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THEORETICAL NOTE

Spiking the Mind: Rethinking the Role of Cortical Feedback in Visual Mental Imagery

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Recent research has revealed similarities between visual mental imagery and visual perception. Visual imagery is supported by cortical feedback involving multiple visual areas, including the primary visual cortex, and functionally interacts with perception. This has led to the assumption that imagery is "perception in reverse," with feedback connections driving action potentials in early visual areas. However, evidence on feedback mechanisms is mixed, often exerting modulation (often as negative gain control) in sensory areas. Here, we examine and interpret the current understanding of feedback mechanisms related to visual imagery, integrating this with its functional effects and neural correlates. Finally, we put forward a new hypothesis, along with testable predictions, proposing that imagery reshapes spontaneous neural activity rather than producing spiking in early visual areas. This new framework explains many of the properties of visual imagery while providing a better general understanding of feedback and brain function.

Keywords: visual mental imagery, feedback, neural mechanisms, spontaneous neural activity, visual perception

For most of us, our brains can produce visual experiences in the form of mental images without any concurrent retinal input. Unlike visual perception, which needs retinal input, voluntary visual imagery is understood to originate in executive areas (Amedi et al., 2005; Dijkstra, Bosch, & van Gerven, 2017; Pearson, 2019; Pearson et al., 2015). This results in an opposite recruitment pattern along the visual pathway. While visual perception engages the visual system in a feedforward fashion, visual imagery does so in a feedback manner. Feedforward begins in the retina, reaching the primary visual cortex (or area V1) and then activating hierarchically organized cortical areas, where neurons generally have larger receptive fields and more complex stimulus selectivity (DiCarlo et al., 2012; Felleman & Van Essen, 1991), see Table 1 for details. In contrast, visual imagery channels signals from executive areas (in the prefrontal cortex) down to the early visual cortex (in the occipital lobe) through long-range feedback connections (Dentico et al., 2014; Dijkstra, Bosch, & van Gerven, 2017; Mechelli et al., 2004). In the context of visual mental imagery, feedback connections are often assumed to deliver information down the visual pathway by recruiting visual neurons in the same way as feedforward connections do, that is, by driving action potentials. However, feedback connections have physiological properties that differ from feedforward connections (Figure 1). Feedback carries contextual, predictive, and attentional signals. Despite outnumbering feedforward connections, feedback communication is weaker and slower and mainly exerts modulatory rather than driving effects in early sensory areas (Briggs, 2020); see Table 2 for details. Feedback connections primarily act as a gain control in existing spike rates rather than causing them, as discussed in the following sections. Even though the communication pathways involved in visual perception and visual imagery differ, research has shown that they activate overlapping brain areas of the brain and can functionally influence one another (see Table 3). This suggests shared neural substrates and raises the question of how visual imagery exerts its effects on the visual system.

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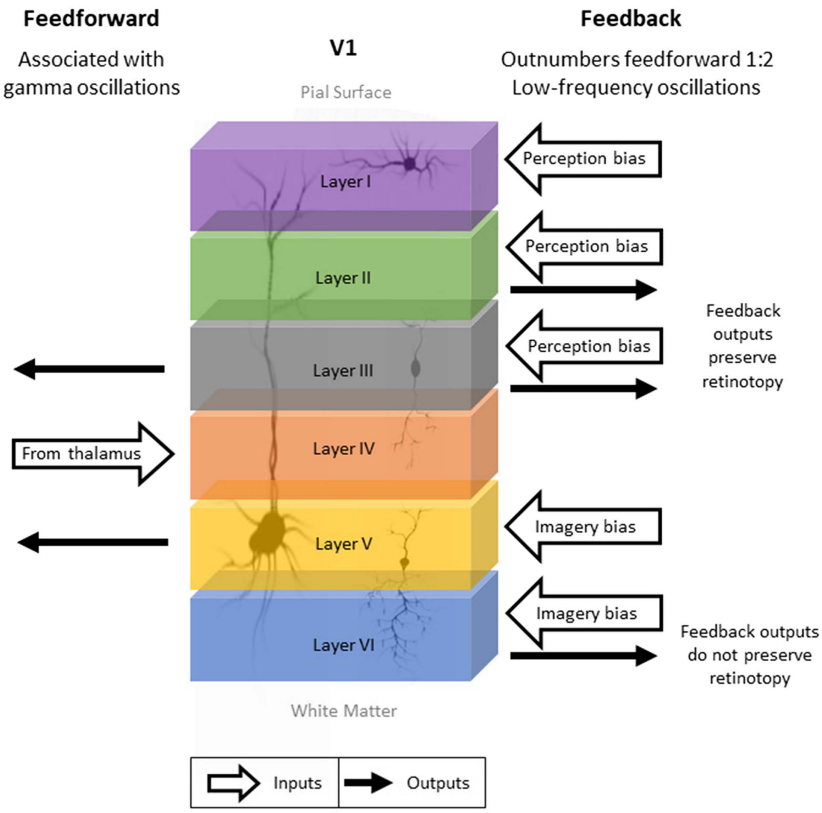
Table 1
Functional Components of the Visual Brain

Component	Definition
Visual hierarchy	Cortical visual areas are organized hierarchically, with neural selectivity becoming more complex and receptive field sizes increasing as one moves up the visual hierarchy. This occurs due to the pooling of multiple receptive fields at each level of the hierarchy. By analyzing laminar patterns of cortical connectivity, researchers have been able to map the hierarchical relationships among various visual areas.
Stimulus selectivity	The optimal perceptual stimuli that trigger action potentials in a specific neuron or cortical area. While neurons in V1 exhibit selectivity for oriented contours, neurons at the top of the visual hierarchy, such as those in the inferior temporal lobe, are selective for more complex stimuli, including faces.
Receptive field (vision)	The region of the visual field from which a stimulus can elicit a response in a specific neuron. While receptive fields in V1 are relatively small, averaging about 1° of visual angle, neurons in the inferior temporal lobe can possess receptive fields of approximately, 30°.
Feedforward	The flow of neural information from lower level areas to higher level areas. Axons originate in lower level cortical areas (presynaptic component) and target neurons in higher level areas (postsynaptic component). Neurons inherit their properties (such as stimulus selectivity and receptive field size) from their feedforward input.
Feedback	The unidirectional flow of neural information from higher level regions to lower level regions. Feedback carries contextual, predictive, and attentional signals. Axons originate in higher level cortical areas (presynaptic component) and target neurons situated in lower level areas (postsynaptic component). It is commonly accepted that feedback only modulates neurons' properties by tuning their spiking patterns, but otherwise, feedback would not drive these properties.

Most of our knowledge of the neural mechanisms and areas supporting visual imagery comes from functional neuroimaging, especially functional magnetic resonance imaging (fMRI). Neuroimaging studies have shown that visual imagery recruits several visual areas, including the early visual cortex (V1/V2; Amedi et al., 2005; Cui et al., 2007; Dijkstra, 2024; Dijkstra, Bosch, & van Gerven, 2017; Kosslyn et al., 1995, 1997, 1999; Naselaris et al., 2015), reinforcing the idea that visual imagery is a sort of visual perception in reverse (Pearson, 2019;

Figure 1
Function and Anatomy of Feedback Connections



Note. This scheme summarizes the main properties of feedforward and feedback connections. Feedforward connections are represented on the left and feedback on the right. White arrows represent inputs and solid black arrows represent outputs. Larger neuron represents a pyramidal cell (excitatory), and smaller ones represent interneurons (inhibitory). See the online article for the color version of this figure.

Table 2
Types of Connections: Drivers Versus Modulators

Driver versus modulator
Synapses have a broad range of effects on the postsynaptic neurons (the neurons that receive the message). Traditionally, synaptic connections are divided into drivers and modulators. Drivers transmit the properties of the receptive field, while modulators regulate specific aspects of these properties (Sherman & Guillery, 1998). In other words, drivers generate action potentials in target neurons (defining their selectivity), while modulators influence spiking rates; otherwise, they do not induce spikes without a feedforward drive (Shipp, 2007). While this distinction was originally based on observations in the thalamus—where retinal inputs act as drivers and cortico-thalamic connections serve as modulators—recent evidence indicates that cortico-cortical connections can likewise be categorized into these two groups (Covic & Sherman, 2011; De Pasquale & Sherman, 2011; Sherman & Guillery, 2011). Functionally, drivers and modulators can be differentiated by the following characteristics: Drivers activate the postsynaptic neuron, resulting in significant depolarizations (i.e., large excitatory postsynaptic potentials) that exhibit depression after repetitive stimulation (i.e., paired-pulse depression). Consequently, driver connections are linked with a high likelihood of spiking in the postsynaptic neuron and adaptation. Conversely, modulators generate smaller initial excitatory postsynaptic potentials but exhibit facilitation after repeated stimulation (i.e., paired-pulse facilitation), which is associated with a low probability of spiking in the postsynaptic neuron and a lack of adaptation. Traditionally, it has been proposed that feedforward connections serve as drivers, whereas feedback connections function as modulators (Crick & Koch, 1998; Sherman & Guillery, 1998; Shipp, 2007). However, subsequent studies in the early visual (V1/V2) and auditory (A1/A2) areas of mice have revealed that short-range feedback connections in these sensory regions consist of both drivers and modulators (Covic & Sherman, 2011; De Pasquale & Sherman, 2011). Contemporary influential models of neural function, on the other hand, suggest that these long-range feedback connections are mainly modulatory, while their "driving" capabilities would serve to activate inhibitory neurons in the target area, particularly those connections terminating in supragranular layers (Auksztulewicz & Friston, 2016; Bastos et al., 2012; Rao & Ballard, 1999). This view is supported by neuroimaging and noninvasive electrophysiology data in humans showing suppressive effects of putative feedback signals (Kok et al., 2012; Wacongne et al., 2011).

Pearson et al., 2015). It is often implied that visual imagery, using feedback, would single handedly activate visual neurons that code for the features contained in the imagined object by increasing their spiking rates above baseline, similar to visual perception (e.g., activating neurons that code for the color red when imagining a red apple). This seems like the most parsimonious mechanistic explanation of visual imagery, and can often be interpreted as the assumed mechanism in several studies (Byrne et al., 2007; W. Chen et al., 1998; Dijkstra, Zeidman, et al., 2017; Kosslyn & Thompson, 2003; Kosslyn et al., 1995; Stokes et al., 2009). However, current views on the physiology of feedback connections challenge the ability of feedback to generate action potentials without visual stimulation, particularly concerning early visual areas, as is the case in visual mental imagery (Briggs, 2020; Crick & Koch, 1998; Hupé et al., 1998; Semedo et al., 2022; Shipp, 2007). Current evidence indicates that the effects of feedback in early sensory areas are mainly modulatory; in other words, feedback would only adjust the firing rate "gain," usually through inhibition, instead of driving or triggering action potentials in excitatory neurons by itself, without visual input. Besides specific cases of perceptual filling in (Murray & Herrmann, 2013), it has been argued that feedback likely lacks the capacity to substantially increase mean firing rates in early sensory areas as perception does (Auksztulewicz & Friston, 2016; Bastos et al., 2012; Briggs, 2020; Crick & Koch, 1998; Rao & Ballard, 1999; Sherman & Guillery, 1998; Shipp, 2007), see Table 2 for details.

As this remains a topic of active research, we discuss evidence for and against the notion that visual imagery (and, more broadly, feedback) drives spiking rates in early visual areas. We refer to this as the spiking hypothesis and contrast it with the idea that visual imagery influences these areas (particularly earlier visual regions) without significantly elevating the spiking rate in neurons coding for imagined features, which we term spontaneous activity reshaping hypothesis (Figure 2). Considering the current physiological and psychophysical evidence, we propose that feedback would increase spiking in (or drive) higher level cortical areas related to memory, higher level visual processing and visual motion. At the same time, it would only have a modulatory (mainly as a negative gain control) or reshaping effect on the spontaneous neural activity of early visual areas. This is important as this new framework reconciles seemingly disparate results on the mechanisms of visual imagery, while also accounting for fundamental properties of visual imagery, such as its lower vividness compared to visual perception and its dynamic nature.

This detailed discussion is further motivated by the significant implications of understanding the neural mechanisms behind visual imagery, which can enhance our comprehension of feedback and overall brain function. Imagery provides a uniquely effective way to study feedback processes in the brain. Unlike perceptual visual attention, such as object- and feature-based attention, which influences perceptual neural representations of external visual stimuli, imagery generates perceptual neural representations internally, without requiring external (retinal) visual stimulation. This separation of feedback from sensory input allows us to explore the boundaries and roles of feedback in isolation, offering a direct way to examine how top-down signals influence or even create neural representations across cortical hierarchies. Gaining insight into these processes not only clarifies the computational role of feedback during imagery, but also shows how top-down mechanisms shape our perception of the world.

The Neural Correlates of Visual Imagery

Directly testing the physiological effects of visual imagery in early visual areas would require invasive recordings in humans. Invasive brain recordings are exceptionally performed for clinical purposes on epileptic patients resistant to pharmacological treatments. The electrode implantation sites on the patients' brains are typically very sparse and determined by strict clinical criteria (Bautista et al., 1999; Mukamel & Fried, 2012). Given the location of the epilepsy foci, action potential or "spike" recordings from early visual areas are exceptionally rare; only relatively recently have such recordings been obtained from V2/V3 in human patients (Self et al., 2016). Therefore, no spike recordings in early visual areas in humans about the effects of imagery are yet available.

However, intracranial recordings from other brain areas in human patients have revealed that neurons in the medial temporal lobe, a

Table 3
Functional Interaction Between Visual Imagery and Perception

Study	Imagery paradigm	Perception paradigm	Result	Putative target area	Hypothesis compatibility
Pace et al. (2023)	Imagine-oriented monochromatic gratings after adaptation	Binocular rivalry dominance and discrimination	Reversing effects of adaptation effects by suppressing competing visual representations	Early visual areas, including V1	Reshaping spontaneous activity hypothesis
S. Zhang et al. (2025)	Imagine-oriented gratings	Orientation discrimination	Suppressive bias in tuning curves elicited by imagery	Early visual areas	Reshaping spontaneous activity hypothesis
Pearson et al. (2008), Chang et al. (2013), Maróthi and Kéri (2018)	Imagine-oriented and colored gratings	Binocular rivalry dominance test on rival gratings	Facilitation: Imagined gratings primed binocular rivalry dominance	Competition among binocular neurons in V1	Reshaping spontaneous activity hypothesis
Winawer et al. (2010)	Imagine moving gratings	Motion direction discrimination of dots at different motion coherence	Adaptation: Imagined movement biased motion discrimination away from the imagined motion (motion adaptation)	Motion-detecting neurons in hV5/MT	Spiking hypothesis
Gilden et al. (1995)	Imagine motion	Motion adaptation prior to imagery	Adaptation: Imagined motion showed adaptation (as a decrease in imagined motion speed) from previously perceived motion	Motion-detecting neurons in hV5/MT	Spiking hypothesis
Seurinck et al. (2011)	Mental rotation	Motion adaptation prior to imagery	Adaptation: Motion after effect leads to longer reaction times in the mental rotation task	Motion-detecting neurons in hV5/MT as revealed by concurrent fMRI	Spiking hypothesis
Chang and Pearson (2017)	Imagine motion	Binocular rivalry dominance test on rivalrous motion dot patterns	Facilitation: Imagined motion primed binocular rivalry dominance toward the imagined motion	Competition among binocular neurons in V1	Reshaping spontaneous activity hypothesis
Mohr et al. (2009)	Imagine tilted lines	Orientation judgment on test lines	Adaptation: Perceived orientation was tilted away from the imagined orientation (tilt after-effect)	Extrastriate areas, mainly V4 as revealed by BOLD adaptation experiment	Spiking hypothesis
Ishai and Sagi (1995)	Imagine oriented Gabor flankers	Oriented Gabor detection	Facilitation: Imagining flankers' reduced detection thresholds for visual targets	Orientation selective neurons, probably located in early visual areas	Reshaping spontaneous activity hypothesis

Note. fMRI = functional magnetic resonance imaging; MT = medial temporal area; BOLD = blood-oxygen-level dependent.

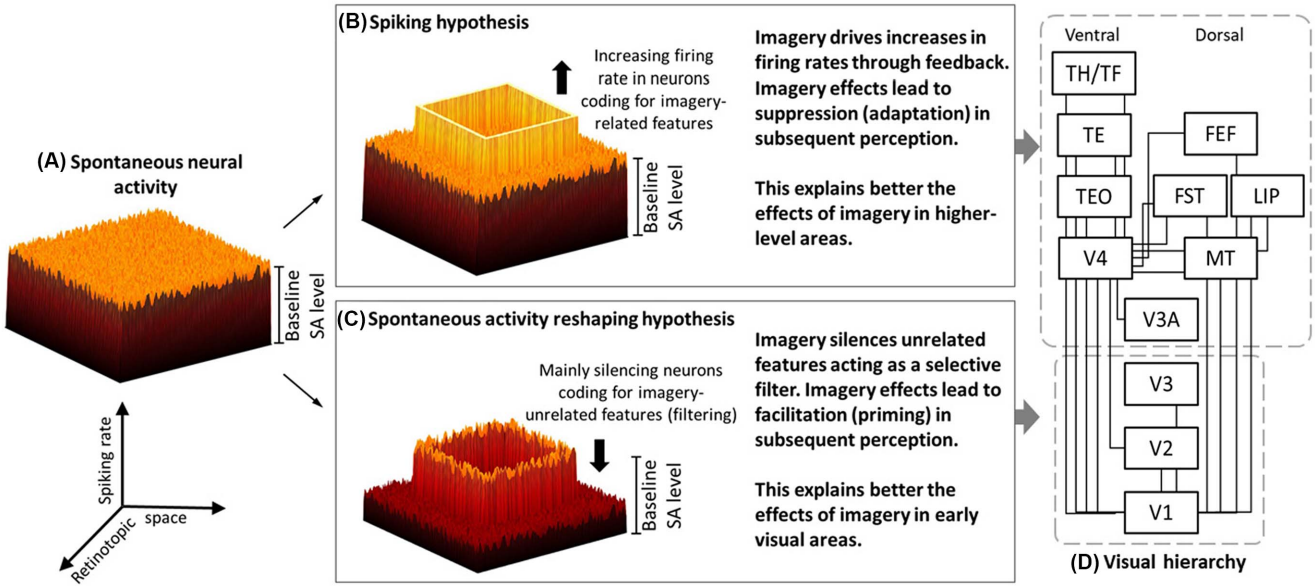
high-level cortical area implicated in memory, are selectively driven (i.e., they respond by increasing their spike rate) by visual imagery (Kreiman et al., 2000). This study showed that most neurons (88%) kept their stimulus selectivity (e.g., a given person's face) independent of whether their preferred stimuli were perceptually presented or imagined. A later study found that some of these neurons even responded to the written name of the stimuli they were selective for, indicating that their responses are highly invariant across modalities (Quiroga et al., 2005). The areas recorded in these studies included the hippocampus, amygdala, entorhinal cortex, and parahippocampal gyrus. Since these areas are not classically regarded as part of the visual system (Felleman & Van Essen, 1991), these results are unlikely to be directly extrapolated to early visual areas.

Noninvasive neuroimaging studies in humans have revealed a network of brain areas engaged during visual imagery, including the occipital, ventral-temporal, parietal, and frontal cortex (Amedi et al., 2005; Dijkstra, Bosch, & van Gerven, 2017; Ishai et al., 2000; Stokes et al., 2009). In addition, several studies have shown changes in the average blood-oxygen-level dependent (BOLD) response in lower visual areas, including the primary visual cortex V1 (Amedi et al., 2005; Cui et al., 2007; Kosslyn et al., 1995, 1997, 1999). It has also been shown that this early visual cortex recruitment is somewhat retinotopic (Klein et al., 2004).

The functional activations observed through standard neuroimaging (i.e., based on the average BOLD or univariate responses across a given region) are, however, not conclusive regarding the neural mechanisms underlying these activations, as they could be triggered by processes that are not specific to the coding of features of visual imagery, such as the overall level of arousal or attention. Do the activations in visual areas represent specific information about the contents of visual imagery? More recently, multivoxel pattern analysis (MVPA) has revealed that several areas along the visual hierarchy contain specific information about the contents of imagery (i.e., is the participant imagining an apple or a carrot?). These analyses do not rely on changes in global activation in a particular area (as classic neuroimaging analyses do) but rather on the spatial pattern of activation in the brain (for a review, see Norman et al., 2006). The MVPA has allowed the decoding of single imagined letters in the lateral occipital cortex (Stokes et al., 2009), imagined visual objects (such as faces, objects, and tools) from different ventral visual areas (Reddy et al., 2010); scenes in ventral visual areas (M. R. Johnson & Johnson, 2014), among many other stimuli. In addition, MVPA has shown that imagery

Figure 2

Schematic Representation of the Neural Mechanisms of Visual Imagery



Note. This scheme depicts the neuron spiking rate along the *z*-axis (the height of the boxes), with retinotopic space represented on the *x* and *y*-axes. In this example, the imagined object is a rectangle, illustrated as a colinear recruitment of neurons forming the shape of a rectangle. This scheme implies that neurons from a given edge code for the same orientation. (A) Spontaneous activity. The visual cortex's state prior to imagery involves neurons displaying internally generated dynamics. In this setting, the intrinsic activation of the visual cortex is understood to fluctuate stochastically over time around a baseline level of SA. (B) Spiking hypothesis. Visual imagery activates visual regions by enhancing spiking above the baseline spontaneous activity level, much like visual perception. This feedback mechanism more effectively explains imagery effects in higher level brain areas (see text for details). (C) Spontaneous activity reshaping hypothesis. Visual imagery engages visual areas through feedback by selectively decreasing the activity of neurons that are not related to the imagined object (e.g., unrelated orientations and irrelevant retinotopic locations), bringing neurons coding for these features below baseline levels. Note that while the figure implies inhibition of all neurons not contributing to the imagined content, suppression of just a set of these neurons could account for the phenomenology of imagery as explained in the main text. This feedback hypothesis more effectively explains imagery effects in early visual areas. (D) Proposed effects of imagery across the visual hierarchy. The reshaping hypothesis explains imagery effects mainly from V1 to V3, while the spiking hypothesis explains imagery effects from about V3a onwards. Note that the representation of a rectangle in this example is relevant to lower visual areas, and less so to higher level areas, but the same principle applies to more complex stimuli. Scheme modified from (Barone et al., 2000). From "Laminar Distribution of Neurons in Extrastriate Areas Projecting to Visual Areas V1 and V4 Correlates With the Hierarchical Rank and Indicates the Operation of a Distance Rule," by P. Barone, A. Batardiere, K. Knoblauch, and H. Kennedy, 2000, *Journal of Neuroscience*, *20*(9), p. 3276 (https://doi.org/10.1523/JNEUROSCI.20-09-03263.2000). Copyright 2000 by Society for Neuroscience. Reprinted with permission. SA = spontaneous activity; FEF = frontal eye fields; TH/TF = temporal areas H/F (parahippocampal cortex); TE = temporal area E (lateral inferior temporal cortex); TEO = temporal area E-occipital (posterior inferior temporal cortex); FST = fundus of the superior temporal sulcus; LIP = lateral intraparietal area; MT = middle temporal area/V5. See the online article for the color version of this figure.

representations are location-specific in high-level visual cortical areas (Cichy et al., 2012). Some of these studies also showed that visual imagery representations share information with visual perception (Albers et al., 2013; Bannert & Bartels, 2013; Chang et al., 2024; Cichy et al., 2012; Harrison & Tong, 2009; Koenig-Robert & Pearson, 2019, 2020; Reddy et al., 2010; Stokes et al., 2009). Importantly, research using encoding models has shown that the visual features encoded in the early visual cortex, represented by orientation preferences across voxels, are adequate to distinguish between many imagined fine art paintings (Naselaris et al., 2015), indicating that visual imagery uses neural coding similar to visual perception. It has also been shown that visual imagery representations in the early visual cortex share information with visual working memory (Albers et al., 2013), indicating overlapping neural substrates. These results show that visual imagery recruits the visual cortex in a content-specific (or visual feature-specific) fashion analogous to visual perception. The results obtained from neuroimaging are important and shed light on which areas participate in constructing mental images. However, as discussed in the next section, these approaches are not well-suited to revealing how visual imagery recruits these early visual areas.

Why Visual Imagery fMRI Responses Do Not Necessarily Mean an Increase in Spiking

It is often implicitly assumed that responses, as revealed by non-invasive neuroimaging (fMRI or positron emission tomography) in visual areas during visual imagery, are a correlate of spiking activity or action potentials (Byrne et al., 2007; W. Chen et al., 1998; Kosslyn & Thompson, 2003; Stokes et al., 2009). However, fMRI and positron emission tomography responses indirectly estimate neural activity by measuring local metabolism, which cannot be directly translated into spiking. fMRI quantifies the BOLD signal, which measures the hemodynamic response following a change in local metabolism. The

hemodynamic response primarily depends on blood flow, oxygenation levels, and volume (Shibasaki, 2008).

A series of studies has well established that BOLD responses are a mixture of sub- and suprathreshold neural activity, that is, nonspiking and spiking activations, respectively (Goense & Logothetis, 2008; Logothetis et al., 2001; Magri et al., 2012), see Table 4 for details. These studies have revealed that the BOLD response is more closely related to the extracellular electrical potentials recorded in the brain by penetrating electrodes. These electrical potentials are a mixture of different sources of brain activity near the electrode's tip: from multiunit activity (neurons spiking) and average peri-synaptic activity (nonspiking) or local field potentials (LFP). LFPs correspond to several so-called "subthreshold activities," including synaptic potentials, afterpotentials of somatodendritic spikes, and voltage-gated membrane oscillations, which mainly reflect the input of a given cortical area, which can be present without any local spiking (Buzsáki et al., 2012).

Studies combining simultaneous BOLD and invasive electrophysiological recordings have shown that the BOLD signal is better predicted by LFP (subthreshold activity) than Multi Unit Activity (spiking; Goense & Logothetis, 2008; Logothetis & Panzeri, 2015; Logothetis et al., 2001; Magri et al., 2012). More strikingly, it has been shown that robust positive BOLD responses can be recorded without an increase or even with a decrease in local spiking, given that LFP modulations are present (Goense & Logothetis, 2008; Logothetis, 2008; Logothetis et al., 2001; Logothetis & Panzeri, 2015). Thus, increases in BOLD without a spiking increase can originate from active long-range inhibition of local neural spiking, explaining both increases in LFP (modulatory inputs from distant areas) and absence (or decrease) in local spiking. This pattern of BOLD responses is consistent with feedback exerting inhibitory modulatory effects, which could result from presynaptic inputs from higher level areas. This is also compatible with MVPA imagery results, as decoding is not based on the global level of BOLD activity but on the spatial patterns of activity, which can be produced using inhibitory mechanisms, as we will see later.

In conclusion, it is still unclear whether increases in BOLD activity in early visual areas during visual imagery represent spiking driven by higher level areas, subthreshold activity or a combination of both. However, electrophysiological studies in animals may provide valuable insights into the likelihood that feedback drives visual neurons across different visual areas, as we will see in the next section.

The Functional Architecture of Feedback Connections

Feedback connections are ubiquitous in the primate visual system (Figure 1). Indeed, studies in primates have shown that feedback connections outnumber feedforward ones in a ratio of 2:1 (Markov et al., 2014; Perkel et al., 1986; Salin & Bullier, 1995). Despite their pervasiveness, the role of feedback connections is still poorly understood. Feedback and feedforward connections are formed by axons of pyramidal neurons, which are mainly excitatory (R. R. Johnson & Burkhalter, 1997). Feedforward connections originate in layers adjacent to the granular layer (L3B and L5) and mainly target synapses in the granular layer (L4). On the other hand, feedback connections originate from superficial (L2/3) and infragranular (L6) layers of the cortex, targeting the same regions (Barone et al., 2000; Kennedy & Bullier, 1985; Markov et al., 2014; Perkel et al., 1986; Rockland, 1994; Van Essen et al., 1986). It has been shown that the interaction between different visual areas is principally dominated by feedforward very shortly after a stimulus is presented, but this interaction reverses quickly after, with feedback dominating the interaction in later evoked responses and the spontaneous activity of visual neurons (Semedo et al., 2022), indicating that feedback is a major contributor to brain activity dynamics.

Traditionally, feedback projections have been thought to be spatially (i.e., retinotopically) diffuse (Kennedy & Bullier, 1985; Rockland & Pandya, 1979), raising questions about the spatial specificity of feedback effects. However, recent studies have shown that the projection fields' diffuseness depends on the origin layer (Markov & Kennedy, 2013; Markov et al., 2014). Feedback projections originating from supragranular layers are often point-to-point (i.e., preserve retinotopy) while also being short range. On the other hand, feedback connections originating from infragranular layers are more diffuse (i.e., do not preserve retinotopy) and span several levels in the visual hierarchy (i.e., long range). Interestingly, most corticocortical connections (~75%) are short to medium range (Markov et al., 2014). Therefore, it is likely that feedback connections generally preserve retinotopy. Further, a recent study has revealed that V2 feedback connections in the macaque cortex modulate V1 responses in a visual feature-specific manner, in a similar manner to feedforward connections, thus indicating the preservation of visual information when transmitted from higher to lower level visual areas (Federer et al., 2021). However, a study in mice recently showed that experience minimizes the spatial overlap between feedback from the lateromedial visual area, a higher order visual area, and V1 neurons (Dias et al., 2024). This is consistent with the loss of spatial specificity in long range (i.e., spanning several hierarchical levels) feedback connections.

Recent studies have suggested that feedforward and feedback connections transmit messages at different frequencies. Feedforward connections seem to convey their message using high-frequency oscillations (e.g., gamma oscillations around and above 40 Hz), while feedback signals do so through low-frequency oscillations such as alpha and beta frequencies, which are below 40 Hz (Bastos et al., 2015; Fontolan et al., 2014; Michalareas et al., 2016; Sedley et al., 2016; van Kerkoerle et al., 2014). Remarkably, these lower frequency alpha oscillations recorded from noninvasive recordings such as electroencephalogram have been used to decode the contents of visual imagery in humans, indicating a functional association between low-frequency oscillations and visual imagery neural representations (L. Chen et al., 2023; Stecher & Kaiser, 2024; Xie et al., 2020).

Both feedforward and feedback connections target primarily pyramidal neurons, which are excitatory neurons, but some connections (10%–20%) project directly onto putative inhibitory neurons (Lowenstein & Somogyi, 1991; Shao & Burkhalter, 1996; Shen et al., 2022). In the top cortical layer, L1, it has been shown that feedback projections are mostly excitatory (glutamatergic), but their overall effect is often inhibitory (Schuman et al., 2021), as this layer is remarkably abundant in inhibitory interneurons (X. Xu et al., 2010). Although less abundant, long-range inhibitory (GABAergic) feedback projections have also been identified in rodents (Melzer & Monyer, 2020). These experimental results support the idea of feedback exerting inhibitory modulatory effects.

A recent layer-resolved fMRI study has found stimulus-specific information feedback from mentally rotated stimuli in both deep and superficial layers of V1 (Iamshchinina et al., 2021), while another study found imagery-related information mainly in deep V1 layers, while perceptual illusory signals mainly in superficial cortical layers (Bergmann et al., 2024). These results are consistent with what is

Table 4
Types of Neural Activities

Neural actvity	Definition
Action potentials or spiking	The all-or-none depolarization of a neuron occurs after it reaches the threshold membrane potential. Action potentials define the type of input a neuron responds to. If a stimulus triggers the action potentials significantly above baseline in a neuron, then that neuron is selective to that stimulus. Action potentials frequently result in the release of neurotransmitters from the axon tip. Continuous spiking can also lead to adaptation, wherein the neuron ceases to respond to stimulation.
Subthreshold activity	Changes in membrane potential below the threshold for generating an action potential can occur. Fluctuations in membrane potential may be depolarizing (bringing the membrane potential closer to the threshold and thus excitatory) or hyperpolarising (moving the membrane potential away from the threshold and thus inhibitory). Shifts in the membrane potentials caused by subthreshold activity often have an effect on the ongoing spiking rate. Subthreshold activity is traditionally measured using intracellular electrophysiological recording techniques.

known about the layer compartmentalization of feedforward and feedback signals, but also suggest that the phenomenological differences between perception and imagery might be rooted in the differential layer recruitment in sensory cortical areas (Koenig-Robert & Pearson, 2021).

In summary, the role of feedback (driving or modulatory) in a particular area will ultimately depend on the implementation of the excitatory and inhibitory circuits, which is a matter of active research and debate (Barzegaran & Plomp, 2022; Born et al., 2021; Markov & Kennedy, 2013; Markov et al., 2014; Rockland, 2022; Shen et al., 2022). However, evidence shows that feedback architectures differ markedly from feedforward ones (Figure 1). Feedback pathways feature denser connectivity, predominantly operate through low as opposed to high-frequency oscillations, differentially target specific cortical layers, and exert modulatory (often as inhibition) rather than driving effects. These characteristics suggest that feedback pathways refine visual processing in a spatially and feature-specific way, complementing rather than mimicking feedforward connections. The following section will review physiological evidence for and against feedback driving spiking.

Physiological Evidence for and Against the Spiking Hypothesis

Several electrophysiological studies have investigated the effects of feedback on the spiking activity and the receptive field properties of neurons in visual areas. The driving effects of feedback are still a matter of debate. Here, we review evidence for and against the spiking hypothesis using invasive neural recordings of behaving and anesthetized animals.

Physiological Evidence for the Spiking Hypothesis

Studies on illusory contours suggest that feedback connections may drive spiking activity in early visual areas, without direct feedforward input to the retinotopic locations where the illusion is represented, leading to its conscious perception. Classic experiments showed that V2 neurons exhibit spiking responses to illusory contours that mimic those evoked by real contours (Peterhans & von der Heydt, 1989; von der Heydt et al., 1984; von der Heydt & Peterhans, 1989). Single-unit recordings from alert macaque monkeys showed heightened spiking activity in V2 neurons in response to illusory contours (discontinuous lines), whereas V1 neurons did not respond to these illusory contours (von der Heydt et al., 1984). In a later study (Lee & Nguyen, 2001), population-averaged responses were simultaneously recorded from the superficial and deep layers of V1 and V2 in awake monkeys as they viewed Kanizsa shapes. This study found that illusory contour responses emerged first in V2 (around 70 ms after stimulus onset), followed by V1 superficial layers (approximately 100 ms). This timing is significantly delayed compared to real contours, which drive V1 neurons within roughly 40–60 ms. The temporal sequence of these events indicates that responses to illusory contours in V1 may be driven by feedback originating in V2. A recent optogenetics study in mice established the role of lateromedial visual area (a higher level visual area) in the neural responses to Kanizsa illusory contours in V1 (Pak et al., 2020). This study showed that when feedback from lateromedial visual area was transiently inactivated, the V1 illusory contour responses were abolished even though V1 responses to actual luminance-defined edges remained largely unchanged. While these results seem to indicate that feedback could, on certain occasions, single handedly drive spiking in early visual areas, other studies have suggested that these effects are the result of the joint influences from feedforward, feedback, and lateral connections (communicating adjacent retinotopic locations within a visual area; Grosof et al., 1993; Ramsden et al., 2001; Redies et al., 1986; Sheth et al., 1996; Sugita, 1999). Therefore, it is generally accepted that illusory contour filling-in mechanisms do not rely solely on feedback, but instead, they depend on recurring processing that involves a combination of feedforward, feedback, and lateral mechanisms (for a review, see Murray & Herrmann, 2013). Interestingly, these effects are robust to anesthesia (Pan et al., 2012; Ramsden et al., 2001; Redies et al., 1986; Sheth et al., 1996), which suggests a significant contribution from automatic local mechanisms (feedforward, lateral connections, and short-range feedback), as it is well established that anesthesia impairs long-range feedback communication in the brain (Alkire et al., 2008; Boly et al., 2012; Imas et al., 2005; Ku et al., 2011; Mashour, 2014). In the context of perceptual filling-in mechanisms, feedback could, for example, release inhibition to feedforward drive or enhance spiking, which is consistent with modulation. Research on the role of feedback in filling-in mechanisms is still in active development, but, taken together, these findings help to define perceptual conditions under which feedback could seemingly drive early visual areas.

More recent studies have expanded on these findings by highlighting the influence of contextual information on spiking activity in early visual areas. A recent study in mice showed a robust contextual drive of V1 neurons (Kirchberger et al., 2023). In this paradigm, the stimulus comprised a full-screen grating with a blank circular section designed to

cover the entire receptive field of the V1 neuron being recorded. The results showed that neurons responded to the contextual stimulation by increasing their spike rate even if there was no stimulus in their receptive field. This increase was significantly smaller and delayed by about 80 ms from the responses recorded to gratings falling within their receptive field, but it was nonetheless robust. Responses to the empty receptive field were located in both supra- and infragranular layers, thus consistent with feedback effects. The study also showed that disinhibitory circuits, which released pyramidal neurons from inhibition, contributed to the responses to contextual stimuli, consistent with a feedforward drive (e.g., from lateral connections) and modulatory feedback influences. A related study performed in macaques showed that information (in the form of multiunit activity) from V1 neurons falling in occluded parts of images was sufficient to decode the images above chance (Papale et al., 2023). This study indicates that perceptual and contextual neural representations overlap. The results from these studies are consistent with increases in spiking, whether due to feedback, feedforward, or a combination of both. Notably, behavioral results using the neon color spreading illusion, a contextual perceptual illusion, revealed that repeated exposure to the illusion leads to adaptation (Chang & Pearson, 2020), which is compatible with increases in spiking.

Feedback can also sustain spiking that was previously initiated by perceptual responses in early visual areas. A study on macaques using layer-resolved recordings in V1 showed that top-down connections could maintain spiking activity initially triggered by perception in V1, even after the cessation of direct retinal input, up to 950 ms (van Kerkoerle et al., 2017). Similarly, recordings in rat V1 showed that after repeated exposure to a moving dot sequence, neurons could recreate the movement path, lasting several hundred milliseconds, in response to the presentation of only the first dot (S. Xu et al., 2012). While it remains unclear whether the animals in these studies experienced a phenomenal sensory experience akin to mental imagery, the results nonetheless highlight the ability of feedback connections to sustain spiking activity in early visual areas, provided that feedforward drive is initially ignited by visual perception in these or nearby neurons.

In higher level brain regions, feedback seems to have a more active role in driving neurons. As discussed before, intracranial recordings from human patients revealed that neurons in the hippocampus, amygdala, entorhinal cortex, and parahippocampal gyrus are driven by visual imagery (Kreiman et al., 2000). However, most of these regions correspond to associative areas beyond the visual cortex, and, to date, there are no studies recording spiking from visual areas during visual imagery in humans. Concerning areas traditionally regarded as visual, a study conducted in macaques investigated feedback between the prefrontal and inferotemporal cortex while performing a memory task (Tomita et al., 1999). This experiment combined split-brain animals (posterior corpus callosum sectioning) with Multi Unit Activity recordings. Spiking activity was recorded in the inferior temporal cortex, temporal area E (lateral inferior temporal cortex) [TE], a high-level visual area representing complex visual objects in response to stimulation in the ipsilateral visual field. Since the posterior corpus callosum was severed, spiking in the ipsilateral TE could not be linked to feedforward information, as sensory signals could not travel to the opposite hemisphere. Instead, these were linked to feedback signals from the prefrontal cortex that could still reach the ipsilateral hemisphere through the remaining anterior corpus callosum. Results showed that the prefrontal cortex could drive spiking in TE, activating it to a lesser extent and later than feedforward stimulation. Another study using a similar paradigm, also using behaving macaques, showed that the activity in the perirhinal cortex (Area 36, a high-level area associated with object memory) preceded that of the inferior temporal cortex (area TE), thus suggesting that Area 36 drives spiking in area TE through feedback (Naya et al., 2001). In another experiment using macaques in an associative memory task, motion-sensitive neurons in the medial temporal area (MT) were activated in the presence of stimuli previously associated with motion (an arrow), but otherwise, a static image (Schlack & Albright, 2007). This result suggests that the association (perhaps analogous to visual imagery) between the real movement and the arrow was enough to drive spiking in MT without physical motion. Another interpretation would be that the cue could reactivate associative memories stored in MT.

In summary, feedback seems to fill in contextual information by increasing spiking in occluded contiguous areas of the early visual cortex (V1/V2), but only during visual stimulation. This contextual feedback is likely mediated by short-range feedback (e.g., V2 to V1), in combination with feedforward and lateral mechanisms, in contrast to the unique influence of long-range feedback required for visual imagery. Evidence also shows that feedback can drive spiking in high-level regions located in the medial and inferior temporal cortex, as well as midlevel visual areas, such as area MT. In the case of the early visual cortex, results show that feedback can only sustain increases in spiking rates in neurons previously driven by perceptual stimulation. In conclusion, the evidence so far is insufficient to assert whether feedback alone can drive spiking without a feedforward drive, such as during visual imagery.

Physiological Evidence Against the Spiking Hypothesis

In a series of experiments, the role of feedback on receptive field responses was recorded as firing rates from V1 to V3 while reversibly inactivating area MT in anesthetized macaques. Interestingly, feedback from MT was found to have an enhancing effect on the center receptive field responses from V1 to V3 while suppressing responses from the receptive field surround (Bullier et al., 2001; Hupé et al., 1998). These results suggest that feedback from MT is important to improve figure/ground segregation in lower level visual areas. While the enhancing effects of feedback were, on occasion, significant, V1/V2 responses were largely feedforward-driven and remained robust even without MT. This led the authors to conclude that feedback is unlikely to drive spiking on the target neurons. This conclusion is supported by previous research showing that most neurons in V2 are silenced after V1 inactivation (Girard & Bullier, 1989). However, strong residual activity was present in MT after V1 inactivation (Girard et al., 1992; Nowak et al., 1995; Rodman et al., 1989). Interestingly, another area in the dorsal stream, V3a, also shows residual responses after V1 inactivation (Girard et al., 1991a). However, no residual activity was found in V3 or V4, which belong to the ventral stream (Girard et al., 1991a, 1991b). Further research showed that the residual responses after the inactivation of feedforward inputs from V1 are driven by subcortical structures that bypass V1 (Berman & Wurtz, 2011; Bridge et al., 2016; Lyon et al., 2010; Rodman et al., 1990; Stepniewska et al., 2000), thus supporting the idea that feedback cannot drive neurons in early visual areas without feedforward input.

Studies performed in cats showed that the inactivation of the postero-temporal visual cortex (homologue to the inferotemporal

area in primates) led to changes in area 17 (V1 homologous) that are consistent with modulatory effects in the classical and extra-classical receptive fields of the primary visual cortex (Bardy et al., 2009; Huang et al., 2007, 2017). A more recent study in marmosets used optogenetics to inactivate feedback from V2 to V1 specifically (Nurminen et al., 2018). Feedback inactivation reduced surround suppression (i.e., decreased contextual inhibition) in V1 receptive fields, resulting in an increase in their size (less spatial specificity). These results indicate feedback inhibitory mechanisms consistent with the filtering role observed in spatial attention.

In an attention paradigm involving behaving macaques, microstimulation of the frontal eye fields (FEF), an area responsible for attentional selection and saccade production, resulted in spiking enhancement in V4 only when stimuli were presented within V4's receptive fields, but not when there was no stimulus in V4's receptive field (Moore & Armstrong, 2003). This result highlights the modulatory nature of the spiking enhancement in V4 by FEF: top-down signals from FEF can increase spiking rates in V4, given that V4 is activated by stimuli presented in its receptive field. Otherwise, when V4 neurons were not stimulated in their receptive fields (no feedforward drive), feedback signals from FEF did not result in an increase in their firing rate.

In a recent spatial attention paradigm in macaques, feedback from FEF to the visual motion processing medial temporal (MT) area was inactivated using optogenetics (Hüer et al., 2024). The study showed that the feedback-mediated attentional modulation suppressed distractors in MT and enhanced the sustained (after 300 ms from stimulus onset) responses in the attended area in a classic "push–pull" effect. This study highlights both the inhibitory and enhancing modulatory properties of feedback.

To summarize, the effects of feedback in early visual areas seem to be, in general, modulatory. These modulatory effects can involve enhancing specific attributes of the feedforward signal (e.g., center receptive field responses) or inhibiting it (e.g., surround response suppression). Importantly, the removal of feedback signals has been shown to have limited effects in early visual areas. On the other hand, inactivating the feedforward drive from V1 silences areas up the visual hierarchy (except for some dorsal visual areas that receive direct drive from subcortical regions), consistent with the idea that feedback cannot drive early visual areas. This suggests that the primary role of feedback is to refine visual processing, complementing rather than replicating or replacing feedforward mechanisms.

Psychophysical Evidence for and Against the Spiking Hypothesis

As an indirect probing method, psychophysics with human participants can serve as a valuable tool to clarify the role of feedback connections during visual imagery. Specifically, visual adaptation can provide insights into the nature of feedback effects. In considering a simplistic view of adaptation that solely examines neural fatigue, sustained increases in firing rates should inevitably lead to adaptation. Conversely, if feedback only exerts modulatory effects, with minimal increases in mean firing rates, we anticipate only priming effects and no adaptation. This perspective has notable limitations since visual adaptation is supported by different mechanisms in various contexts (Kohn, 2007; Webster, 2015). However, it is reasonable to assume that a sustained rise in spiking rate in the temporal scales necessary for visual imagery (from seconds to minutes) would eventually lead to adaptation, as observed for perceptual stimulation (Müller et al., 1999; Patterson et al., 2013).

Priming and adaptation paradigms thus provide complementary tools to disentangle driving from modulatory feedback during imagery. Adaptation can reveal whether feedback directly drives feature-selective neurons: If imagining a stimulus reduces subsequent sensory responses, it suggests that feedback has a driving component capable of reactivating those neural populations. In contrast, if imagery only causes facilitatory or priming effects, independent of previous adaptation (see Psychophysical Evidence Against the Spiking Hypothesis section for details), this indicates that feedback influences neural activity through modulation rather than driving it.

Adaptation has been abundantly used as a tool to probe the mechanisms of perception (Clifford et al., 2007; Kohn, 2007; Krekelberg et al., 2006; Mather et al., 2008; Webster, 2011). By applying this framework to visual mental imagery, research has found both adaptation (suppression) and priming (facilitation) from imagined stimuli, depending on the paradigm and imagery content. These seemingly disparate effects can be reconciled by considering which visual areas (i.e., early visual cortex or higher level visual areas) are targeted by each paradigm and imagery content, as discussed below.

Psychophysical Evidence for the Spiking Hypothesis

Several studies have shown adaptation effects associated with imagining moving stimuli. Static natural images depicting motion have been shown to induce motion after-effects on random dot displays (Winawer et al., 2008). The same effect has also been found after imagining motion repeatedly in one direction (Winawer et al., 2010). It has also been reported that motion imagery is affected by prior perceptual motion adaptation by decreasing the reported imagined motion speed after perceiving motion in the same direction and vice versa (Gilden et al., 1995). Perceptually induced motion after-effects have been shown to slow down reaction times in a mental rotation task, an effect found to be mediated by hV5/MT (Seurinck et al., 2011). These adaptation results associated with the mental imagery of visual motion are consistent with feedback driving motion-sensitive neurons in MT, a middle-level visual area.

Another study examined orientation-specific adaptation to imaginary lines and identified a perceptual tilt aftereffect induced by imagery (Mohr et al., 2009). Interestingly, simultaneous fMRI confirmed a descending gradient of adaptation from V4 to V1 in BOLD responses, with significant adaptation in V4 and V3a but not in early visual areas V1 and V2. This contrasts with results from perceptual stimuli, which demonstrate significant adaptation of BOLD responses from V1 to V4 (Fang et al., 2005; Larsson et al., 2006). These results are compatible with a decrease in the driving effects of imagery as one descends the visual processing hierarchy and a feedback drive in visual areas beyond the early visual cortex.

Notably, although not imagery per se, a visual illusion that is phenomenologically comparable in strength to visual imagery: The neon color spreading illusion, was shown to produce suppressive effects on subsequent binocular rivalry (Chang & Pearson, 2020). This adaptation effect suggests an increase in the excitatory drive of neurons coding for the illusory color. This is consistent with neurophysiological studies in animals showing that contextual perceptual stimulation induces spiking in early visual areas mediated by mechanisms including short-range feedback (Murray & Herrmann, 2013).

The studies discussed here indicate that visual imagery can lead to visual adaptation when the visual features of imagined stimuli are encoded beyond early visual areas, consistent with driving effects of feedback in visual areas beyond V1 and V2.

Psychophysical Evidence Against the Spiking Hypothesis

Early experiments indicated that visual imagery has a priming effect on perceptual detection rates (Farah, 1985; Segal & Fusella, 1970), followed by reports of facilitatory effects of imagery in contrast detection thresholds (Ishai & Sagi, 1995, 1997). Further, a series of experiments has established that visual imagery biases subsequent ambiguous perception toward the imagined stimuli (Chang & Pearson, 2017; Chang et al., 2013; Keogh & Pearson, 2014; Kwok et al., 2019; Maróthi & Kéri, 2018; Pearson et al., 2008). This imagery-perception priming paradigm uses short binocular rivalry presentations preceded by a period of imagery. Results show that imagining one of the rival images; or even stimuli that share attributes, such as color, with the rival stimuli (Kwok et al., 2019) biases binocular rivalry dominance toward the imagined stimulus. Several experiments have shown that the effects of imagery on binocular rivalry can be disrupted by manipulating low-level stimulus properties such as background luminance, retinotopic location and orientation, thus indicating that these effects depend, at least in part, on the early visual cortex (Bergmann et al., 2016; Chang et al., 2013; Keogh & Pearson, 2011; Pearson & Kosslyn, 2015; Pearson et al., 2008; Sherwood & Pearson, 2010). Moreover, while current evidence indicates that binocular rivalry is likely resolved at different levels throughout the cortical hierarchy, an essential aspect of this phenomenon is the competition among monocular neurons in the primary visual cortex (Tong et al., 2006), thereby making binocular rivalry an effective tool for investigating mechanisms related to early visual areas.

Research has shown that the priming effects of visual imagery on binocular rivalry mimic weak perceptual stimulation (Pearson et al., 2008, 2015). The priming effects of perception have been explained by a model based on the stimulus energy (Brascamp et al., 2007). Priming effects are generated by low-intensity or very brief perceptual stimuli, while high-intensity or lengthy perceptual stimuli lead to suppressive effects due to adaptation. Intriguingly, unlike perception, visual imagery consistently leads to priming effects (facilitation) even for extended imagery periods and high vividness (Pearson et al., 2008). This stands in stark contrast to what a visual stimulus can produce, as it can either elicit priming or suppression (adaptation) during subsequent rivalry based on its energy level—weak or strong, respectively.

An issue arises with the above results, as it remains unclear whether the lack of adaptation stems from visual imagery's inability to produce increases in spiking and subsequent adaptation, or if imagery does increase spiking, but the increase is too weak to lead to any adaptation by itself. Instead of trying to induce adaptation with visual imagery, a recent study directly tested whether visual imagery can add to perceptual visual adaptation for features believed to be coded in the early visual cortex (Pace et al., 2023). In this experiment, monochromatic-oriented Gabor gratings were used to induce adaptation. Then, participants imagined such gratings and the effect of imagery on the adapted neurons was indirectly tested using binocular rivalry priming and perceptual discrimination. The rationale was as follows: If visual imagery were to increase firing rates, imagining the adapted grating should further increase adaptation, as a weak perceptual stimulus should do. If, on the other hand, imagery does not increase firing, then imagery should not add to adaptation. The results showed that imagery not only failed to demonstrate any increases in adaptation but instead reversed the effects of prior perceptual adaptation by suppressing the representation of the orthogonally oriented grating, as shown by a discrimination experiment. This study also tested whether the effects of visual imagery could be replicated by using a weak perceptual stimulus, that is, whether small increases in firing rates elicited by weak Gabor gratings could reverse adaptation. The results revealed that weak perceptual stimuli increased adaptation instead of reversing it as imagery did. Recently, an independent psychophysics study inspired by the abovementioned results confirmed that imagery exerts its effects via suppression rather than activation, while also expanding on previous findings (S. Zhang et al., 2025). The study employed a series of psychophysical discrimination tests preceded by imagery, with systematic variations in stimulus orientation in the test stimuli. The results show that imagery produced bias patterns consistent with a W-shaped, suppressive tuning profile, thereby supporting the suppression hypothesis. Conversely, perception generated activation-like biases in the form of a bell-shaped curve. These two independent studies provide strong empirical support for the reshaping hypothesis.

To summarize, some psychophysical results have revealed imagery-induced adaptation, while others have shown priming (for a summary, see Table 3). Notably, a study investigating the effect of imagery on adapted representations showed that imagery reverses the functional effects of adaptation in binocular rivalry, consistent with an inhibitory modulatory effect of feedback. We argue that these disparate effects can be reconciled by considering where, in the visual hierarchy, the effects of imagery are tested. The results discussed so far indicate that visual imagery in areas beyond the early visual cortex (such as medial superior temporal area, MT, and V4) is likely to yield suppressive effects (adaptation). Conversely, visual imagery experiments that involve detecting low-intensity stimuli and binocular rivalry consistently result in priming, with these paradigms likely engaging early visual areas. It is worth noting also that a contextual perceptual illusion, the neon color spreading illusion, induces suppressive effects consistent with results from neurophysiology. All-in-all, these results suggest that the driving effects from long-range feedback decrease from high-level regions to lower level visual areas, showing mostly modulatory effects on early visual areas in the absence of visual stimulation.

The Spontaneous Activity Reshaping Hypothesis

If feedback connections do not drive spiking in early visual areas in the absence of visual stimulation, how does visual imagery create the conscious experience of seeing with the mind's eye? How are mental images' fine details (likely coded in early visual areas) generated? How do early visual areas produce and store specific information about the contents of imagery, as evidenced by MVPA experiments? One clue to resolve this mystery could be hidden in the ongoing activity dynamics of visual areas, known as spontaneous activity. Early visual areas have a significant baseline level of spontaneous or ongoing activity in the absence of visual stimulation (Arieli et al., 1995; Goldberg et al., 2004; Greenberg et al., 2008; Omer et al., 2019; Pezzulo et al., 2021). Research has shown that this phenomenon is not limited to sensory cortices but encompasses the entire brain, which, instead of mainly responding to changes in the

external environment through sensory stimulation, is fundamentally intrinsically driven, displaying internal dynamics largely invariant to external stimulation (Engel et al., 2013; Raichle, 2010; Q. Zhang et al., 2022). This has led to the notion that the brain is not in a silent state waiting for sensory stimulation but is instead always active, showing intrinsic activity dynamics, which in turn interact with external stimulation (Arieli et al., 1996; Avitan & Stringer, 2022; Pezzulo et al., 2021; Uddin, 2020). Interestingly, as opposed to the intuition that V1 dynamics are primarily driven by photic stimulation, neurophysiology has shown that the spontaneous activity dynamics in V1 (its spatiotemporal spiking pattern) are only modestly modulated by perceptual input (Fiser et al., 2004), explaining, for example, why trial-to-trial neural responses, and also behavior, are so dependent on the ongoing state of the cortex (Roitman & Shadlen, 2002; Samaha et al., 2020; Truccolo et al., 2002).

Recent research has shown that spontaneous activity has some remarkable properties: Most of the brain's metabolism is devoted to it (Raichle, 2010), is highly structured, resembling perceptually evoked activity (Avitan & Stringer, 2022; Cai et al., 2005; Cossart et al., 2003; Omer et al., 2019; Tsodyks et al., 1999), represents internal models of the environment (Berkes et al., 2011; Pezzulo et al., 2021), may represent sensory predictions (Arnal & Giraud, 2012), accounts for the large variability in behavior (Fox et al., 2006, 2007), and it is organized in harmonic wave patterns (Atasoy et al., 2016). Of interest for our discussion, it has been shown that visual representations in early visual areas can emerge spontaneously from spontaneous activity in the absence of sensory stimulation (Han et al., 2008; Kenet et al., 2003).

Next, we ask: How does visual imagery connect to spontaneous activity in visual areas? We propose that visual imagery leverages the spontaneous neural activity in the early visual cortex rather than driving spikes, explaining many of the functional effects of imagery, including the lack of adaptation in early visual areas. We call this the spontaneous activity reshaping hypothesis. This hypothesis posits that feedback elicited by imagery acts as a selective filter (through inhibitory modulation) applied to spontaneous neural activity in early visual areas, analogous to (and likely using the machinery of) selective visual attention (Heeger & Zemlianova, 2020; Hüer et al., 2024; Reynolds & Heeger, 2009). Feedback connections would tune the spontaneous spiking activity toward the imagined percept by suppressing neurons that code for unrelated features (see Figure 2). Under this framework, the spontaneous activity in early visual areas would provide a sort of "constant feedforward drive" on which modulatory feedback mechanisms act. This hypothesis can explain the neural and behavioral effects of imagery (and feedback in general) in early visual areas while being consistent with the suppressive mechanisms mediated by feedback that are at the center of current models of brain function (Alink et al., 2010; Auksztulewicz & Friston, 2016; Bastos et al., 2012; Rao & Ballard, 1999; Shipp, 2016; Spratling, 2008).

The proposal that visual mental imagery might employ inhibitory mechanisms builds upon extensive evidence from attention and visual working memory for multiple forms of internally guided top-down suppression. For example, it has been shown that spatially specific inhibition in V1 reduces activity at unattended locations (Slotnick et al., 2003), while feature-based mechanisms suppress task-irrelevant features across the visual field (Störmer & Alvarez, 2014), with attention-related inhibition operating throughout the visual hierarchy from V1 to V4, becoming stronger as receptive fields enlarge (Desimone & Duncan, 2025; Luck et al., 1997; Moran & Desimone, 1985). These suppressive mechanisms extend beyond attention to internally maintained representations in visual working memory (Dube et al., 2016; Feldmann-Wüstefeld & Vogel, 2019; Lu et al., 2017; Sawaki & Luck, 2011), operating through both rapid direct suppression and learned predictive filtering (Moher et al., 2014; van Moorselaar & Slagter, 2020; van Moorselaar et al., 2020, 2021). Most critically for imagery, internally guided suppression demonstrates precise feature-specificity (Wegener et al., 2008), and feature-based attention can even inhibit ongoing endogenous neural activity before distractor presentation (van Moorselaar et al., 2020), suggesting a plausible framework for how visual mental imagery might suppress non imagined representations within spontaneous visual activity.

A schematic representation of the differences between the spontaneous activity reshaping hypothesis and the spiking hypothesis of visual imagery on population spiking in visual areas is depicted in Figure 2. In this example, if one imagines a square, according to the spontaneous activity reshaping hypothesis, feedback would retinotopically suppress neurons that code for unrelated contour orientations (Figure 2), thus effectively creating the representation of the imagined object by "carving" it in the spontaneous activity. While it is physiologically plausible that this "selective filter" mechanism would also enhance activity related to the imagined object, we believe this is likely to be of limited effect in early visual areas, as strong enhancement of spiking rates for imagined features would otherwise lead to adaptation. We want to emphasize that we propose these two feedback function hypotheses (the spontaneous activity reshaping and spiking hypotheses) are not mutually exclusive, but rather exist at different levels of the visual system hierarchy (as previously suggested; Dijkstra et al., 2025). As discussed above, the spiking hypothesis accounts best for the effects of imagery in higher visual areas, while the spontaneous activity reshaping hypothesis accounts for the effects in early visual areas. The spontaneous activity reshaping hypothesis also explains why imagery is invariably subjectively weaker than perception, as it does not drive spiking in early visual areas. Naturally, this hypothesis also explains why the effects of imagery in lower visual areas are often facilitatory (i.e., priming) and not suppressive (adaptation) after long exposures or high intensities (vividness).

Besides the hypothetical shared neural mechanisms between feature-selective attention and imagery, is there empirical evidence supporting the mechanisms required to implement the spontaneous activity reshaping hypothesis? According to this hypothesis, imagery would need to code for visual objects by silencing rather than activating neurons in early visual areas. It has been recently shown that perceptual stimuli can be encoded by specific patterns of inactivation in V1 neurons (the offsemble, representing ~26% of neurons), along with activated neurons (the onsemble, ~20% of neurons), and, importantly, that the information contained in the silenced neurons is sufficient to decode such stimuli accurately (Pérez-Ortega et al., 2024). These findings suggest a plausible neural mechanism for encoding imagined content in early visual areas, where only an offsemble is recruited through inhibition. Does this mean that all neurons coding features not being imagined need to be inhibited? Most likely not. First, as noted above, offsemble neurons represent about a quarter of V1 neurons during perceptual encoding, from which only a fraction is recruited to code for a given stimulus (Pérez-Ortega et al., 2024). In addition, it has been shown that only a

surprisingly small number of neurons, about 14 pyramidal neurons, are required to support perception (Dalgleish et al., 2020). This implies that suppressive mechanisms would only have to make subtle changes to the spontaneous activity to bias it toward encoding imaginary content. Referring back to our visual illustration, this suggests that the example square in Figure 2 could be represented using broken edges rather than continuous lines, with notably less inhibition than what is implied by the figure. It is also possible that the inhibition could be targeted at features that help discriminate the imagined stimuli, such as local orthogonal orientations—as suggested by the selectivity of offsemble neurons (Pérez-Ortega et al., 2024)—rather than all other orientations at all other locations. Such sparse inhibitory coding could explain why the phenomenology of visual imagery is less vivid and weaker than visual perception with retinal input. At the same time, presently, it remains largely unknown how extensive the inhibition is during visual imagery. Is there evidence of widespread cortical inhibition that could support versions of the spontaneous activity reshaping hypothesis involving significant mass inhibition? A series of studies has indicated that mass inhibition is a feature implemented in the brain. Indeed, extensive inhibition seems to be crucial to stabilize brain activity (i.e., impede runaway excitation) and forms part of cortical computation (Herstel & Wierenga, 2021; Mongillo et al., 2018; Sadeh & Clopath, 2021). This, in addition to findings showing that inhibition dominates sensory responses (Haider et al., 2013) and that most recurrent activity produces net inhibition (Oldenburg et al., 2024), shows that the neural mechanisms that could support versions of the ongoing activity reshaping hypothesis with mass inhibition are not only plausible but already implemented, and currently shown to support other functions. A final question is why imagery would need to be coded through inhibition rather than excitation in the early visual cortex, given that both mechanisms might seem equally plausible at first glance? There may be a significant reason why coding imagery would favor inhibition over driving, and this could relate to preventing imagined stimuli from being confused with "bottom-up" perceptual stimuli content. Similarly, this may explain why feedback interacts with visual sensory signals in early visual areas, boosting spiking through attention, but it would not do so with imagined representations. Clearly differentiating the neural mechanisms and functional effects of actual perception and imagined content most likely offers adaptive benefits by preventing the confusing overlap between reality and imagination, as evidenced by the harm caused by psychosis. This is compatible with and adds to existing proposed frameworks that explain how imagined content is separated from visual perception (Dijkstra et al., 2022; Dijkstra & Fleming, 2023).

The hypothetical framework we propose here generates testable predictions. The spontaneous activity reshaping hypothesis suggests that, on average, the spiking rate in early visual areas will be lower during imagery compared to spontaneous activity because of the trade-off between the inhibition of unrelated features and the enhancement of the imagined ones. Second, because spontaneous activity is dynamic, the experience of visual imagery is expected to change over time. This means that mental images will feel constantly shifting (in contrast to the stability experienced during static visual perception), regardless of our efforts to stabilize them, as the unfiltered, spontaneous activity evolves, thus altering the foundation on which visual imagery operates.

A direct test of whether the spiking rate in early visual areas decreases during imagery compared to spontaneous activity would likely require invasive recordings. However, noninvasive methods can be used to indirectly test core predictions of the reshaping hypothesis. For instance, functional magnetic resonance spectroscopy (fMRS) can be used to test whether visual imagery is mediated by extensive local inhibition rather than excitation in early visual areas. Another predicted feature of visual imagery is its fluctuating nature over time. This can be assessed and measured using psychophysics, such as tracking trial-to-trial changes in imagery strength (Pearson et al., 2011), but also by tracking changes within each trial (variability from time point to time point), enabling us to infer its temporal dynamics and compare them with the spontaneous activity dynamics. Crucially, the reshaping hypothesis predicts that imagery should not add to perception-driven adaptation, which was successfully tested for stimuli coded in early visual areas (Pace et al., 2023). Indeed, this study found that imagery suppresses features absent from the imagined stimulus, akin to attentional filtering, as predicted. Similar experiments can be designed to test stimuli coded higher up in the visual hierarchy (such as faces) and determine whether visual imagery would add to adaptation as predicted in this case.

How does our proposed neural mechanism explain the variations in imagery vividness and strength among individuals and account for extremes like aphantasia and hyperphantasia? Since the spontaneous activity reshaping hypothesis requires inhibitory mechanisms to encode imagined content in early visual areas, the relative strength of inhibitory circuits or the balance between excitation and inhibition in these regions should predict the subjective vividness of visual imagery. Accordingly, stronger inhibitory gain would translate into a stronger reshaping of the spontaneous activity through inhibition, which in turn should correlate with higher vividness. On the other hand, increased visual cortex excitability, which implies weaker inhibitory gain, should relate to lower vividness. Indeed, early visual cortex excitability, as measured by phosphene thresholds, has been linked to decreased imagery strength (Keogh et al., 2020). Moreover, this study demonstrated a causal role of excitability in imagery strength by showing that reducing visual cortex excitability with transcranial direct current stimulation (tDCS) enhances imagery strength. In summary, this research suggests that strengthening inhibitory tone results in stronger imagery. Therefore, changes in the excitation-inhibition balance, particularly the relative strength of inhibition in the visual cortex, could account for the spectrum of imagery strength from aphantasia to hyperphantasia, due to weak and strong inhibitory control, respectively.

Concluding Remarks

In conclusion, we have explored the potential neurophysiological mechanisms through which imagery recruits visual areas via feedback. We have observed that while it is implicitly assumed that visual imagery induces spiking in early visual areas without visual stimulation, both neurophysiological and psychophysical data contest this assumption. We propose a reshaping spontaneous activity hypothesis that aligns with neurophysiological evidence, drawing upon established neural mechanisms employed by attention, perceptual encoding, and network dynamics and reconciling the varied impacts of visual imagery and feedback, as found in the literature at both neural and behavioral levels. We believe this proposed hypothesis will be

beneficial for future investigations into the mechanisms of visual imagery and feedback, not by resolving the debate but rather by invigorating the discussion and ultimately inspiring experiments to test these hypotheses directly. We contend that studying visual imagery may be the ideal model for addressing some of the fundamental classic questions regarding the role of feedback in brain function.

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