. In addition, to test the dynamic core hypothesis, it will be necessary to go beyond the capabilities of present MEG methods. Whereas these methods have shown that awareness of a signal in binocular rivalry is accompanied by a burst of synchronous reentrant activity in widely distributed neuronal groups in the cortex (23), they are not yet able to measure or record thalamic responses in humans. On the neurophysiological side, more sophisticated methods capable of recording multiple brain areas simultaneously in conscious behaving animals would be a great help in analyzing reentrant interactions and binding events in greater detail.

Summary

According to the framework proposed here (Fig. 2), consciousness arises as a result of integration of many inputs by reentrant interactions in the dynamic core. This integration occurs in periods of <500 ms. Selection occurs among a set of circuits in the core repertoire; given their degeneracy, a number of different circuits can carry out similar functions. As a result of the continual interplay of signals from the environment, the body, and the brain itself, each integrated core state is succeeded by yet another and differentiated neural state in the core. This capability confers an evolutionary advantage on individuals possessing it, for, by these means, richly structured events can be related adaptively to the past history of value-dependent learning events in an individual animal.

The sequences and conjoined arrays of qualia entailed by this neural activity are the higher-order discriminations that such neural events make possible. Underlying each quale are distinct neuroanatomical structures and neural dynamics that together account for the specific and distinctive phenomenal property of that quale. Qualia thus reflect the causal sequences of the underlying metastable neural states of the complex dynamic core. The relationship of entailment between these neural states and the corresponding states of consciousness has the property of fidelity. Given the hyperastronomical functional connectivity patterns of the dynamic core, however, no two subjects can have identical core activity. This is consistent with the TNGS, which views the brain as a selectional system in which myriad neural states provide degenerate repertoires for matching a rich array of signals. Degenerate patterns (24) in the reentrant dynamic core provide an adaptive system for dealing with the enormously complex combinations of such signals.

The qualia that constitute these discriminations are rich and subtle. The fact that it is only by having a phenotype capable of giving rise to those qualia that their “quality” can be experienced is not an embarrassment to a scientific theory of consciousness. Looked at in this way, the so-called hard problem is ill posed, for it seems to be framed in the expectation that, for an observer, a theoretical construct can lead by description to the experiencing of the phenomenal quality being described. If the phenomenal part of conscious experience that constitutes its entailed distinctions is irreducible, so is the fact that physics has not explained why there is something rather than nothing. Physics is not hindered by this ontological limit nor should the scientific understanding of consciousness be hindered by the privacy of phenomenal experience. At the end of our studies, when we have grasped its mechanisms in greater detail, consciousness will lose its mystery (4, 25) and be generally accepted as part of the natural order.

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