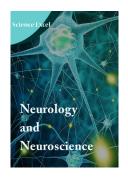
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# What Current Theories of Consciousness are Missing

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#### Abstract

Notwithstanding the power of the cell assembly concept, which holds that specific patterns of neuronal activity constitute the substrate of perceptual awareness that rises into consciousness, a explanatory gap remains between the phenomenological experience of consciousness and the brain processes from which that experience arises. A number of compelling and insightful theories have been offered that attempt to bridge that gap, but most of them fall short by failing to [a] specify which of many options other than hard-wired cell assemblies carry the information that becomes conscious, or [b] identify the brain mechanism for monitoring the functional events that become conscious. This Viewpoint article points to a number of possibilities that could be considered for both the *substrate* and *monitor* that give rise to consciousness.

#### Introduction

Underlying most current theories about the neural correlates of consciousness (NCCs) is the assumption that fragments of conscious experience are coextensive with specific patterns of neuronal activity. The circuits that mediate this activity have variously been called 'cell assemblies' [1,2], 'structured neuronal groups' [3], or 'selector circuits' [4], among others, and are assumed to be local neuronal ensembles whose pattern of activity varies for different qualia or for diverse units of perception. These would be the elementary, or primary, NCCs.

Different theories of consciousness propose different mechanisms for raising the primary NCCs to conscious awareness, and there is no consensus on which theory or mechanism is likely to provide the most accurate account of how consciousness is generated. However, three current models are among those frequently advanced as being most promising [5]. The Dynamic Thalamocortical Core holds that consciousness is a form of awareness that arises from integration of reentrant interactions between the thalamus and higher brain regions [6-11]. The Global Neuronal Workspace (GNW) views that access to consciousness occurs when incoming information is made globally available to multiple brain systems through a network of neurons with long-range axons densely distributed in the cerebral cortex [12,13]. A distinct but compatible concept is that of Higher-Order Thought (HOT), which proposes that conscious awareness occurs when

nonconscious primary sensory information is cognitively re-represented in a higher-order mental state [14-19].

Integrated Information Theory, which offers a sophisticated model of how integrated information that rises to consciousness differs quantitatively from the activity of unconscious information processing [20], enjoys widespread attention but offers less in terms of specific structural or functional details related to specific neural circuits.

The Dynamic Thalamocortical Core, GNW, and HOT models of consciousness share a number of overlapping features, and generally reinforce one another [15,21,22]. They all implicitly accept the view that activity in neuronal ensembles constitutes the NCCs that give rise to phenomenological experience, as do most other contemporary theories of consciousness. However, two features of brain function consistently missing from nearly all these theories is leaving a gap between the proposed NCCs and the phenomenology, or mental experience, of consciousness. The first is incomplete consideration of which dynamic brain activities provide the actual substrate for conscious experience. The second is the lack of ideas about the mechanism that monitors the specific NCCs required for conscious awareness. For simplicity, I will refer to these two features of brain activity as substrates in the first case, and *monitors* in the second case.

#### Substrates of NCCs

The concept of the cell assembly is powerful, and the evidence that qualitative

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information arises from the spatiotemporal pattern of activation of discreet neuronal assemblies is strong. It could be that activation of specific neuronal cell assemblies constitutes both the necessary and sufficient NCCs for phenomenological experience. But the brain is more than a complex of hard-wired and otherwise indistinguishable cells, so other possibilities require consideration. They include but are not limited to the following:

Neurons come in a variety of sizes and architectures. Some transmit excitation through electrotonic junctions, and the majority that communicate through neurotransmitter release or response use a variety of different transmitters and neuromodulators. Perhaps some but not all of these variations participate in the processing of information that comprises a network of NCCs.

All the cells of the brain are bathed in hundreds of peptides, hormones and neuromodulators, in addition to a rich repertoire of neurotransmitters. That the pattern of their distribution or the spatiotemporal dynamics of their presence could be the substrate of or contributor to phenomenological experience – either directly or by modulating cell assemblies — needs to be considered.

Astrocytes, oligodendroglia, and microglia far outnumber neurons. They are excitable, release and respond to neurochemical messengers, and modulate the extracellular environment in contact with all the cells in the brain. Over 60 years ago, Galambos [23] suggested that glial activity could constitute fields or patterns of activity in themselves, or act to modulate neuronal cell assemblies that constitute NCCs. Adey [24] long championed the concept of a tricompartmental model, in which neuronal, neuroglial, and extracellular compartments would constitute a micrometabolic module, in which neuronal elements appear to influence the behavior of neuroglial and extracellular elements in their immediate surroundings. As a pertinent example, microglia have been shown to sculpt neuronal interconnections by an activity-dependent process [25,26].

The microenvironment of all cells in the brain is a dynamic space, with a locally fluctuating ionic composition interacting with polyelectrolytes such as glycoproteins and gangliosides protruding from the surface of cells [27]. Local variations in the availability of these electrolytes can influence the mobility and availability of these ions. These extracellular fields could modulate cell firing patterns, entrain EEG rhythms, alter neurotransmitter release and modulate behavioral states [28,29].

To the extent that any of these processes could constitute NCCs, they do not call into question the strong evidence that information pertinent to phenomenological experience, imagination, or memory correlate with the specific circuitry of cell assemblies at some point. What they do show is that cell assembly circuitry may not be the only substrate from which consciousness arises. A specialized subpopulation of neurons, dispersed fields of ionic conductance, superimposable and interacting groups of neuroactive peptides or other neuromodulators, or even localized patches of cell surfaces containing unique cell-surface components or receptors — these could all potentially be the source of variations in conscious perceptions.

#### **Monitors of NCCs**

Neuronal activity is widespread and constant throughout the brain, in all states of awareness, *without* giving rise to conscious experience [30,31]. So what is the mechanism that monitors

A reasonable assumption is that the agency of consciousness — the 'witness' to the relevant neural processes — is itself a specific neural process. The well-known role of the brain stem reticular formation in controlling arousal, attention, and motivation (32) would appear to be a good candidate for detecting NCCs, but it could merely serve to arouse the brain to a level of consciousness detected by some other process.

and selects the substrates of NCCs — the filter that determines

It may be that not all the cells of the brain are involved in manifestations of consciousness. There could be a select population of neurons, glia, or both which some focusing mechanism monitors, driven by other determinants of interest or necessity (conveyed from other neural centers) at any given moment. This could be the function of the reticular activating system, or a parallel process.

But it could also be the ebb and flow of impedance changes in the fluid of the extracellular space [28] rather than the activity of the cells that the focusing mechanism monitors in giving rise to phenomenological experience.

Perhaps the critical monitoring mechanism of the relevant NCCs resides in electrophysiological (EEG) activity. Evidence from a variety of neuroscience areas, including the reversible electrophysiological changes observed with loss and return of consciousness in anesthesia as well as distinctive EEG profiles of various psychiatric disorders, provides an empirical foundation for this theory of consciousness [33]. For example, Hameroff [34] proposed that cognitive neurocomputation with consciousness is accompanied by 30- to 90-Hz gamma synchrony electroencephalography. A concept for the involvement of slow cortical potentials in the emergence of consciousness was proposed by He and Raichle [35]. Evidence for such a process can also be seen in the work of Fernandez-Ruiz, et al. [36] in which pathway-specific gamma oscillations appear to route taskrelevant information between distinct neuronal subpopulations in the entorhinal-hippocampal circuit.

Thompson and Varela [37] proposed a different approach, growing out of an 'enactive' viewpoint in cognitive science, which emphasized the need to map NCCs at the level of large-scale, emergent and transient dynamical patterns of brain activity (rather than at the level of particular circuits or classes of neurons).

It may well be that what the 'mind' focuses upon is not what is happening at any local place or process in the brain, but in the totality of the brain's activity, as predicted by the GNW and HOT theories of consciousness, in particular. Yet the need for a focusing mechanism remains. Toward that end, the spotlight features of the brain stem reticular formation, or some similar process, is more compatible with the Dynamic Thalamocortical Core concept.

Dennett [38,39] has been adamant in laying to rest any dualistic explanations of consciousness. Dennett has derided the notion of a 'Cartesian Theater' where neural activity giving rise to consciousness is put on display. Dennet's own Multiple Drafts model in which multitrack processes of interpretation and elaboration of sensory inputs are under continuous 'editorial revision' leaves open the question of what is doing the editing and revising. Therefore, it seems clear that some compartment of the brain [11,40,41] or some facet of brain activity [42] admits some neural activity into consciousness while all other activity in that moment is excluded. Metaphorically, at least, a screening room (Cartesian Theater) in which or by which such a process takes place may be a fit analogy.

## **Summary and Conclusions**

Notwithstanding the power of the cell assembly concept, which holds that specific patterns of neuronal activity constitute the substrate of conscious awareness, a gap remains between the phenomenological experience of consciousness and the brain processes from which that experience arises. While contemporary theories of consciousness provide fruitful insights into the brain mechanisms possibly involved, but most of them fall short by failing to [a] specify which of many options other than hard-wired cell assemblies carry the information that becomes conscious, or [b] identify the brain mechanism for monitoring the functional events that filter the information that becomes conscious.

This Viewpoint article points to a number of possibilities that could be considered for both the *substrate* and *monitor* that give rise to consciousness. The suggestions offered here are speculative in lacking empirical evidence, but this should change as specialized technologies increasingly improve the visualization of brain dynamics in unprecedented detail and in real time. These methodologies include optogenetic means for tracing the population of cells activated by specific percepts [43,44], the ability to record simultaneously the activity of multiple individual neurons [45,46], quantitative microelectrophoretic techniques for assessing ionic and neurotransmitter fluxes at highly localized sites [47]; and a tool kit for pinpointing the activity of specific neuroactive peptides [48].

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