Beyond the Feedforward Model: Towards a Richer Understanding of Visual Perception

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Abstract

Understanding conscious visual perception remains one of neuroscience's central challenges. While traditional models of vision emphasize feedforward processing, growing empirical and theoretical evidence suggests that this model is insufficient to account for the richness, flexibility, and subjective nature of conscious experience. Conscious vision emerges not from sequential processing of sensory inputs but from dynamic, recursive interactions between bottom-up signals, top-down feedback, and intrinsic brain activity. Recurrent processing is essential: conscious experience involves resolving ambiguity, integrating contextual information, and incorporating prior knowledge, all of which unfold over time and require feedback activity. Additionally, spontaneous neural activity prior to stimulus onset — including oscillatory and aperiodic neural activity — shapes perceptual outcomes. Hallucinations, in which internal models dominate perception in the absence of sensory input, are an interesting case study that underscores the generative and constructive nature of visual consciousness. Finally, although deep neural networks (CNNs) have demonstrated remarkable performance in object recognition tasks, computational models capable of capturing the abilities and features of conscious vision remain lacking. Together, these insights converge on a view of conscious vision as an emergent property of recursive, predictive, and contextually embedded neural dynamics, thus demanding a new generation of computational models to bridge human and computer vision that integrate recurrence, spontaneous activity, and biologically grounded principles.

Introduction

Our understanding of visual perception has long been dominated by the feedforward paradigm: a cascade of processing steps beginning with retinal input and ascending through increasingly complex cortical hierarchies, operating passively as a function of the strength of incoming stimuli. This framework has garnered substantial empirical support: fMRI and electrophysiological studies show that early visual areas (V1–V4) respond robustly and predictably to stimulus features like contrast, edges, and spatial frequency, which is consistent with a feedforward cascade that extracts increasing levels of abstraction from raw inputs (Felleman and Essen, 1991; DiCarlo and Cox, 2007). Moreover, MEG and EEG studies reveal that object categories can be decoded from brain activity as early as 150 ms post-stimulus, a timing that is consistent with rapid, bottom-up processing (Cichy et al., 2014). Further support comes from deep convolutional neural networks (CNNs), which are explicitly based on feedforward architectures and achieve remarkable performance in object recognition tasks (DiCarlo et al., 2012; Kheradpisheh et al., 2016). These findings build on classic neurophysiological work demonstrating feature selectivity in V1-V4 (Hubel and Wiesel, 1968) and are complemented by more recent MEG/EEG decoding studies showing early object representations across the visual hierarchy (Carlson et al., 2013; Clarke et al., 2015).

However, while the feedforward model has been highly successful in accounting for rapid visual categorization and low-level feature processing, it fails to capture core aspects of conscious visual experience – such as perceptual illusions, context-dependent interpretations, and the dynamic integration of prior experience (Yuille and Kersten, 2006; Ayzenberg and Behrmann, 2022). These limitations have prompted a shift away from purely feedforward models toward frameworks that view perception as an active, inference-driven process shaped not only by incoming sensory data, but also by internally generated signals. These include top-down influences such as prior knowledge and expectations — formed over a lifetime or acquired from a single exposure — as well as the contribution of spontaneous neural activity ongoing before stimulus onset. Together, these processes suggest that perception is not a passive reflection of the external world, but an active construction shaped by both the past and the brain's internal dynamics. This chapter will explore the experimental findings and theoretical advances that call for a more dynamic and generative understanding of vision.

Beyond Feedforward: Conscious Vision Requires Recurrent and Top-down Processing

Building on the feedforward model, recent work emphasizes that additional computational mechanisms are necessary to account for the full richness of visual perception. Conscious experience demands more than rapid categorization; it requires the flexible interpretation of ambiguous inputs, the resolution of conflicting information, and the incorporation of context and prior expectations, all of which unfold over time and vary with internal brain states. For instance, phenomena such as perceptual filling-in, bistable perception, and the modulation of sensory processing by attention suggest that perceptual representations are not dictated by incoming stimuli alone but instead are dynamically constructed and maintained. These observations point to the essential role of recurrent processing – the ongoing exchange of information between different levels of the visual hierarchy – as well as top-down influences that modulate sensory processing based on prior knowledge, goals, and predictions. Understanding how these recurrent and top-down mechanisms interact with feedforward streams is thus crucial for developing a more complete theory of conscious vision.

Empirical studies increasingly support the centrality of recurrent processing in conscious vision. Neurophysiological recordings reveal that activity within early visual areas, such as primary visual cortex (V1), does not simply reflect bottom-up stimulus-driven inputs, but is modulated by feedback from higher-order areas over time. For example, laminar recordings in macaque V1 show that early stimulus-evoked responses are dominated by feedforward inputs to granular layers, whereas later activity reflects feedback arriving in superficial and deep layers (Self et al., 2019).

Moreover, disrupting recurrent interactions – such as by masking stimuli shortly after presentation – selectively impairs conscious report without abolishing early sensory responses (Lamme and Roelfsema, 2000). In another approach, paired-pulse TMS was used to probe the causal role of feedback in conscious motion perception (Pascual-Leone and Walsh, 2001). Phosphenes were induced with the first TMS pulse in motion-sensitive area V5 (MT) and then a second TMS pulse was applied over V1 at varying delays relative to the V5 stimulation. Disruption of phosphene perception occurred when V1 was stimulated 5 to 45 ms after V5, suggesting that feedback from V5 to V1 is critical for the conscious experience of motion. This experiment demonstrates that although initial activation of higher visual areas may encode motion signals, recurrent feedback to early visual cortex is required for these signals to enter conscious awareness. Other studies using TMS or lesion methods have similarly demonstrated the necessity of feedback for conscious perception (Silvanto et al., 2005; Fahrenfort et al., 2007), and electrophysiological work in macaques shows that feedback signals from higher-order areas contribute to shape and object recognition in early visual cortex (Hupé et al., 1998; Bullier et al., 2001).

Together, these findings suggest that while initial feedforward sweeps rapidly convey basic feature information, recurrent processing is critical for integrating features into coherent percepts, resolving ambiguities, and stabilizing perceptual representations over time. Importantly, recurrent interactions are not confined within local circuits but often span long-range connections, linking early sensory cortices with higher-level regions. These top-down signals are not merely general modulators of neural activity, but instead convey specific predictions and learned expectations that shape how incoming sensory inputs are interpreted, and thus influence the content of conscious perception. The next section explores how such knowledge, accumulated over time, or formed on the fly, systematically guides the interpretation of incoming sensory data.

Prior Knowledge

Our understanding of how prior knowledge influences perception provides compelling evidence for the essential role of top-down feedback. Prior knowledge and experiences, acquired both over a lifetime and in the moment, systematically guide the interpretation of sensory inputs, allowing perception to be faster, more efficient, and generally more successful. This view echoes the classic proposals of Helmholtz (1925) and Gregory (1997), who emphasized vision as an inference process guided by prior knowledge.

First, long-term priors become embedded into the synaptic architecture of visual pathways through repeated exposure to stimuli over time, which in turn biases how new stimuli are perceived. For instance, in bistable perception, participants are shown ambiguous stimuli, such as the Rubin face-vase image and the Necker cube, which can be perceived in more than one way (Leopold and Logothetis, 1999; Sterzer et al., 2009). For each ambiguous image, the percept that a participant reports seeing for a greater proportion of time is considered their 'preferred' percept and reflects the individual's long-term priors. A recent study, using intracranial recordings from neurosurgical patients, found that the 'preferred' percept was associated with increased top-down feedback from higher-order temporal regions to lower-order occipital visual areas (Hardstone et al., 2021). Conversely, perceptions incongruent with their typical preference elicited stronger feedforward signals. This study further demonstrated that a computational model incorporating long-term priors, implemented as biases in higher layers, exhibited to increased top-down predictions during preferred percepts and heightened bottom-up prediction errors during non-preferred percepts, mirroring the empirical observations. The observed modulation of perception by long-term priors through feedback mechanisms emphasize the critical role of top-down processes in shaping perceptual experience and highlight perception as a dynamic interplay between incoming data and prior knowledge.

Second, one-shot perceptual learning refers to the remarkable ability of the brain to form lasting changes in perception after a single exposure to a stimulus. Mounting evidence from recent studies on this phenomenon challenges traditional feedforward-dominant models of visual perception and suggests the critical role of top-down feedback in shaping conscious experience. A well-established paradigm used to study how prior experience shapes perceptual processing is the Mooney image paradigm (Mooney, 1957). Mooney images are black-and-white degraded images that are, at first, difficult to recognize. Yet, once a subject is exposed to the original, non-degraded grayscale image (a process called 'disambiguation'), their recognition of the corresponding Mooney image becomes effortless, and this effect can last for days to months, or even a lifetime (Albright, 2012), demonstrating that experience can shape perception in a remarkably fast and robust manner. What is striking about this phenomenon is that an identical visual stimulus input results in distinct perceptual outcomes depending on whether a perceptual prior is available (Hsieh et al., 2010). A whole-brain 7T fMRI study found that after the encoding of perceptual priors via disambiguation, Mooney images were represented more differently from each other, and more similarly to the grayscale images that had induced the perceptual priors (González-García et al., 2018). This was the case throughout the cortical hierarchy, from early visual areas to frontoparietal and default-mode networks. The perceptual priors induce a gradient of sharpening effects along the cortical hierarchy: higher-order frontoparietal regions enhance predicted content, while visual cortices exhibit suppressed responses to unexpected inputs (Gonzalez-Garcia and He, 2021). A follow-up study combining fMRI and MEG further revealed that, after prior knowledge has been learnt, recognition-related activity involves a feedback wave from ventral temporal and frontoparietal areas into early visual cortex (Flounders et al., 2019). Together, these studies establish the critical role of top-down feedback processes in shaping conscious visual experience in combination with bottom-up feedforward sensory processes.

In addition to long-term and one-shot priors, intermediate forms of expectation also provide converging evidence that feedback activity from higher-order cortical areas plays a central role in shaping conscious visual perception. A key line of evidence comes from a phenomenon known as prediction suppression, in which predicted stimuli elicit attenuated activity relative to unpredicted stimuli (Summerfield et al., 2006; Summerfield and Koechlin, 2008). For instance, an fMRI study demonstrated that expected stimuli evoke reduced neural responses in category-selective regions of visual cortex (Summerfield et al., 2008). Crucially, when repetitions were expected, neural responses in the fusiform face area (FFA) were attenuated, but when repetitions were unexpected, this suppression was diminished, indicating that top-down expectation influenced sensory processing. Beyond response attenuation, other findings show that prior expectations increase the precision of stimulus-specific representations in early visual areas. In one study, orientation expectations were manipulated while participants viewed gratings. Although expected orientations elicited lower overall BOLD responses in V1, multivariate pattern analyses revealed enhanced orientation selectivity, indicating that expectations sharpen sensory representations, improving signal fidelity without increasing neural gain (Kok et al., 2012). Converging evidence from neuroimaging further shows that contextual information enhances responses in higher-order areas while reducing activity in lower-level visual cortex, consistent with hierarchical models of predictive processing (Murray et al., 2002). These findings align with longstanding theoretical accounts that emphasize perception as an inference process shaped by top-down knowledge (Gregory, 1997) and more recent predictive coding formulations in which prior expectations modulate sensory processing by minimizing prediction error (Rao and Ballard, 1999; Friston, 2005). Taken together, these results indicate that feedback activity is integral to constructing ongoing conscious perceptual experience. More broadly, these findings complement classic work on attention and orienting (Posner, 1980; Kastner and Ungerleider, 2000) and fit with recent ideas highlighting how prior knowledge and expectation guide perceptual decision-making through hierarchical feedback mechanisms (Summerfield and de Lange, 2014).

Visual Illusions

Although the feedforward model has been highly successful in explaining certain aspects of visual processing, such as rapid categorization and low-level feature extraction, it largely fails to explain perceptual illusions. Perceptual illusions such as the Müller-Lyer or Kanizsa figures demonstrate that our visual system is highly influenced by spatial and temporal context, and these effects cannot be explained by a straightforward, bottom-up flow of information (Zipser et al., 1996).

In the Müller-Lyer illusion, the same physical lines are perceived as having different lengths depending on the surrounding arrows, an effect that requires the integration of surrounding context with the perception of the central stimulus. An fMRI study of the effect showed that viewing the illusion activated both lateral occipital cortex (LOC) and the right superior parietal lobule (SPL), with dynamic causal modeling suggesting that models where the strength of bidirectional connectivity between LOC and SPL was modulated by the strength of the illusion (Weidner and Fink, 2007). Thus, SPL, which is involved in spatial cognition, might send feedback to LOC to modify the percept based on the spatial context.

Similarly, in the perception of Kanizsa figures, observers report seeing illusory contours though no corresponding edges exist, an effect that requires the integration of contextual information. A study combining electroencephalography (EEG) with transcranial magnetic stimulation (TMS) provided evidence that recurrent feedback is necessary for this phenomenon (Wokke et al., 2013). Early neural responses (<100 ms) to illusory contours were similar to those evoked by real contours, reflecting initial feedforward processing. However, at later stages (~200 ms), responses specific to illusory contours emerged, a timing consistent with recurrent interactions. Critically, when TMS was applied over early visual cortex (V1/V2) around 100–135 ms after stimulus onset — targeting the presumed time window of feedback — the perception of illusory contours was selectively disrupted, whereas earlier TMS (at ~80–100 ms) had little effect. This temporal specificity suggests that the perception of illusory contours depends not merely on early feedforward signals but on recurrent feedback from higher-order areas to early visual cortex, supporting the integration of contextual information necessary for constructing the percept. Consistent with this, a study used population receptive field mapping to explore how Kanisza illusory shape perception modulates V1 activity (Kok and de Lange, 2014). The authors found that perceiving an illusory shape both enhances activity in V1 regions representing the missing shape and suppresses activity in regions where bottom-up input conformed to prediction. This bidirectional modulation supports the idea that feedback amplifies activity where input is absent and dampens it where input is as expected. A follow-up 7T fMRI study further demonstrated that predictive effects preferentially recruit deep layers of V1, consistent with the anatomical profile of feedback pathways. Specifically, illusory Kanisza shape perception produced selective activation in the deep layers of V1, whereas bottom-up stimulation activated all layers, most strongly the middle and superficial ones, consistent with feedforward processing (Kok et al., 2016). Together, these findings support a model in which the brain constructs illusory percepts through top-down signals that modify activity in early sensory areas to reflect not just the physical input, but the inferred structure of the visual scene.

Another class of illusions that speaks directly to the mechanisms of conscious access is figure-ground segregation. Work by Lamme and colleagues has shown that while early visual cortex encodes local features in a largely feedforward manner, the conscious perception of figure-ground relationships depends critically on recurrent interactions between higher-order and early visual areas (Lamme and Roelfsema, 2000; Lamme, 2006). For example, V1 neurons respond differently to identical local inputs depending on whether they are part of the figure or the background, an effect that emerges relatively late in the response and is abolished when recurrent processing is disrupted. Thus, figure-ground stimuli provide a particularly clear demonstration that recurrent processing is essential for conscious perception, transforming initial feature maps into percepts of coherent objects.

In sum, while top-down feedback has traditionally been studied primarily in the field of selective attention, a wealth of findings now suggests that top-down feedback carrying the influences of prior knowledge—acquired both over a lifetime and in the moment—plays an enormous role in shaping conscious vision. Thus, a framework of visual perception needs to incorporate feedback, recurrence, and context to fully account for the quality of conscious experience.

Limitations of Feedforward Models: Importance of Spontaneous Activity

In addition to top-down feedback, spontaneous brain activity plays a fundamental role in shaping conscious visual experience. Several early fMRI studies demonstrated that pre-stimulus brain activity influences conscious visual perception. One study showed that spontaneous pre-stimulus BOLD fluctuations in visual cortex predicted which interpretation of an ambiguous visual stimulus participants perceived, indicating that ongoing local brain activity biases perceptual outcomes (Hesselmann et al., 2008). Other studies revealed that spontaneous fluctuations in large-scale brain activity, including in the default mode and attentional networks, can shape perceptual outcomes across sensory modalities (Boly et al., 2007; Sadaghiani et al., 2009). More recent work using EEG and MEG has offered additional insights into the spontaneous neural dynamics that predict whether a stimulus will enter conscious awareness. Two prominent signatures have emerged: the power and phase of pre-stimulus oscillations, particularly in the alpha (8 – 12 Hz) and beta (13 – 30 Hz) ranges, and aperiodic, low-frequency slow cortical potentials (SCPs).

Oscillations

Spontaneous alpha oscillations, especially over occipital cortex, have been robustly linked to perceptual thresholds: lower pre-stimulus alpha power is associated with increased likelihood of detecting near-threshold visual stimuli (van Dijk et al., 2008; Mathewson et al., 2009; Hanslmayr et al., 2013; Samaha et al., 2020; Iemi et al., 2021). This effect is thought to reflect changes in cortical excitability (Bollimunta et al., 2011; Haegens et al., 2015) and is modulated by both endogenous attentional fluctuations (Worden et al., 2000; Thut et al., 2006; Voytek et al., 2017) and neuromodulatory influences related to arousal, such as noradrenergic and cholinergic tone, which can alter how incoming sensory signals are processed and prioritized (de Gee et al., 2014; Gelbard-Sagiv et al., 2018; Johnston et al., 2022).

Samaha et al. (2020) reviewed and extended this body of work by combining meta-analytic and empirical approaches. They confirmed that pre-stimulus alpha power not only predicts whether a stimulus will be detected, but also influences subjective confidence – the degree to which individuals feel certain about their perceptual judgments. Crucially, this relationship holds even when objective performance, defined as the accuracy of the perceptual decision, remains unchanged. This dissociation was originally demonstrated in a study that showed that lower alpha power prior to stimulus onset increased confidence ratings without affecting discrimination accuracy (Samaha et al., 2017). Similarly, another study found that alpha power modulates sensory gain, or the amplitude of early sensory-evoked responses, thereby influencing the intensity of perceptual experiences regardless of actual stimulus content (Iemi and Busch, 2018). These effects also extend to metacognitive evaluation, or the ability to monitor and judge one's own perceptual decisions (Benwell et al., 2017; Wöstmann et al., 2019).

Though less extensively studied, beta oscillations have also been implicated in conscious perception, especially in contexts involving top-down attention, cognitive control, and decision processes. For instance, changes in selective attention have been associated with long-range phase synchrony in the beta band in the frontoparietal attentional network (Gross et al., 2004), resulting in more accurate target processing and suppressed nontarget processing in a visual task. Similarly, higher parietal beta power is predictive of the accuracy of perceptual choices (Donner et al., 2007). Beyond observational findings, causal manipulation using repetitive TMS at beta frequencies over the frontal eye field was shown to enhance conscious visual perception in a near-threshold task, supporting a functional role for beta oscillations in facilitating conscious access (Vernet et al., 2019). Moreover, pre-stimulus beta activity has been linked to the biasing of perceptual reports, particularly in tasks requiring maintenance of prior expectations or rule-based categorization (Engel and Fries, 2010; Arnal and Giraud, 2012). This supports the idea that beta may reflect an anticipatory top-down template that shapes the processing of incoming sensory input. For example, increased beta power has been associated with greater confidence in perceptual decisions (Wöstmann et al., 2019) and the stabilization of perceptual representations across trials (Spitzer and Haegens, 2017), pointing to a role in sustaining the internal context against which new stimuli are evaluated. These findings align with the broader notion that beta oscillations coordinate top-down influences over sensory cortices (Engel and Fries, 2010; Arnal and Giraud, 2012), allowing spontaneous or internally generated activity to modulate perceptual outcomes in a manner not predicted by feedforward processing alone.

Slow Cortical Potentials

Complementing these oscillatory markers are slow cortical potentials, which capture non-oscillatory fluctuations in neural excitability and are increasingly recognized as powerful predictors of conscious perception. SCPs reflect relatively slow (<5 Hz) shifts in the baseline voltage of the local field potential, thought to arise from the summation of synaptic activity across populations of neurons (Birbaumer et al., 1990; He and Raichle, 2009). These slow fluctuations thus effectively shape the neural context within which sensory inputs are interpreted.

Indeed, the phase and amplitude of SCPs prior to stimulus onset have been shown to modulate the detection and recognition of visual stimuli. Indeed, a study using whole-head MEG and a task utilizing low-level visual stimuli found robust single-trial decoding of seen versus unseen perceptual outcome only in the SCP band (Baria et al., 2017). Further, a follow-up study relying on the recognition of high-level visual stimuli also found that SCP activity was predictive of recognition outcome (Podvalny et al., 2019). Importantly, this study uncovered different types of spontaneous processes in the SCP band that influence conscious recognition in distinct manners — modulating detection criterion vs. sensitivity. The latter type of spontaneous SCP activity is correlated with moment-to-moment arousal fluctuations as indexed by pupil size fluctuations, while the former type is not linked to arousal. In this way, SCPs seem to serve as a dynamic backdrop that influences conscious visual perception by biasing the brain's responsiveness to external stimuli, thereby affecting both the likelihood of stimulus detection and the subjective clarity of perceptual experience. This coupling between SCPs and global brain dynamics underscores their critical role in bridging spontaneous neural activity and the moment-to-moment variations in conscious awareness.

SCPs have also been implicated in perceptual alternations in bistable visual perception, with recent work demonstrating that they allow the decoding of moment-to-moment content of perceptual experience (Hardstone et al., 2022). In contrast, alpha power was found to predict the duration of a given percept, thus reflecting its stability rather than its specific content. This double dissociation suggests distinct functional roles: whereas SCPs track what is perceived, alpha oscillations reflect how long a percept remains dominant. These findings underscore the importance of intrinsic neural dynamics not only in setting the overall excitability of sensory systems, but in shaping both the content and dynamics of conscious perception.

Building on the complementary roles of oscillatory activity and slow cortical potentials in shaping conscious perception, a recent study used magnetoencephalography (MEG) to investigate the relationship between SCPs and oscillations in their influences on conscious visual perception across two different near-threshold tasks involving both low- and high-level stimuli (Koenig and He, 2025). Specifically, large-scale pre-stimulus SCP activity, as well as alpha and beta oscillatory power, consistently predicted whether a stimulus was consciously seen or recognized, regardless of stimulus complexity. However, these perceptually-predictive signals were uncorrelated across trials, and their spatial and temporal patterns only partially overlapped, suggesting that SCPs and oscillatory power influence perceptual awareness through distinct and largely independent neural mechanisms.

Finally, although most of the studies discussed above were carried out in human subjects, recent neurophysiological work in non-human primates have also underscored the impact of pre-stimulus spontaneous activity on conscious perception. Van Vugt and colleagues (2018) showed that weak visual stimuli evoke early responses in V1 and V4 regardless of report, but only when these signals are amplified and sustained in dorsolateral prefrontal cortex, emerging around 100–200 ms after onset, do they reach conscious report. Importantly, this study also showed that pre-stimulus neuronal firing rates in V4 and dlPFC, as well as pre-stimulus power in the alpha and gamma frequency bands of the local field potential, predicted detection behavior including false alarms. These findings were interpreted in the context of the Global Neuronal Workspace (GNW) Theory, which focuses on the mechanism of conscious access and proposes that conscious access happens when feedforward activity (aided by suitable pre-stimulus brain states) crosses a nonlinear 'ignition' threshold and triggers amplification and widespread broadcasting of sensory signals through recurrent fronto-parietal networks.

Taken together, these findings reveal that the pre-stimulus brain states strongly shape whether and how stimuli are consciously perceived. They support a dynamical systems view of consciousness (He, 2023), in which internal neural context – structured by both oscillatory and aperiodic activity – interacts with external input to determine conscious experience.

When Perception Goes Awry: Hallucinations as A Case Study

Hallucinations offer a compelling case study for challenging feedforward models of conscious visual perception. Visual hallucinations can happen in a variety of psychiatric and neurological disorders, including schizophrenia, neurodegenerative disorders, and age-related macular degeneration. Hallucinations are vivid and involuntary perceptual experiences that occur in the absence of external stimuli or that do not match external reality. Their very existence demonstrates that conscious visual experiences can arise independently of external sensory input, though they may still engage bottom-up neural pathways activated by spontaneous or subcortical activity. As outlined above, our current understanding is that conscious visual perception relies on an interaction of sensory input and both prior knowledge and spontaneous neural activity in the brain. Below, we outline two frameworks that attempt to explain hallucinations, and they underscore the centrality of feedback processes and spontaneous brain activity in conscious visual perception.

One theory proposes that hallucinations occur when top-down prior knowledge exerts a disproportionate influence on perception (Powers et al., 2016; O'Callaghan et al., 2017; Parr et al., 2018; Corlett et al., 2019; Zarkali et al., 2019). Indeed, early psychosis and psychosis proneness were shown to both be associated with a basic shift in visual information processing which favored prior knowledge over incoming sensory evidence (Teufel et al., 2015). Similarly, Lewy body disease (LBD) patients who experienced hallucinations showed greater benefit from prior knowledge in a Mooney image disambiguation task compared to LBD patients who do not experience hallucinations and healthy controls, such that the degree of top-down influence measured by this behavioral task was predictive of hallucination severity (Zarkali et al., 2019). At the neural level, functional connectivity analyses revealed altered coupling between visual regions and the default mode network in hallucinators with LBD, implicating disrupted top-down modulation as a contributing factor (Firbank et al., 2024). In addition, a recent dynamic causal modeling study in these patients found reduced bottom-up connectivity from the lateral geniculate nucleus to visual cortex, alongside increased top-down connectivity from prefrontal to visual regions (Thomas et al., 2023). Together, these findings point to hallucinations in psychosis-related conditions as arising, at least in part, from a shift in the perceptual system's balance, favoring internally generated predictions over externally driven sensory input.

In other cases, spontaneous activity in early visual cortex appears to be the primary driver of hallucinations. This is illustrated in Charles Bonnet Syndrome (CBS), a condition in which individuals with peripheral visual degeneration (e.g., macular degeneration) experience vivid visual hallucinations. In these cases, it is proposed that damage to the sensory input pathways releases early visual areas from the constraints of feedforward input, allowing intrinsic cortical activity to dominate. Burke's (2002) deafferentation theory posits that loss of afferent sensory input leads to disinhibition and subsequent hyperexcitability of cortical circuits, triggering spontaneous perceptual experiences. Consistent with the deafferentation theory, the 'release from inhibition' hypothesis (Ffytche, 2007) suggests that in the absence of sensory input, early visual areas become disinhibited, and that this disinhibition results in spontaneous activity in early visual areas becoming unregulated, driving the emergence of hallucinatory percepts. Supporting these ideas, two studies scanned individuals with CBS using fMRI and observed a gradual build-up of spontaneous neural activity in early visual cortex and extrastriate visual cortex preceding the onset of hallucinations (Ffytche et al., 1998; Hahamy et al., 2021). This activity then propagated through the visual hierarchy, suggesting that, in the absence of external stimuli, internally generated fluctuations can activate the visual system to produce conscious visual experiences. In addition, patients with CBS exhibited a higher steady-state visual evoked response (SSVEP) amplitude than patients with macular degeneration but without CBS, or healthy controls, suggesting that their visual cortex might be hyper-excitable (Painter et al., 2018).

In sum, both feedback processes and spontaneous activity contribute to visual hallucinations. Hallucinations exemplify the broader principle that conscious visual perception arises from an interplay between bottom-up input, top-down predictions, and intrinsic cortical activity.

Deep Neural Networks (DNNs) as Models of Visual Perception

Deep convolutional neural networks (CNNs) provide strong evidence for the importance of feedforward pathways in visual processing. These models mimic the hierarchical structure of the ventral visual stream, where early stages encode simple features like edges and higher stages represent complex objects and categories (DiCarlo and Cox, 2007; DiCarlo et al., 2012). Despite the remarkable successes exhibited by feedforward CNNs in visual tasks such as object recognition and image classification, where they often achieve human-level performance on benchmark datasets like ImageNet (Krizhevsky et al., 2012), they struggle to explain recurrent and feedback-dependent phenomena which are central to conscious vision, such as visual illusions, masking, and figure-ground segmentation.

However, their strictly feedforward architecture imposes critical limitations when modeling human conscious vision. CNNs typically excel in scenarios where high-level object categorization can be computed directly from low-level image features but struggle with tasks involving context, ambiguity, or noisy inputs. For example, CNNs have been shown to rely disproportionately on texture information rather than shape, in contrast to human perception which emphasizes shape and contextual cues (Geirhos et al., 2018). This texture bias in CNNs illustrates the inadequacy of purely feedforward models to capture the rich, flexible, and context-sensitive nature of conscious visual experience (Geirhos et al., 2018; Kubilius et al., 2019). Moreover, CNNs tend to lack robustness against image distortions and adversarial noise, often failing to generalize outside their training distributions (Kubilius et al., 2019). These deficits reflect fundamental limitations of feedforward architectures, which do not incorporate iterative or predictive processes that characterize biological vision (Tang et al., 2018; Kar et al., 2019).

The Promise and Limitations of RCNNs

Standard CNNs operate in a strictly feedforward manner, passing information from one layer to the next without recurrence. In contrast, the primate ventral pathway contains both within-area and across-area recurrent connections, a feature thought to be crucial for robust object recognition, especially under challenging visual conditions such as occlusion, noise, or ambiguity. To address this discrepancy, recurrent CNNs (RCNNs) have been developed, which incorporate lateral and feedback recurrence to mimic the dynamics of the ventral stream. The CORnet family exemplifies this approach: its simplest version, CORnet-Z, is a shallow feedforward model, whereas recurrent variants such as CORnet-R and CORnet-S include lateral and feedback connections that improve biological plausibility and better capture aspects of the temporal dynamics observed in primate visual cortex (Kubilius et al., 2019).

Empirical work further supports the importance of recurrence: for instance, Tang et al. (2018) showed that recurrent computations enable pattern completion and object recognition under occlusion. More generally, RCNNs outperform feedforward CNNs on tasks involving degraded or ambiguous inputs, highlighting the benefits of feedback for visual inference (Spoerer et al., 2017; Kar et al., 2019). By supporting iterative integration of information and disambiguation of inputs over time, these models provide a computational analogue for the recurrent and top-down mechanisms thought to enable conscious perception in humans. However, current RCNNs still fail to capture human-like error patterns in vision, highlighting the remaining gap between artificial and biological perceptual mechanisms (Geirhos et al., 2020).

In recent work, rather than optimizing models for object classification, models have been built that explicitly incorporate neurophysiological constraints derived from single-unit recordings in macaque face patches. For example, a topographic deep artificial neural network (TDANN) was designed to match the known topographic organization and representational geometry of inferotemporal cortex (Lee et al., 2020; Margalit et al., 2024). This approach shifts the modeling goal from performance on engineering benchmarks to fidelity to neural data (Schrimpf et al., 2018).

The recurrent architecture implemented in RCNNs resonates with the “analysis-by-synthesis” framework in vision science (Yuille and Kersten, 2006), which posits that perception involves the brain generating and testing internal hypotheses against sensory data through feedback mechanisms*.* This iterative, hypothesis-driven computation mirrors the kinds of recurrent and predictive processes proposed to underlie conscious visual experience. The next frontier in computational modeling of conscious vision lies in developing architectures that combine feedforward, feedback, and spontaneous neural dynamics to reflect the brain’s multi-level inferential processes more accurately. A key ongoing challenge will be determining exactly how to incorporate these dynamics into models such that they match not only human perceptual behavior but also human brain mechanisms.

Finally, it is important to critically examine the assumption that conscious vision can be captured by implementing the correct computations, a view known as computational functionalism. According to this view, consciousness arises once the appropriate computational processes are in place, regardless of the physical substrate executing them. Although computational functionalism is widely embraced in computer science and cognitive science, it remains a conjecture and serious doubts on this view have been raised (Seth, 2024). One critical view on computational functionalism adopts the analogy of weather simulations: "If you simulate a rainstorm in the computer, it is not wet." (Ned Block, 2024, ASSC symposium "Computational Functionalism or Not" in Tokyo, organized and chaired by Biyu He).

At present, whether one adopts computational functionalism or not remains largely a matter of philosophical stance. However, even if computational functionalism is incorrect, a detailed computer simulation of brain circuit dynamics underlying conscious vision can represent our mechanistic understanding in a more quantitative and concrete form than otherwise possible, and enable novel predictions that can be tested through further empirical experiments. We are convinced that it will be important for any such model, DNN or not, to incorporate the effects of top-down feedback, prior knowledge, and spontaneous activity.

Conclusions

A consistent picture emerges from the evidence reviewed above: conscious perception is not merely the result of a sequential progression of stimulus processing through hierarchical layers, but instead reflects a dynamic and context-sensitive interplay between bottom-up sensory signals and top-down expectations, priors, and intrinsic activity patterns.

We first reviewed empirical evidence showing that conscious vision relies on dynamic interactions between feedforward, recurrent, and top-down processes. Top-down influences, shaped by long-term experience, one-shot learning, and expectations, guide sensory and perceptual processing to generate conscious perception. This feedback is evident in various visual illusions, which depend on the integration of contextual cues and learned predictions.

We subsequently focused on the role of spontaneous neural activity in conscious visual perception. The brain's baseline state is not a blank slate awaiting sensory input but contains a rich and structured pattern of ongoing activity that shapes perception even before a stimulus appears. This background activity, along with fluctuations in attention, expectation, and arousal, biases which sensory inputs reach conscious awareness and how they are interpreted. This suggests that the brain might be continuously engaged in hypothesis testing even in the absence of external stimuli. Understanding the variability and structure of spontaneous activity, and how it interacts with sensory processing, are thus integral to explaining the conscious experience.

Hallucinations are an illustrative case of perception that is decoupled from sensory input. Hallucinations seem to arise when top-down expectations or internal models override or distort incoming sensory signals, leading to vivid conscious experiences in the absence of appropriate external stimuli. This phenomenon further supports the idea that perception is generative and constructive rather than reactive and highlights that the brain's capacity for conscious experience is not contingent on sensory stimulation per se, but on the dynamics of internally generated predictions and their interplay with bottom-up input.

Finally, we discussed deep neural networks like CNNs, which have achieved impressive successes in modeling object recognition and other visual tasks. However, next-generation models that better incorporate recurrent processing and spontaneous activity will be necessary to better capture brain mechanisms underlying conscious vision. These models should accommodate the constructive nature of perception, explain the neural underpinnings of hallucinations and illusions, and better reflect the biological realities of the brain's architecture.

In sum, the research reviewed here converges on a view of conscious vision as an emergent property of recursive, dynamic interactions between sensory input and internal models carried by spontaneous activity and top-down feedback. These dynamic interactions endow conscious experience with its flexibility, context sensitivity, and subjective nature.

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