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Dendritic Integration Theory as a Cellular Bridge for the Current Major Consciousness Theories

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Abstract

Consciousness is often described as the final frontier in science, tackled from multiple disciplines including philosophy, neuroscience, and computer science. Consciousness is most commonly defined as what exists from a first-person perspective, as the feeling of what it is like to be something, as well as through neuronal mechanisms that generate and support this phenomenology. Countless theories on consciousness have emerged to try to elucidate this complicated phenomenon. In our review, we aim to examine the three dominant theories of consciousness - Global Neuronal Workspace Theory (GNWT), Recurrent Processing Theory (RPT), Higher-order Theory (HOT) - and the Dendritic Integration Theory (DIT) as a newer, less prominent, theory that focuses on the cellular basis of consciousness. We propose that DIT may complement the postulations of the other three theories through its cellular approach that bridges state and content consciousness. Finally, we discuss the future of consciousness research more generally.

Keywords: Consciousness Theory, GNWT, RPT, HOT, DIT

Introducing the Problem of Consciousness

Consciousness has long been discussed in philosophy, literature, and the arts, while it entered scientific discourse much later. Academic psychology first bypassed consciousness, as did cognitive neuroscience. The first theory of consciousness in

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the cognitive sciences was Bernard Baars's "cognitive theory of consciousness" (Baars, 1988). Following Baars's theory, Francis Crick's "Astonishing Hypothesis: The Scientific Search for the Soul", published in 1994 lead to an expansion of neuroscientific research, particularly in the 21st century (Crick, 1994).

While there is no real consensus among researchers and it remains an ambiguous term, Thomas Nagel first defined consciousness in the most general sense as "the feeling of what it is like to be something" (Nagel, 1974). Put another way, consciousness may be whatever exists from a first-person perspective when not in a state of dreamless sleep. Nagel's definition was later adopted by David Chalmers who expanded consciousness into the so-called "easy problems" and "hard problem" (Chalmers, 1995). The easy problems of consciousness refer to the behaviours and functions that are associated with consciousness, while the hard problem relates to the phenomenal or subjective elements of conscious experience (Seth & Bayne, 2022).

Chalmers's "easy problems" encompass content consciousness where the conscious content can be perceptual, cognitive, or affective. The easy problems of consciousness involve understanding the cognitive and neural processes that underlie conscious experience but can easily be addressed empirically through scientific investigation and accessed and reported on by an individual. Content, i.e., access consciousness therefore refers to an experience that can be investigated using verbal report, which is why it is commonly considered easier to study (Chalmers, 1995). The "hard problem", on the other hand, commonly refers to state or phenomenal consciousness as the raw experience of consciousness, or so-called "qualia". Qualia refers to the subjective qualities of conscious experience such as taste, smell, or colour (Crick & Koch, 2003). Phrased another way, the "hard problem" mainly references an explanatory gap between the subjective experience of consciousness and the report of the conscious experience (Seth & Bayne, 2022).

Researchers have taken different views on the easy-hard problem of consciousness. Crick and Koch (2003) claim that studying the easy problems of consciousness, i.e., content consciousness, will eventually resolve the hard problem. They suggest an integrated approach that includes both philosophical and experimental aspects of consciousness, as well as the neurobiological and cognitive mechanisms that underpin it. Similarly, prominent neuroscientist Stanislas Dehaene opposes Chalmers's claim, suggesting the opposite: the subjective experience is not a problem in itself (Dehaene & Naccache, 2001). In fact, Dehaene and Naccache (2001) dispute the existence of state consciousness. They posit we must simply study and describe what is reportable, and therefore focus on content consciousness while rendering state consciousness redundant (Dehaene & Naccache, 2001). Anil Seth (2021) recently proposed a novel way of solving the easy-hard problem of consciousness by framing the issue in a third way: as the "real" problem of consciousness. Seth (2021) proposes that the primary goal of science is to explain, predict, and control the phenomenological properties of conscious experience. In short, this approach to the problem aims to explain why certain patterns of brain activity (and other physical properties) map to a certain type of conscious experience, and not a general awareness that contains a multitude of mental sensations, e.g., experiencing the colour of a red car, thinking about a chess problem, or feeling pain. Finally, philosopher Daniel Dennett (1998) has claimed that granting state or phenomenal consciousness a special status is only a "cognitive trick" that does not help understanding conscious content. In Dennett's view, it may be impossible to scientifically distinguish between state and content consciousness because all empirical studies require some form of report.

Several researchers have recently claimed to have exclusively studied state consciousness by using no-report paradigms (Aru et al., 2012; Tsuchiya et al., 2015). In these studies, participants are allowed to make no choice or no report of perceiving a stimulus. Although a potentially promising approach, critics have taken issue with no-report paradigms because there is no way to prevent participants from thinking and thought-processes may also reflect the contents of perception in neuroimaging studies (Pitts et al., 2018). The issues in the paradigms widely used nowadays are important to consider for most consciousness research as they relate to the so-called "measurement problem": detailed and comprehensive theories of consciousness are unlikely to be helpful if the phenomenon cannot be adequately empirically tested and measured (Browning & Veit, 2020). It is difficult to ascertain whether there is a single phenomenon of consciousness that can be captured by a single scientific concept since measures of consciousness have produced different findings (Irvine, 2014; Wiese, 2020). A pervasive concern is whether researchers are probing the same phenomenon in their studies as their results come from different paradigms with a wide range of ways in which participants respond to different stimuli, presented in different tasks and task contexts, and analysed differently.

A wide range of brain regions have been implicated in generating conscious experience, involving a wide coalition of not only cortical but subcortical structures and neurons (Koch, 2019). Aspects of higher-level functions such as planning, problem-solving, imagination or creativity seem to crucially rely on unconscious components that are often related in the literature to subcortical structures (Newman, 1995). Yet, importantly, we can neither equate activity in the cortex to the conscious, or activity of subcortical neurons to the unconscious: as stated by Dehaene (2014a), regions of the brain that produce conscious content also produce unconscious processes, and the opposite is also thought to be true. According to the major theories of consciousness, even though the cortex is crucial for conscious experience (Baars & Geld, 2019) cortical areas do not create consciousness, but rather upkeep unconscious cognition and a number of brain processes (Baars & Geld, 2019).

Many theories of consciousness have evolved over the years. Arguably the most influential one is Dehaene and Naccache's (2001) **Global Neuronal Workspace Theory (GNWT)**. Other major theories that are considered to best attempt to tackle consciousness are Victor Lamme's (2006) **Recurrent Processing Theory (RPT)**, and the **Higher-Order Theory (HOT)** (Lau & Rosenthal, 2011)**.** GNWT and RPT, in particular, hold different views on state and content consciousness as well as other key features of consciousness such as where it lies in the brain, i.e., the front-versus-back of the brain debate. HOT is also firmly rooted in this debate: HOT highlights the prefrontal cortex (PFC) as essential for consciousness since it is implicated in higher cognitive or metacognitive mechanisms, although this view is contested within the HOT community (Brown et al., 2019). The three aforementioned major theories will be described in detail in this review.

Numerous other theories have been proposed that will not be discussed in this review (see Seth & Bayne, 2022 for a recent review). To briefly mention one, the Integrated Information Theory (IIT) proposed by Giulio Tononi in 2007, as a new theory that suggests that consciousness is the same as a certain kind of information, measured by the metric *phi*. According to IIT, consciousness requires a group of elements within a system that have a physical cause-effect power over each other (Tononi et al., 2016). Yet, despite its relative popularity (Sattin et al., 2021), especially with non-experts (Michel et al., 2018), we will not consider IIT in this review as it has been criticised by many as being unscientific, and its approach of equating consciousness to integrated information has been extensively questioned (Bayne, 2018; Cerullo, 2015). It also, despite its popularity among non-experts (Michel et al., 2018), has not received nearly as much support in the empirical literature as GNWT, RPT, or HOT.

In this review article our main proposition is that the DIT theory both supplements and complements the current dominant theories of consciousness. In the review we first focus on the three dominant contemporary theories of consciousness: the GNWT, RPT, and HOT. We then expand upon each theory and its contribution to the debate on consciousness before discussing how the theories relate to each other in more depth. We hope to not only increase the understanding of each theory independently, but also depict how they might complement each other. The main original contribution of this article to the literature is therefore to present the argument for how DIT may bridge the gap between the three other major theories in terms of its cellular approach to consciousness. We propose it does so by describing the ideas in the theories on a cellular level through the L5p neurons to merge state and content consciousness. The L5p neurons may be crucial in this sense as single units to build the conscious experience, also in their dual role as they interact with the thalamus as well as cortical areas (Aru et al., 2023). They hold a central position in both thalamo-cortical and cortico-cortical loops. Not only do we suggest that DIT connects cortico-cortical and thalamo-cortical loops, and pairs state and content consciousness convincingly, but we also suggest that DIT can convincingly relate to, and combine insights from, the other major theories of consciousness (Aru et al., 2023). For example, DIT can explain phenomena such as ignition-like dynamics that are associated with the conscious perception of stimuli. DIT is in this sense compatible with the GNWT as it provides the cellular basis for the workspace outlined in the GNWT. We end the article on a discussion of the field of consciousness research as it stands, discussing open questions and avenues for future research, as well as our recommendations on how the field can best advance.

Contemporary Theories

Global Neuronal Workspace Theory

Global Neuronal Workspace Theory (GNWT) is currently one of the most influential theories of consciousness, based on Bernard Baars's Global Workspace Theory (Baars, 1988, 2005; Dehaene, 1998). The theory rests on the theoretical perspective of a cortico-thalamic core in the brain, believed to underlie conscious aspects of higher cognitive processes such as thinking, learning, and executive control (Baars et al., 2013). The C-T core is thought to consist of many anatomical hubs, yet conscious percepts are always unitary and internally consistent at any given moment. The global workspace in the brain therefore cannot be localised to a single anatomical hub but should be sought in a functional hub (Baars et al., 2013). The hub contains a dynamic capacity for the binding and propagation of neural signals over multiple networks (Shanahan, 2012).

GNWT suggests there are unconscious local peripheral processes represented by coalitions of neurons that compete for conscious access to a global workspace in a winner-takes-all fashion. The "winner" broadcasts information into the global workspace, which propagates the information throughout the whole brain (Baars, 2005). The global workspace is composed of mobilised excitatory neurons with long-range cortico-cortical and thalamo-cortical connections, consequently creating patterns of global activity. Dominant sensory neural coalitions are thought to trigger workspace neurons in the frontal and parietal cortex, forming an active reverberating network that makes sensory information available for higher cognitive processes (Dehaene & Changeux, 2011).

The theory comprises three stages of conscious processing: subliminal, preconscious, and conscious stages. Subliminal processing only occurs in the specialised local neural nodes that operate in isolation (Dehaene & Changeux, 2011). Activity here is triggered automatically, and refers to activity in early sensory cortices, limited to the periphery of the workspace. The preconscious stage is a step between subliminal and access consciousness, where stimuli almost have access to the workspace, but require additional top-down attention to enter the workspace and become reportable. Finally, the conscious stage refers to stimuli that are in the workspace and completely reportable, which corresponds to access consciousness (Dehaene & Changeux, 2011).

GNWT accordingly suggests that consciousness is a non-linear, rather than a linear process. It posits that consciousness arises from information processing where specialised programs have access to smaller, divided information repositories. Once the dispersed information is broadcast into the workspace, it becomes globally accessible, and the subject becomes conscious of it (Dehaene, 2014b). This global broadcasting is also referred to as global ignition, or non-linear network ignition (Mashour et al., 2020).

The workspace, which acts as a window of consciousness, is extremely limited in its broadcasting. The theory therefore suggests that one can be aware in a given moment of a limited amount of sensory (visual, auditory, mnemonic, imaginative, etc.) information (Dehaene & Naccache, 2001).

Importantly, in GNWT, consciousness is always accessible and, in this way, the theory focuses exclusively on access rather than phenomenal consciousness. Moreover, the neural network thought to send, share, transmit and air the messages is thought to be located in the frontal-parietal areas, supported by neuroimaging studies that consistently find activity in fronto-parietal regions during conscious processing of stimuli (Mashour et al., 2020), as well as in evidence from bilateral lesion studies (Odegaard et al., 2017). The GNWT thus places consciousness in the front of the brain, as opposed to other theories we will shortly discuss.

In general, evidence from brain imaging suggests that both conscious and unconscious stimuli trigger activity in sensory regions, and this activity then propagates into the cortex (Baars et al., 2013; Mashour et al., 2020). Yet, neuroimaging studies suggest that conscious processing is connected to more widespread and high-fidelity activity in the brain compared to unconscious stimuli (Dehaene & Naccache, 2001). The central idea of the GNWT is that conscious cognitive content is globally available for different cognitive processes that include attention, evaluation, memory, and verbal report. It is also thought that state consciousness and its properties are separate to what is probed in GNWT studies that measure and report on access consciousness.

Recurrent Processing Theory

Victor Lamme's Recurrent Processing Theory (RPT) connects consciousness to recurrent processing with a feedforward-feedback dichotomy (Lamme, 2006). RPT first posited that this feedforward-feedback dichotomy in neuronal processing helps to understand the differences between pre-attentive and attentive vision, as well as between unconscious and conscious awareness in vision (Lamme & Roelfsema, 2000).

One similarity between RPT and the original GNWT is a division of conscious processing into three main stages (Dehaene et al., 1998; Lamme, 2006). Lamme (2006) identifies three types of processing: a feedforward sweep, localised recurrent processing, and widespread recurrent processing. The feedforward sweep occurs from the visual cortex to motor areas, within 150 – 200ms after stimulus onset. It includes feature extraction in, and rapid categorization of stimuli, where low- and high-level features are extracted and translated into a (potential) motor output. The feedforward sweep is unconscious, and thus does not include or lead to conscious experience.

The second type of processing is localised recurrent processing for unattended stimuli. This starts within 100ms after stimulus presentation, at first between low-level visual areas, and then more widespread between the low-level areas and the visual cortex. This processing stage can be compared to Dehaene's preconscious stage, except the stimuli are thought to be phenomenally conscious.

The last stage is widespread recurrent processing, for attended stimuli that are not masked. Stimuli here are conscious and fully reportable, connected therefore to access consciousness. This would correspond to entry in the global workspace in GNWT. The recurrent interactions enable phenomenal consciousness of the visual stimulus. Eventually, recurrent interactions spread through the whole brain, causing 'global ignition'. At the neural level this is expressed in P300 responses, and the involvement of fronto-parietal areas. The result is access consciousness, the ability to cognitively manipulate the stimulus, your reaction to it, its consequences, and so on. In short, recurrent processing is the cortico-cortical activity that appears after the feedforward sweep of information processing in the brain, and this process is directly connected to visual awareness (Lamme, 2006; Lamme & Roelfsema, 2000).

Importantly, the two theories are dissimilar on this issue, as well as in other aspects, including where they place consciousness in the brain. While GNWT places consciousness in anterior brain areas, primarily areas in the PFC, RPT places consciousness in posterior brain areas, since the theory arose from explanations of visual processing and how perception is formed (Lamme & Roelfsema, 2000). Evidence in the RPT that complements the idea that localised recurrent processing is conscious comes mainly from partial report studies and postdictive effects. In partial report studies, similar to reports in general, a subject's partial report is taken as evidence that they are conscious of the information presented sensorially only when the information is cognitively accessed (Stazicker, 2018). Yet, philosophers have recently argued that the partial report paradigm is the wrong paradigm to use to investigate consciousness. Wu (2018), for one, criticises the idea that subjects are conscious only of partial information as this requires a "decay of information" that is not supported by the so-called "overflow hypothesis", that is, the hypothesis argued by philosophers and cognitive scientists that conscious perception overflows cognitive access, i.e., reportability. Wu (2018) argues that the interpretations predicted by the alternative hypothesis, the "consciousness hypothesis", in which conscious perception is conflated with cognitive access or reportability (Stazicker, 2018), involves the same decay of visual information between visual processing and the lower-capacity processes in cognitive access to the visual information (Wu, 2018). Block (2014) similarly argues that inattention does not make visual responses less precise, suggesting that subjects are only conscious of non-detailed, vague information outside of the focus of attention in a scene. Both the consciousness and overflow hypotheses, even though they oppose each other in their views on partial reportability and whether consciousness overflow reportability, predict that the loss of detailed information occurs at the point of cognitive access, rather than early in the stream of visual processing (Stazicker, 2018).

Postdictive effects refer to when the majority of effects happen after the fact, for example, when a stimulus presented after another stimulus seems to causally affect the percept of the earlier stimulus (Shimojo, 2014). Long-lasting postdictive effects have been considered evidence for discrete perception. More specifically, long-lasting postdiction requires high-capacity buffers that store incoming information for long periods of time (Herzog et al., 2020). Evidence from postdiction favours a two-stage model in which discrete conscious percepts are preceded by continuous unconscious processing. Recurrent networks are thought to dynamically store information about the duration of incoming stimuli (Goudar & Buonomano, 2018).

Higher Order Theories

Higher-order theories of consciousness attempt to explain consciousness as higher-order representations (HOR) of mental states. Higher-Order Thought Theory (HOT) suggests that consciousness is created from higher-order observations of first-order processes (Rosenthal, 2005). In other words, consciousness is not comprised of current sensations, but rather higher-order perceptions of those sensations. The HOR of a mental state can be seen as a meta-psychological state, i.e., a second, higher mental state directed toward the first mental state (Gennaro, 2004). A key characteristic of higher-order theories is, therefore, a hierarchical or iterative structure.

HOT theorists argue that the first-order state, which arises from processing sensory stimuli, is not enough in itself to generate a conscious experience of a stimulus (Lau & Rosenthal, 2011; Rosenthal & Weisberg, 2008). Instead, they claim a higher-order representation of that experience is necessary for consciousness. Cognitive processes such as attention, working memory or metacognition are critical in creating a conscious experience. These processes are related to the prefrontal and parietal cortices, which can be thought of as the higher-order regions that make first-order input from the visual cortex, in the posterior part of the brain, conscious (Lau & Rosenthal, 2011). This way, consciousness can be described as the interaction between first-order sensory regions of the brain and cortical regions for higher cognition.

The higher-order representation of representation (HOROR) theory is a modified version of the HOT theory, conceptualised and proposed by Brown (2014) and further elaborated by Brown and colleagues (2019). The theory rests on the idea that the phenomenal experience is, in fact, an introspective awareness of the unconscious higher-order representation (HOR). In other words, a HOR of the first order goes through a HOR of the second order, where only the second-order representation becomes conscious.

In addition to HOROR, LeDoux and Brown (2017) investigated a higher-order theory of emotional consciousness and introduced the concept of a self-HOROR. A self-HOROR is created when we add, along with semantic and episodic memory, autobiographical knowledge. The self-HOROR can in this sense be viewed as a self-schema with multiple aspects of the Self. With these aspects we gain phenomenal consciousness of the Self in our working memory.

The self-HOROR does not include emotions until survival circuits are activated, which in turn activate the arousal system. LeDoux and Brown (2017) suggest that, to generate cognitive consciousness, we need input from the senses, memory, and schemas relating to the Self, while to create an emotional state, input from survival circuits or body-sensing circuits (interoceptors) are necessary.

HOT can be considered more of a state consciousness than content consciousness theory as it is more concerned with the phenomenology of consciousness rather than the conscious content itself. It posits that what makes a mental state conscious is the presence of a higher-order thought directed at that state. According to HOT, a mental state becomes conscious when there is a separate mental state that represents or is about the original mental state. This higher-order thought is typically described as a state of introspection or self-awareness. In other words, the HOT proposes that conscious experiences involve not only the first-order mental states (such as perceiving an object or feeling pain) but also the second-order thoughts or mental representations of those first-order states. The presence of these higher-order thoughts is what confers consciousness to the initial mental states. HOT approaches consciousness in terms of mental phenomena in the local state such as introspection and cognition. Although HOT provides key neurobiological predictions, it is overall more concerned or reliant on cognition as a complex cognitive theory. Relatedly, it retains criticism toward some mental functions that are described through the neurobiological impulse-motivation limbic system, such as emotions, expanding to the complex concepts of Self, emotions, introspection, and metacognition. The theory claims that we must elaborate on and differentiate between different mental phenomena that pertain to consciousness, such as how the Self functions in the passive or active way, or qualitatively different types of introspection. HOT overall suggests there may be too little contact between the theories of consciousness and theories of emotion.

For a conscious experience, we need a complex interaction between the circles of the general network of cognition (GNC), the sensory cortex, and other cortical areas, especially those implicated in memory in the medial temporal lobe. Regions of the GNC such as the prefrontal cortex and the parietal cortex (forming the frontoparietal network) cognitively process and make conscious sensory information represented in the secondary visual cortex (LeDoux & Brown, 2017).

Fleming (2020) highlights how the two streams of "first order" and "second order" in neuroscience differ in whether we need higher cognitive mechanisms to generate consciousness. In first-order theory, metacognition is thought to be necessary for reflection and report of one's experience, but not necessarily for creating consciousness (Fleming, 2020). Fleming (2021), as a higher-order theorist, believes that what we are in essence conscious of our thoughts (the mental), as well as our capacity or ability to reflect and generate thoughts and feelings. Without metacognitive consciousness, we can adapt or behave complexly, to process information and react to stimuli, but we cannot be "fully" conscious (Fleming, 2021).

A major new direction for HOT seems to be perceptual reality monitoring (Gershman, 2019). Reality monitoring involves discriminating between real and imagined stimuli in memory. It is different to reality testing in this way, which refers to discriminating between real and imagined stimuli in perception. Past experiences are crucial parts of consciousness and understanding conscious perception, where the imagination may influence past stored experiences then also used by the brain to make predictions about reality. Gershman (2019) proposed an adversarial framework for computation in the brain that includes feedback and feedforward generators as well as a prefrontal discriminator. The feedback and feedforward terminology was chosen to map the generators respectively onto the feedback and feedforward pathways in posterior cortical regions (Gershman, 2019). The feedback pathways are thought to compute predictions about incoming or upcoming sensory data, while feedforward pathways have a supposed role in computing inferences about the latent causes of sensory data. The framework may also have clinical applications, as the author proposes the breakdown of the generator and discriminator in this framework could lead to the delusions observed in some psychological or psychiatric disorders (Gershman, 2019).

Perceptual reality monitoring has received much traction and has particularly been adopted by HOT proponents. For example, Michel and Lau (2020) utilise perceptual reality monitoring to tackle the criticisms of HOT, such as the criticism that it cannot be generalised to other systems. While the two theories are not the same, they can be conflated when understanding the principles of HOT and how it is a two-step computation system (Michel & Lau, 2020).

Dendritic Integration Theory

Along with the three dominant theories, in 2020 a new theory arose that updates the classic thalamo-cortical theory of consciousness: the dendritic integration theory (DIT) (Bachmann et al., 2020). DIT takes a cellular neuroscience approach to consciousness, based on the cellular mechanisms of cortical pyramidal neurons. This theory is sparsely evaluated (Gidon et al., 2022), but we find it holds great potential for elucidating the neurobiological underpinnings of consciousness by integrating cellular processes into investigating how the brain generates conscious experience.

Cellular approaches to consciousness have also been proposed in the past (Sevush, 2006). Sevush's (2006) single neuron theory, for example, posited that each neuron in the nervous system is conscious, but also highlighted the role of layer 5 pyramidal neurons, particularly in the lateral prefrontal cortices. The electrical activity within a portion of the apical dendritic tree of these neurons was thought to be complex and diverse enough itself to account for the complexity and diversity of complex experiences that would usually be ascribed to activity from the whole brain (Sevush, 2006).

In general, it is considered that consciousness is connected to distributed patterns of activity in the large-scale network, but it remains unclear what the role of individual cells is, i.e., how the pyramidal neurons contribute to the dynamics on the macroscales. Most theories of consciousness are based on cortical process and separating the anterior and posterior areas of the cortex. This separation or divide of the information streams is mirrored on the level of individual cortical pyramidal neurons, but also plays a key role in the cortical-thalamic processing. Here especially we can highlight the role of the higher-order thalamus, a cluster of thalamic cores that are included in the relay of information from the early sensory processing areas to the cortex (Aru et al., 2020).

The idea that the thalamocortical system is the crucial constituent of the neurobiological mechanisms of consciousness has a long history (Sevush, 2006). For the last few decades, however, consciousness research has, to a large extent, overlooked the interplay between the cortex and thalamus. According to a thalamo-cortical theory of consciousness, no one part of the cortex is related to consciousness: rather, the interaction between the cortex and the thalamus is what creates consciousness, including both conscious state and conscious content (Aru et al., 2019).

DIT aims to reconcile cortical and thalamo-cortical theories: processes in the brain that create consciousness interact at the level of single cortical neurons, providing evidence that non-specific thalamic nuclei affect the coupling between the apical and somatic (basal) compartments of the pyramidal cells, thereby coupling or decoupling the thalamo-cortical loop (Aru et al., 2020; Gidon et al., 2022).

The theory rests on two main claims. First, the theory claims the global dynamics of a conscious brain rest on cellular mechanisms in the pyramidal cells of the fifth cortical layer. Second, the authors propose that the conceptual basis for consciousness is the flexible integration of bottom-up and top-down information streams at this cellular level.

The theory highlights processing between the apical and basal compartments of layer 5 pyramidal cells as central to generating conscious experience. The apical part of the pyramidal neuron lies towards the cortical surface and integrates contextual information from cortico-cortical and thalamo-cortical loops. The basal compartment is centred around the cell body of the pyramidal neuron, toward the basal dendrites that control the spiking of the output cell (Aru et al., 2020). In addition, the coupling compartment within the L5p cells also crucially acts as a mediator, receiving signals from the higher-order thalamus.

While the cell bodies of L5p neurons lie in the fifth cortical layer, their dendrites stretch through all layers of the cortex all the way to the first. The L5p dendrites, considering both their location and morphology, also cast long-range projections within and outside the cortex and encapsulate input-output functions of cortical columns. These pyramidal cells, given their long-range projections and morphology, serve as the primary way the cortex exerts control over behaviour (Aru et al., 2020; Bachmann et al., 2020). Deep pyramidal neurons are cortical output units that encapsulate the combined activity of cortical columns. Different L5p cell populations project to either other cortical or subcortical areas (Petrof et al., 2012). DIT proponents advocate for an essential role of the L5p neuron dendrites in conscious experience because the projections of these neurons span between cortical and subcortical areas of the brain, connecting them to form conscious perception or a conscious experience.

The architecture and biological characteristics of the L5p neurons enables the flexible integration of segregated data streams. This segregation and integration of the data streams within pyramidal neurons forms the conceptual basis of how cognitive high-level processes and phenomenological consciousness are rendered.

According to DIT theorists, conscious content depends on conscious state, and both conscious state and conscious content depend on the activity of L5p neurons that activate, integrate, and modulate cortico-thalamic processing by activating cortico-cortical and thalamo-cortical nodes together and, by doing so, form a broadcasting system where the L5p neurons are a central element and mechanism to establish and disrupt consciousness. From this, DIT theorists posit that cortical processing that does not include L5p neurons is not available to consciousness, rather, it is unconscious (Aru et al., 2019). DIT overall emphasises how the pyramidal cells, with their biophysical properties, act as the gates to control patterns of global activation in the brain relating to consciousness. When a person is conscious, the gate within a cell is open to enable signals to propagate within the brain and activate cortico-cortical and thalamo-cortical loops. In unconscious processing, cortical pyramidal cells are decoupled, so activity does not spread within the thalamo-cortical system.

Importantly, Bachmann and colleagues (2020) highlight how the theory is compatible with the other most prominent consciousness theories: DIT, they claim, addresses the other theories' claims about consciousness on the cellular level. How the theory supports other theories of consciousness will be further discussed below.

Discussion

For now, there is no consensus over which theory offers the best explanation, so the theories are still in competition, even though each is in part corroborated by experimental research. While GNWT, RPT, and HOT attempt to primarily explain conscious content and conscious state and can be divided according to which of the two components they primarily focus on, DIT aims to integrate conscious state and content.

To understand the complicated phenomenon of consciousness we need multiple levels of explanation, from the molecular basis to neural networks, to understand how behaviour and mental phenomena form the subjective experience (Baars & Geld, 2019). So far, there has not been a single unifying theory of consciousness. We chose to discuss the selected theories of consciousness (GNWT, RPT, and HOT) because, in addition to being some of the most widely cited and discussed in the field (Sattin et al., 2021), we believe that together they encapsulate the greatest extent of knowledge on consciousness to-date.

The theories share some commonalities. For instance, GNWT and RPT both take a neurobiological approach to investigating consciousness that is predominantly based on visual perception. To support its claims, HOT also makes clear neurobiological predictions that rely heavily on visual perception studies, although it in general takes a more cognitive approach to consciousness by mostly focusing on mental experiences such as thoughts, memory, planning, and emotions (Baars & Geld, 2019; Rosenthal & Weisberg, 2008).

Nevertheless, the theories differ on major points, where the first key difference concerns their anatomical predictions regarding consciousness in the brain. GNWT, as the leading theory, emphasizes the relationship between consciousness and cognitive processing, and in an explanation of this relationship includes thalamo-cortical projections (Dehaene & Changeux, 2011). Yet, the thalamo-cortical system plays a minor role in GNWT compared to the cortical fronto-parietal broadcasting system emphasized in GNWT (Dehaene & Changeux, 2011). On the other hand, RPT is a “purely” cortical theory (Lamme, 2006), and HOT emphasizes that consciousness crucially relies on the PFC (Lau & Rosenthal, 2011). GNWT and HOT relate consciousness to anterior areas of the brain, while RPT relates it to posterior sensory areas in the front-versus-back of the brain (Boly et al., 2017; Gennaro, 2018). HOT emphasizes activity in the PFC as necessary for the higher-order state of consciousness, as prefrontal areas are implicated in higher cognitive or metacognitive processes (Lau & Rosenthal, 2011). Lau and Rosenthal (2011), in particular, propose that the dorsolateral and polar regions of the PFC play key roles in conscious experience. By adding the ventrolateral PFC to their model, they were able to generalise the model to the other senses, as it was at first based solely on visual perception.

Even though HOT emphasises the role of the PFC in consciousness and forming conscious content, the theory remains slightly more open to the interpretation of the exact role of the PFC in consciousness (Brown et al., 2019). In their opinion piece, Brown and colleagues (2019) suggest that the original model for higher-order thought might too narrowly focus on some areas of the PFC. A wider, more complete model may also include medial and insula prefrontal areas. Alternatively, they propose the higher-order network might in fact extend beyond the PFC to more posterior areas of the parietal and temporal lobes. So, while HOT heavily implicates the PFC in the higher-order network and conscious experience, the theory proponents are slightly more flexible in their view of the PFC's role, and how closely consciousness is in fact linked to the PFC alone. Moreover, HOT proponents disagree on what the PFC contributes to consciousness. Koch (2019) has even argued completely against any constitutive involvement of the PFC in consciousness based on findings from patients with partial lesions to the PFC.

GNWT and HOT both rely on studies of activity in the PFC (Dehaene et al., 2006; Rosenthal, 2005). In contrast, RPT argues that the PFC is not sufficient or necessary for consciousness, rather suggesting that conscious content is based on a local sensory system. More specifically, it suggests the underlying process of phenomenal consciousness is connected to local recurrent processing, while widespread processing in motor and frontal regions may correlate with access consciousness (Lamme, 2006). In summary, RPT finds local sensory regions and their integration of signals to be sufficient for consciousness, while GNWT highlights fronto-parietal communication and global ignition in the workspace, or non-linear network ignition, in the brain as necessary for a conscious experience.

Here, as explained earlier, DIT finds a cellular basis for regulating the conscious experience in the fifth cortical layer pyramidal neurons and their dendrites (Aru et al., 2021). DIT does not focus per se on specific regions of the neocortex to investigate consciousness, but rather bridges two long-standing perspectives on the neural mechanisms of consciousness by proposing that cortical and thalamo-cortical processing interact at the level of single cortical pyramidal cells (or single column) generate conscious experience (Bachmann et al., 2020).

Another key difference between the theories is how they view the functions of consciousness. GNWT views consciousness as essential for executive functions such as flexibility or the integration of information. This relates to how the theory anatomically places consciousness in anterior areas of the brain including the PFC, and the PFC is typically correlated with executive functions (Baars et al., 2013; Yuan & Raz, 2014). Here, consciousness is found to be essential not only for bringing items into awareness, but also for being able to report on those items. RPT, on the other hand, relates consciousness to perceptual awareness, where perceptual organisation is mediated by recurrent cortico-cortical connections (Lamme, 2010).

GNWT also suggests that attention is necessary for consciousness (Dehaene et al., 2006), whereas other theories such as the RPT do not (Lamme, 2006). This claim has been supported by studies using change blindness, a phenomenon where changes in stimuli are undetected even though they are actively searched for (Beck et al., 2001). RPT, in contrast to the GNWT, argues for the independence of consciousness from attention, access, or report. RPT addresses the issue of report specifically, suggesting that consciousness and reportability should be viewed as entirely independent (Block, 2007).

Accordingly, proponents of RPT suggest that (visual) consciousness should not be equated with access, report, or metacognition (Tsuchiya et al., 2015). RPT, as opposed to GNWT or HOT, proposes that consciousness is created in localised recurrent processing, which leads to perceptual integration and therefore consciousness. Accepting localised recurrent processing as a marker of consciousness implies that we can be conscious of a stimulus without the ability to introspect about our conscious perception of the stimulus (Billeke et al., 2020; Silvanto et al., 2007). Rather, we can to an extent be conscious without the understanding that we are conscious of the stimulus. The relationship between consciousness and attention is a currently highly debated topic, and how it is viewed differs significantly between the dominant consciousness theories (van Boxtel et al., 2010).

Higher-order theorists propose that attention enhances the way we are aware of our perceptual experiences. HOT proponents, therefore, also do not place an emphasis on attention for consciousness, despite the temptation for one to say that some attention is needed for higher-order awareness to form (Rosenthal, 2012). Instead, newer research finds ample evidence of a double dissociation between attention and the mental states' being conscious, at least according to HOT proponents (van Boxtel et al., 2010; van Gaal & Fahrenfort, 2008).

HOT proposes that "attention occurs in connection with states that are not conscious and is absent with many states that are conscious" (Rosenthal, 2012), thus suggesting that attention is not directly necessary for consciousness. Rosenthal (2012) additionally argues that, for example, many peripheral visual states are conscious even though they are seemingly unattended to.

The theories, mainly RPT and HOT, also attempt to relate consciousness to top-down processes of meaning and prediction (Lamme, 2018). Theories of consciousness should offer a way to explain why conscious experience is determined by the synergy between top-down and bottom-up information flow. One of the main findings of the last decade of research is how prior information holds a pervasive effect in processing new, incoming information by facilitating prediction in conscious perception (Samaha et al., 2015). In this sense, expectation manipulates conscious experience: in fact, the expectation that a stimulus will occur can create the experience of a stimulus even when it is not present, suggesting that top-down effects strongly influence perception (de Lange et al., 2018).

DIT is conceptually most similar to RPT (Lamme, 2006) since both theories have dual-stream architecture, although it can also relate to HOT if the streams are conceptualised as a first-order and higher-order stream. RPT has a "two-stream feedforward and feedback activity" architecture, while DIT focuses on cellular activity specifying how the two streams interact on the level of single L5p neurons that connect apical and basal streams. We can also conceptualise these two streams as the first-order representation – the basal compartment (bottom-up), or the higher-order representation in the apical compartment (top-down) when relating DIT to the HOT theory (Aru et al., 2023).

Crucially, the integration of cortical and thalamic structures in DIT relate to the integration of state and content consciousness. Thalamo-cortical loops relate to state consciousness, while cortico-cortical loops relate to content consciousness (Aru et al., 2019). As DIT includes both thalamo-cortical and cortico-cortical loops and shows how they are coupled or integrated in the fifth cortical layer, the theory directly integrates state and content consciousness. Two distinct subpopulations of neurons may exist in the fifth cortical layer where it seems that the neurons in the upper part of the fifth layer (L5A neurons) are more involved in cortico-cortical loops, while the neurons in the lower part of the fifth cortical layer (L5B neurons) are more involved in thalamo-cortical loops (Aru et al., 2019). Relating to conscious state, research has shown that anaesthesia, for example, specifically affects the apical dendritic compartment of the L5p cells (Phillips et al., 2019). It was long previously suspected that these cells form, at least to an extent, the basis of consciousness, and the integration of inputs from cortico-cortical loops in the upper part of the layer with the integration of input from thalamo-cortical loops from the lower part of the layer forms the basis of merging conscious content (relating to cortico-cortical loops) with conscious state (relating to thalamo-cortical loops).

As mentioned, measurement procedures also differ between studies, where some studies use subjective measures while others tend to use objective (Overgaard et al., 2010). This preference is mainly based on the views of the authors (as proponents of different theories) on access compared to phenomenal consciousness. Namely, if the authors place emphasis on phenomenal consciousness as the “true” consciousness, they will deny that reportable, subjective measures probe “true” consciousness. For example, the RPT denies that reportability has much to do with consciousness (Lamme, 2006). On the other hand, a focus on access consciousness such as that in GNWT holds reportability as an essential component of conscious experience (Odegaard et al., 2017).

It is an open question whether null findings in studies of prefrontal theories of consciousness can falsify the claims of these theories (Odegaard et al., 2017). While the literature seems to highlight the essential role of the PFC in enabling a subjective perceptive experience, conflating it with the objective capacity to perform visual tasks can be a source of confusion. For instance, critics of the PFC theories claim that activity in the PFC in studies of conscious perception does not reflect conscious perception per se but is rather confounded by the task demand to report the stimulus (Koch et al., 2016; Tsuchiya et al., 2015). Recent studies have found null findings for PFC activity when subjects were not required to make explicit reports (Frässle et al., 2014; Pitts et al., 2018; Tsuchiya et al., 2015).

Odegaard and colleagues (2017) emphasise how the recent excitement over no-report paradigms as a way to falsify PFC theories may be misguided, as PFC activity in conscious perception has, according to the authors, already survived such tests. In general, Odegaard and colleagues (2017) argue that for all criticisms of studies of the PFC in conscious perception, individual null findings for one measure, even if true, do not generalise to other measures. A similar discussion regards lesion patients and their role in investigating whether the PFC is essential for generating conscious experience. Individual case studies are often problematic because of incomplete documentation and limited data (Odegaard et al., 2017). Yet, recent research (Del Cul et al., 2009; Fleming et al., 2014) has investigated how PFC lesions, sometimes even incomplete, seem to impact subjective perceptual experiences in representative patients with PFC lesions, with a pronounced effect on their subjective ratings of objects or experiences.

Overall, the architecture of consciousness comprises different neuronal signals from specific regions of the neocortex, and GNWT, RPT, and HOT primarily differ on how they view the dynamics and architecture of neural signals and how these neural signals propagate over the cortex. RPT emphasizes the role of the occipital cortex (the primary visual regions), while GNWT focuses on the parietal cortex, and HOT finally highlights the essential communication between the parietal and prefrontal cortices. DIT does not focus on specific areas of the cortex (e.g., the occipital, parietal, or prefrontal regions), but rather sees consciousness as arising from the integration of pyramidal neurons of the fifth cortical layer. While the other theories speak of the activity of signals and cortical pathways in specific areas of the cortex, DIT highlights thalamo-cortical signals in addition to cortico-cortical signals as necessary for generating consciousness (Aru et al., 2020).

Unfortunately for consciousness research, conscious state is most often studied separately from conscious state (Bachmann & Hudetz, 2014). As mentioned, state consciousness research mainly revolved around the thalamus and thalamo-cortical interactions (see reviews by Alkire et al., 2008; Laureys et al., 2005; and Schiff, 2007). In contrast, the search for the correlates of conscious content in the brain mostly focuses on cortical processing (see reviews by Rees et al., 2002; and Koch et al., 2016).

We will now more generally expand upon how DIT may complement the other theories. In general, DIT reconciles the traditional separation between content and state consciousness, as well as cortex-based compared to thalamo-cortical foundations of consciousness (Bachmann et al., 2020). While it has long been known that the cortex may "encode" the content of consciousness and content experience, state consciousness has been omitted from discussions. Moreover, prior research also suggests the thalamus, and connections between the cortex and the thalamus, are essential to generate conscious experience and integrate both content and state consciousness (Bachmann et al., 2020). For example, whether the brain is asleep or awake depends on non-specific pathways from the thalamus to the cortex (Aru et al., 2020). The idea that certain thalamic nuclei affect how information is integrated in single cortical neurons highlights how tight this coupling is between the thalamus and the cortex. Cortical layer 5 pyramidal neurons are central in both cortico-cortical and thalamo-cortical loops (Bachmann et al., 2020). In this sense, they effectively couple the two loops, and bridge the gap between the cortex and the thalamus, highlighting that the thalamus is far more than just a relay station for sensory input as it travels to the cortex.

As discussed, the difference between non-conscious and conscious states in DIT is found at both the thalamic and the cortical levels. Every theory that suggests that conscious state and conscious content interact in the brain should be able to answer two key questions. First, why are conscious state and content so closely related? DIT answers that this is because the two phenomena are interwoven on the level of L5p neurons (and individual cortical columns). According to Bachmann and colleagues (2020), the thalamo-cortical and cortico-cortical loops intersect at the cortical layer 5 pyramidal neurons, and the coupling mechanism is found within single pyramidal neurons. In a conscious state, signals propagate from the apical compartment to the somatic one, whereas this propagation does not occur in non-conscious states. The propagation relates to how consciousness is considered continuous by the DIT: even though the combination of L5p neurons that participate in conscious experience changes, the integration that happens with these neurons is always supported by the non-specific pathway of the thalamus (Bachmann et al., 2020). Moreover, DIT considers conscious experience to always be integrated. The thalamus here is in the central position to integrate the various aspects of processing that occur at different nodes in the cortex. Here, DIT can more closely relate to the other theories of consciousness, as it highlights the role of the thalamus, and the thalamus is densely connected to all areas of the cortex both within and between specific regions (Sherman & Guillery, 2001).

The second key question concerns unconscious processing of conscious content (as 90% of cognitive processes are thought to be unconscious), i.e., how does unconscious content arise in conscious states? Cognitive processing of mental information can be in the subliminal mode, as not all sensory signals that are correctly encoded and adequately responded to reach conscious perception, i.e., are consciously experienced. In fact, conscious experience only has access to a specific level of representation or computation while other levels are completely inaccessible to consciousness. When we speak or write in sentences, we do not have a conscious experience of how our brain constructs the sentences, selects words, or orders them correctly in the sentence with the correct grammatical formulation. Conscious experience is constrained to specific contents and specific computations. DIT emphasizes the natural neurobiological explanation that unconscious processing is tied to subcortical and cortical processing that does not include L5p neurons. Why does conscious content depend on conscious state? It is thought this is because the processes in thalamo-cortical and cortico-cortical networks are mechanistic in the interactions on the level of L5p neurons, which functionally corresponds to the integration and entanglement of state and content consciousness. Here, DIT has a theoretical potential to reconcile and integrate thalamo-cortical and cortico-cortical theories of consciousness since L5p neurons influence both thalamo-cortical and cortico-cortical processing (Aru et al., 2019).

As DIT theorists themselves point out, it is difficult to study state and content consciousness separately since they are exceptionally intertwined and interconnected as concepts. The intertwinement of state and content consciousness is often inadequately tackled or even ignored in other major theories of consciousness, as the theories focus on either state or content consciousness and probe one or the other in their experimental paradigms. We therefore posit that DIT is a key theory to supplement but also integrate the other consciousness theories to better integrate state and content consciousness and, through that, to generate a better understanding of consciousness overall. The missing component in other theories has also been the neurobiological, cellular level to the understanding of consciousness. DIT complements other theories of consciousness by providing an explanation on the cellular level as well. Namely, for example, GNWT suggests that consciousness arises when information is shared and integrated across multiple brain regions. DIT then adds to the theory by proposing that the dendritic processing and integration of information on the level of the L5p neurons plays a critical role in creating the global workspace. As mentioned and discussed, DIT complements other theories of consciousness by providing a framework for understanding how conscious experience is generated at the level of individual neurons. It thus provides a more detailed understanding of the micro-level neural processes that contribute to consciousness (Aru et al., 2023).

Finally, we want to highlight how the neuroscience of consciousness is as a field, as evident from the competing theories, highly fractionated, and this influences the allocation of funding, as well as biases in research. There are not a lot of collaborators or mutual influences between the theories (Yaron, 2022). Each consciousness theory seems to support itself, with little crosstalk between the theories. Moreover, there seems to be a confirmatory bias, where new articles about a theory tend to support rather than challenge it (Yaron, 2022). This may also be a consequence of the field being relatively young. Evidence for limited cross-talk also comes from the fact that the success of one theory does not seem to affect the success of another. In other words, the growth in popularity or citations of one theory does not seem to influence how popular or cited the other dominant theories are (Yaron, 2022).

The evident lack of consensus in consciousness research has led some philosophers to even argue, somewhat radically, that the pursuit to tackle consciousness in scientific research should be completely abandoned (Irvine, 2012). Some philosophers have claimed that, by evaluating historical and contemporary research into consciousness, consciousness does not seem to be a viable scientific concept (Irvine, 2012). In contrast, in 2019, a large group of influential consciousness researchers published a commentary on the opportunities the maturing science of consciousness has now, and those it may bring in the future (Michel et al., 2019). The commentary highlights how scientific research on consciousness is indispensable, and that consciousness research has already made significant contributions to science, including for clinical applications or biomedical research. Despite the lack of consensus on a theory, findings in consciousness research have had many positive practical consequences or implications, including in medical, legal, and ethical issues. These translational applications include not only neurological disorders such as vegetative state patients, but also psychiatric disorders including anxiety (Michel et al., 2019). Thus, while it may seem like a frustrating pursuit, consciousness research, as a young field, may be important to keep and pursue.

Conclusion

While there are multiple theories of consciousness, cognitive and neurobiological research cannot seem to confirm any one theory unambiguously or unanimously for now. Moreover, the possibility for unanimous agreement over one of the current contemporary dominant theories among researchers seems limited given the fractioned state of the consciousness research field.

In this review article we propose that the three currently most popular theories of consciousness should, at least to an extent, integrate their findings with DIT for its cellular that provides a neurobiological perspective on consciousness research, as well as bridging state and content consciousness at the cellular level. DIT more specifically focuses on the neurobiological thalamo-cortical mechanisms of consciousness, where this complex interplay between the cortex and the thalamus may complement the other three theories as they mostly focus on different areas of the cortical surface when examining consciousness in the brain. Crucially, DIT is concerned with the integration of conscious state and content, emphasizing that these phenomena are incredibly related on a neurobiological, cellular basis. It examines these phenomena in tandem rather than separately. We posit that DIT tackles and integrates conscious state and content in a more convincing way compared to the other theories of consciousness, which is why we consider DIT as an important theory in and for the future of consciousness research.

Regardless of how and whether this integration of DIT with the other dominant theories will take place, and in spite of the fractioned nature of the field, researchers seem to agree on one thing: despite all frustrations and limitations, consciousness is worth researching, and a better understanding of consciousness through a more integrated theory is worth pursuing.

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Teorija dendritičke integracije kao stanični most za dominantne suvremene teorije svijesti

Sažetak

Svijest se često opisuje kao posljednja granica u znanosti kojom se bavi više disciplina, uključujući filozofiju, neuroznanost i informatiku. Svijest se najčešće definira kao ono što postoji iz perspektive prvoga lica, kao osjećaj kako je to biti nešto, kao i kroz neuronske mehanizme koji stvaraju i podržavaju tu fenomenologiju. Postoje nebrojene teorije o svijesti koje pokušavaju razjasniti taj složeni fenomen. Cilj je ovoga pregleda ispitivanje triju dominantnih teorija svijesti – teorije globalnoga neuronskoga radnog prostora (GNWT), teorije rekurentne obrade (RPT) i teorije višega reda (HOT), te teorije dendritičke integracije (DIT) kao novije, manje istaknute teorije koja se usredotočuje na staničnu osnovu svijesti. Predlažemo da DIT može dopuniti pretpostavke ostalih triju teorija kroz svoj stanični pristup koji premošćuje svijest o stanju i sadržaju. Nakraju se raspravlja o budućnosti istraživanja svijesti općenito.

Ključne riječi: teorija svijesti, GNWT, RPT, HOT, DIT

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