

Is V1 a Cognitive Map?

Short Description

A ‘Cognitive Map’ is an internal model of space upon which we can scaffold our judgments about the world [1]. The question this GAC seeks to resolve is whether V1 acts as a ‘Cognitive Map’ in humans? In answering this question, our goal is to connect Cognitive Science back to the Computational Neuroscience of V1. There’s been a raft of suggestive evidence of ‘cognitive’ processing in V1 over the last 20 years, but comparatively little stepping back and asking ‘what does it all mean?’ By contrast, the goal of Cognitive Computational Neuroscience is not just to link neural processes with computational principles, but also to explore what they mean for our experience of the world?

Scientific Question and Background

There is a fundamental tension at the heart of the literature on the Primary Visual Cortex (V1). On the one hand, there is suggestive evidence of multisensory and cognitive processing in V1, suggesting that V1 operates as a 3D ‘Cognitive Map’ with visual and non-visual signals integrated together in 3D space. By contrast, in other areas of the literature, V1 is treated merely as a preliminary stage in visual processing. For instance, the general consensus in the 3D vision literature is that our perception of 3D space emerges much later along the dorsal and ventral streams [2], [3], [4], [5], and so V1 is merely a preliminary processing step. To explain these very different approaches to V1:

1. Standard Model (1970s-1990s) – Feedforward Processing in V1

The ‘Standard Model’ of V1, which dominated the field in the 1970s-90s, treats V1 as feedforward, and pretty well understood: “*V1 is one of the best understood areas of the cerebral cortex, and constitutes a prime workbench for the study of cortical circuits and of computations. ... we understand the nature of its main inputs, we know what stimuli make its neurons fire...*” [6]. The ‘Standard Model’ is based on three components: 1. a weighted sum [7], [8], 2. rectification [9], and 3. normalization [10], [11], and has the effect of enhancing edges and contours, the first step in traditional image processing [6], [12].

The first question for this GAC is how much of V1 can be explained by the ‘Standard Model’? One of the perennial challenges to the ‘Standard Model’ is how much variance in V1 responses it explains? This came to a head with a series of articles in 2005-6: ‘How Close Are We to Understanding V1?’ [13], ‘Do We Know What the Early Visual System Does?’ [14], and ‘What is the other 85% of V1 doing?’ [15], the argument being that the ‘Standard Model’ only explains roughly 10%-20% of V1 responses to natural stimuli. 20 years on, and numerous discoveries about V1 later, to what extent can V1 responses be explained by the ‘Standard Model’? [16], [17], [18].

2. Questioning the Standard Model (2000s-Present) – Feedback and Recurrent Processing in V1

The key challenge for the ‘Standard Model’ is that V1 receives considerable feedback from higher visual areas, as well as long-range connections, and engages in recurrent processing. The question is, what is this processing doing?

1. ‘Standard Model’ with Attention: The first attempt at capturing feedback responses in V1 was to add attentional modulation to the ‘Standard Model’ [19], [20]. As Lee & Mumford [21] noted in 2003: “*A prevalent view in the biological community on the role of feedback among the cortical areas is that of selective attention modeled by biased competition.*”

2. Bayesian Processing: The alternative, which Lee & Mumford [21] and Rao & Ballard [22] advanced, is that V1 should be understood as part of larger Bayesian processing chain that spans across the visual cortices: “*recurrent feedforward/feedback loops in the cortex serve to integrate top-down contextual priors and bottom-up observations so as to implement concurrent probabilistic inference along the visual hierarchy.*” [21] It’s important to note that under this account “low level visual computation cannot be completed before high level computations are begun” [23]. Others suggest V1 itself may be the site of Bayesian processing [24], [25], [26]. Bayesian accounts are popular accounts of perception [27], but do they apply to V1? Lee & Mumford (2003) [21] hoped that their account would “revolutionize how we think about neural and computational processes underlying vision.” 20 years later, does the evidence support this?

3. ‘Cognitive Map’: A ‘Cognitive Map’ is an internal model of (2D or 3D) space upon which we can scaffold our judgments about the world. We traditionally think of the Hippocampus as a ‘Cognitive Map’ (internal model) of *allocentric* space. Might V1 play a similar role as an internal model of *retinotopic* / *egocentric* space? [28]. Mumford [29] suggested that V1 might act as a ‘Visuospatial Blackboard’ where V1 functions as “*the one and only high-resolution visual buffer in the neo-cortex, which is involved in all the computations which need high resolution, such as recognizing objects and discovering differences between memories and current stimuli, when details are crucial.*” This approach has been developed today by Roelfsema & de Lange [30]. By contrast, Zhaoping argues that the visual pathway from V1 to higher cortical areas acts as an ‘attentional bottleneck’, and so V1 has to guide attentional selection by creating a ‘Saliency Map’ and engaging higher brain areas by feedforward and feedback connections through this ‘attentional bottleneck’ [31], [32].

3. Linking V1 to Perceptual Experience

In 1995, Crick & Koch [33] asked: ‘**Are we aware of neural activity in primary visual cortex?**’ Similarly, in ‘What is the other 85% of V1 doing?’, Olshausen & Field [15] ask: **What is V1’s relation to perceptual experience?**

The last 30 years has seen considerable debate on this question [34], [35]. However, one key point that has been largely overlooked in the Consciousness literature is that whilst our visual experience is three-dimensional, the general consensus in the 3D vision literature is that 3D visual experience happens much later than V1 [2], [3], [4], [5].

But this consensus is worth reconsidering. As Olshausen & Field [15] note: “*We live in a three-dimensional world, and the fundamental causes of images that are of behavioral relevance are surfaces, not two-dimensional features such as spots, bars, edges, or gratings. ... It thus seems quite reasonable to think that the visual cortex has evolved effective means to parse images in terms of the three-dimensional structure of the environment*”. On the one hand, there is some suggestive evidence of 3D processing in V1: First, modulation of V1 with eye movements arguably suggests that V1 cells “are dedicated to certain volumes of visual space” [36]. Second, one of the leading accounts of perceptual ‘size constancy’ is that it relies on distorting the receptive fields of V1 neurons [37], [38]. On the other hand, as we have already noted, when it comes to 3D visual experience, the general consensus in the 3D vision literature is that it occurs much later [2], [3], [4], [5].

Challenge or Controversy

This GAC is an opportunity to definitively resolve these questions which have remained open for the last 20 years, and to consider what impact the last 20 years of research into V1 has had on our understanding. We will ask:

1. **How much of V1 processing can be accounted for using the ‘Standard Model’?**
2. **What evidence is there of V1 acting as a ‘Cognitive Map’ and/or reflecting Bayesian Processing?**
3. **How (if at all) is perceptual processing in V1 related to our visual experience?**

Plan for GAC Kickoff Workshop

These are questions that have remained unresolved for 20 years, so the CCN Kickoff Workshop is a crucial opportunity to engender a discussion within the CCN community. The idea is to break the GAC Kickoff into two parts: **1. Debate:** First, a 1-hour debate between the two sides with 3 talks for the ‘Cognitive Map’ hypothesis and 3 talks against, each talk strictly limited to 10 minutes. This will give everyone at CCN an introduction to the issues at stake. **2. CCN Community Discussion:** Second, a 45-minute open discussion within the CCN Community that is focused on devising experimental strategies that would resolve these key tensions in our understanding of V1.

Competing hypotheses and proposed approach for resolution

The **Debate** and **Discussion** at CCN will be structured around the three aspects of *Cognitive Computation Neuroscience*:

1. Neuroscience

First, we will evaluate the evidence of ‘cognitive’ processing in V1 that has emerged over the last 20 years, including:

1. Figure-Ground / Object-Based Attention: Whilst V1 identifies edges / boundaries in the feedforward sweep, the spread of attention to the rest of the object typically relies on feedback from higher visual areas to V1 [39], with V1 implicated in this spread of attention when the details that the visual system needs to resolve are small enough to require V1’s resolution [40]. Here, [41] find evidence for V1’s causal role: if the late phase of V1 responses are inhibited in mice, mice can’t carry out figure-ground segmentation, even though they do see simple contrasts.

2. Decision Related Signals: There is accumulating evidence of decision related signals in V1 [42], [43]. However, the evidence continues to go both ways. On the one hand, [44] find that decision related feedback is not spatially selective in the way that we might expect if it was task specific, and [45] find only weak evidence for decision related signals in V1. On the other hand, [46] find evidence that primate V1 can process multiple decisions in parallel, [47] find evidence that attentional signals in visual and frontal cortex of primates emerge at the same time, and [48] find that V1 responses reflect task uncertainty (with microstimulation inducing appropriate errors in macaques).

3. Visual Routines: Activity in V1 activation also mirrors the ordering in time of different cognitive tasks [49], and [50] exploit this to recover the time of individual stages of a self-timed sequential cognitive task in macaques.

4. Imagery: Does V1 represent the visual scene in the absence of visual stimulation? A series of fMRI studies [51], [52], [53] have shown that when a section of a familiar image is blanked out (removing visual stimulation), contextual feedback still activates V1. These results have now been replicated using electrophysiology in macaques, showing as much correlation between humans and macaques, as between individual humans [54].

5. Multisensory Processing: [55] argue that “convergence and integration of information from different senses within low-level cortices is a rule rather than an exception...” For instance, the semantic category of sounds (bird song vs traffic vs talking) can be decoded from peripheral V1 activation in blindfolded human fMRI subjects [56], leading [57] to “endorse the [view] that V1 acts as a screen where the brain projects its internal world...”

6. Bodily Movement: The last decade has seen well documented evidence of bodily motion being processed in the mouse V1 [58], [59], [60]. However, this is one area where non-visual processing in V1 does not appear to extend to primates [61], [62](see [63] for discussion). For instance, [62] found evidence of bodily motion modulating the macaque V1, but this effect largely disappeared once changes in the retinal image were controlled for, concluding that “activity in the primate visual areas is only minimally modulated by the animal’s own body movements.”

2. Computation

Second, the presence of non-visual feedback does not tell us what (if anything) V1 is doing with it. Consistent with later iterations of the ‘Standard Model’, it could be attention. But it could also be evidence of Bayesian processing, higher-level cognitive processing, and/or V1 functioning as a ‘Cognitive Map’. We will evaluate these alternatives.

3. Cognition

Third, we connect these discussions back to perception. Specifically, what predictions about experience and behavior do the different models of V1 make? And how can these predictions be tested? Here we will focus on engendering a discussion within the CCN Community with the intention of developing testable experimental hypotheses.

Benefit to the Community

As we have outlined, many of these questions were raised 20 years ago, and yet have never been definitively answered. Part of the reason is that two communities – those treating V1 as largely feedforward, and those treating V1 as largely ‘cognitive’ – exist relatively independently of each other. This GAC brings them into conversation with each other.

Concrete Outcomes

Beyond the review article, the aspiration of this GAC is that we will identify key experiments that would resolve these fundamental tensions in our understanding of V1 and build collaborations across these two communities.

Team

Senior Members	Nikolaus Kriegeskorte (Columbia University) (Lead Senior Member): Computational models of vision, with a focus on deep neural networks and recurrent neural networks.
<i>Pro-Cognitive Map</i>	<p>Lars Muckli (University of Glasgow): Work from lab on human fMRI indicating both multisensory (sound) and imagery (occluded scenes) feedback to V1.</p> <p>Pieter Roelfsema (Netherlands Institute for Neuroscience): Advocate for ‘visuospatial blackboard’. Work from lab on both the feedforward and feedback aspects of V1.</p> <p>Petra Vetter (University of Fribourg): Work on multisensory processing in V1 as well as V1 processing in the congenitally blind (‘Mapping Space in the Blind Brain’).</p> <p>Li Zhaoping (Max Planck Institute for Biological Cybernetics): Developed framework that argues for V1’s role in vision in light of an ‘attentional bottleneck’.</p>
<i>Anti-Cognitive Map</i>	<p>David Heeger (New York University): Along with Tony Movshon, played a key role in the development of the ‘Standard Model’ of V1.</p> <p>Tony Movshon (New York University): Along with David Heeger, played a key role in the development of the ‘Standard Model’ of V1.</p> <p>Hendrikje Nienborg (National Eye Institute): Work from lab shows that modulation of V1 by bodily movement in macaques largely due to changes in retinal image.</p> <p>Andrew Parker (Otto von Guericke University of Magdeburg): Work from lab indicates that stereo vision, and 3D vision in general, is post-V1 in humans.</p>
Junior Members	<p>Paul Linton (Kriegeskorte Lab) (Lead Junior Member) Lucy Petro (Muckli Lab)</p> <p>Paolo Papale (Roelfsema Lab) Cheng Xue (Marlene Cohen Lab)</p>

Commitment: We are committed to the GAC process and look forward to engaging with the CCN Community.

References

- [1] J. O’Keefe and L. Nadel, *The Hippocampus as a Cognitive Map*. Clarendon Press, 1978.
- [2] A. J. Parker, J. E. T. Smith, and K. Krug, “Neural architectures for stereo vision,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 371, no. 1697, p. 20150261, Jun. 2016, doi: 10.1098/rstb.2015.0261.
- [3] B. G. Cumming and G. C. DeAngelis, “The physiology of stereopsis,” *Annu Rev Neurosci*, vol. 24, pp. 203–238, 2001, doi: 10.1146/annurev.neuro.24.1.203.
- [4] A. E. Welchman, “The Human Brain in Depth: How We See in 3D,” *Annual Review of Vision Science*, vol. 2, no. 1, pp. 345–376, 2016, doi: 10.1146/annurev-vision-111815-114605.
- [5] A. J. Parker, “Binocular depth perception and the cerebral cortex,” *Nature Reviews Neuroscience*, vol. 8, no. 5, Art. no. 5, May 2007, doi: 10.1038/nrn2131.
- [6] M. Carandini, “Area V1,” *Scholarpedia*, vol. 7, no. 7, pp. 12105, revision #137292 (30th October 2013), 2013 2012, doi: 10.4249/scholarpedia.12105.
- [7] C. Blakemore and F. W. Campbell, “On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images,” *J Physiol*, vol. 203, no. 1, pp. 237–260, Jul. 1969.
- [8] F. W. Campbell and J. G. Robson, “Application of Fourier analysis to the visibility of gratings,” *J Physiol*, vol. 197, no. 3, pp. 551–566, Aug. 1968, doi: 10.1113/jphysiol.1968.sp008574.
- [9] J. A. Movshon, I. D. Thompson, and D. J. Tolhurst, “Spatial summation in the receptive fields of simple cells in the cat’s striate cortex,” *J Physiol*, vol. 283, pp. 53–77, Oct. 1978.
- [10] D. J. Heeger, “Normalization of cell responses in cat striate cortex,” *Vis Neurosci*, vol. 9, no. 2, pp. 181–197, Aug. 1992, doi: 10.1017/s0952523800009640.
- [11] D. J. Heeger, “Nonlinear model of neural responses in cat visual cortex,” in *Computational models of visual processing*. Cambridge, MA, US: The MIT Press, 1991, pp. 119–133.
- [12] D. Marr, *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. Cambridge, MA: MIT Press, 1982.
- [13] B. A. Olshausen and D. J. Field, “How close are we to understanding v1?,” *Neural Comput*, vol. 17, no. 8, pp. 1665–1699, Aug. 2005, doi: 10.1162/0899766054026639.
- [14] M. Carandini *et al.*, “Do We Know What the Early Visual System Does?,” *J. Neurosci.*, vol. 25, no. 46, pp. 10577–10597, Nov. 2005, doi: 10.1523/JNEUROSCI.3726-05.2005.
- [15] B. A. Olshausen and D. J. Field, “What Is the Other 85 Percent of V1 Doing?,” in *23 Problems in Systems Neuroscience*, J. L. van Hemmen and T. J. Sejnowski, Eds., Oxford University Press, 2006, p. 0. doi: 10.1093/acprof:oso/9780195148220.003.0010.
- [16] P. Papale *et al.*, “The influence of objecthood on the representation of natural images in the visual cortex.” *bioRxiv*, p. 2021.09.21.461209, Sep. 24, 2021. doi: 10.1101/2021.09.21.461209.
- [17] S. Rawat, D. Heeger, and S. Martiniani, “A comprehensive large-scale model of primary visual cortex (V1),” presented at the COSYNE, 2024.
- [18] S. A. Cadena *et al.*, “Deep convolutional models improve predictions of macaque V1 responses to natural images,” *PLOS Computational Biology*, vol. 15, no. 4, p. e1006897, Apr. 2019, doi: 10.1371/journal.pcbi.1006897.
- [19] G. M. Boynton, “A framework for describing the effects of attention on visual responses,” *Vision Research*, vol. 49, no. 10, pp. 1129–1143, Jun. 2009, doi: 10.1016/j.visres.2008.11.001.
- [20] J. H. Reynolds and D. J. Heeger, “The Normalization Model of Attention,” *Neuron*, vol. 61, no. 2, pp. 168–185, Jan. 2009, doi: 10.1016/j.neuron.2009.01.002.
- [21] T. S. Lee and D. Mumford, “Hierarchical Bayesian inference in the visual cortex,” *J. Opt. Soc. Am. A, JOSAA*, vol. 20, no. 7, pp. 1434–1448, Jul. 2003, doi: 10.1364/JOSAA.20.001434.
- [22] R. P. N. Rao and D. H. Ballard, “Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects,” *Nature Neuroscience*, vol. 2, no. 1, Art. no. 1, Jan. 1999, doi: 10.1038/4580.
- [23] T. S. Lee, D. Mumford, R. Romero, and V. A. F. Lamme, “The role of the primary visual cortex in higher level vision,” *Vision Research*, vol. 38, no. 15, pp. 2429–2454, Aug. 1998, doi: 10.1016/S0042-6989(97)00464-1.
- [24] R. D. Lange and R. M. Haefner, “Task-induced neural covariability as a signature of approximate Bayesian learning and inference,” *PLOS Computational Biology*, vol. 18, no. 3, p. e1009557, Mar. 2022, doi: 10.1371/journal.pcbi.1009557.

- [25] L. Muckli, “What are we missing here? Brain imaging evidence for higher cognitive functions in primary visual cortex V1,” *International Journal of Imaging Systems and Technology*, vol. 20, no. 2, pp. 131–139, 2010, doi: 10.1002/ima.20236.
- [26] D. J. Heeger, “Theory of cortical function,” *Proceedings of the National Academy of Sciences*, vol. 114, no. 8, pp. 1773–1782, Feb. 2017, doi: 10.1073/pnas.1619788114.
- [27] D. C. Knill and W. Richards, *Perception as Bayesian Inference*. Cambridge: Cambridge University Press, 1996.
- [28] P. Linton, “V1 as an egocentric cognitive map,” *Neuroscience of Consciousness*, vol. 7, no. 2, pp. 1–19, Sep. 2021, doi: 10.1093/nc/niab017.
- [29] D. Mumford, “Banishing the homunculus,” in *Perception as Bayesian Inference*, D. C. Knill and W. Richards, Eds., Cambridge: Cambridge University Press, 1996, pp. 501–505. doi: 10.1017/CBO9780511984037.015.
- [30] P. R. Roelfsema and F. P. de Lange, “Early Visual Cortex as a Multiscale Cognitive Blackboard,” *Annual Review of Vision Science*, vol. 2, no. 1, pp. 131–151, 2016, doi: 10.1146/annurev-vision-111815-114443.
- [31] L. Zhaoping, “A new framework for understanding vision from the perspective of the primary visual cortex,” *Current Opinion in Neurobiology*, vol. 58, pp. 1–10, Oct. 2019, doi: 10.1016/j.conb.2019.06.001.
- [32] Z. Li, “A saliency map in primary visual cortex,” *Trends Cogn Sci*, vol. 6, no. 1, pp. 9–16, Jan. 2002, doi: 10.1016/s1364-6613(00)01817-9.
- [33] F. Crick and C. Koch, “Are we aware of neural activity in primary visual cortex?,” *Nature*, vol. 375, no. 6527, Art. no. 6527, May 1995, doi: 10.1038/375121a0.
- [34] M. Boly, M. Massimini, N. Tsuchiya, B. R. Postle, C. Koch, and G. Tononi, “Are the Neural Correlates of Consciousness in the Front or in the Back of the Cerebral Cortex? Clinical and Neuroimaging Evidence,” *J. Neurosci.*, vol. 37, no. 40, pp. 9603–9613, Oct. 2017, doi: 10.1523/JNEUROSCI.3218-16.2017.
- [35] V. A. F. Lamme, H. Supér, R. Landman, P. R. Roelfsema, and H. Spekreijse, “The role of primary visual cortex (V1) in visual awareness,” *Vision Research*, vol. 40, no. 10, pp. 1507–1521, Jun. 2000, doi: 10.1016/S0042-6989(99)00243-6.
- [36] Y. Trotter and S. Celebrini, “Gaze direction controls response gain in primary visual-cortex neurons,” *Nature*, vol. 398, pp. 239–242, 1999, doi: 10.1038/18444.
- [37] S. P. MacEvoy and D. Fitzpatrick, “Visual Physiology: Perceived Size Looms Large,” *Current Biology*, vol. 16, no. 9, pp. R330–R332, May 2006, doi: 10.1016/j.cub.2006.03.076.
- [38] S. O. Murray, H. Boyaci, and D. Kersten, “The representation of perceived angular size in human primary visual cortex,” *Nature Neuroscience*, vol. 9, no. 3, pp. 429–434, Mar. 2006, doi: 10.1038/nn1641.
- [39] J. Poort, F. Raudies, A. Wannig, V. A. F. Lamme, H. Neumann, and P. R. Roelfsema, “The Role of Attention in Figure-Ground Segregation in Areas V1 and V4 of the Visual Cortex,” *Neuron*, vol. 75, no. 1, pp. 143–156, Jul. 2012, doi: 10.1016/j.neuron.2012.04.032.
- [40] A. Pooremaeli and P. R. Roelfsema, “A growth-cone model for the spread of object-based attention during contour grouping,” *Curr Biol*, vol. 24, no. 24, pp. 2869–2877, Dec. 2014, doi: 10.1016/j.cub.2014.10.007.
- [41] L. Kirchberger *et al.*, “The essential role of recurrent processing for figure-ground perception in mice,” *Science Advances*, vol. 7, no. 27, p. eabe1833, Jun. 2021, doi: 10.1126/sciadv.abe1833.
- [42] A. G. Bondy, R. M. Haefner, and B. G. Cumming, “Feedback determines the structure of correlated variability in primary visual cortex,” *Nat Neurosci*, vol. 21, no. 4, pp. 598–606, Apr. 2018, doi: 10.1038/s41593-018-0089-1.
- [43] H. Nienborg and B. G. Cumming, “Decision-Related Activity in Sensory Neurons May Depend on the Columnar Architecture of Cerebral Cortex,” *J. Neurosci.*, vol. 34, no. 10, pp. 3579–3585, Mar. 2014, doi: 10.1523/JNEUROSCI.2340-13.2014.
- [44] K. R. Quinn, L. Seillier, D. A. Butts, and H. Nienborg, “Decision-related feedback in visual cortex lacks spatial selectivity,” *Nat Commun*, vol. 12, no. 1, p. 4473, Jul. 2021, doi: 10.1038/s41467-021-24629-0.
- [45] R. D. Lange *et al.*, “Weak evidence for neural correlates of task-switching in macaque V1,” *J Neurophysiol*, vol. 129, no. 5, pp. 1021–1044, May 2023, doi: 10.1152/jn.00085.2022.
- [46] J. A. M. Lorteije, A. Zylberberg, B. G. Ouellette, C. I. De Zeeuw, M. Sigman, and P. R. Roelfsema, “The Formation of Hierarchical Decisions in the Visual Cortex,” *Neuron*, vol. 87, no. 6, pp. 1344–1356, Sep. 2015, doi: 10.1016/j.neuron.2015.08.015.
- [47] A. Pooremaeli, J. Poort, and P. R. Roelfsema, “Simultaneous selection by object-based attention in visual and frontal cortex,” *Proceedings of the National Academy of Sciences*, vol. 111, no. 17, pp. 6467–6472, Apr. 2014, doi: 10.1073/pnas.1316181111.

- [48] C. Xue, S. K. Markman, R. Chen, L. E. Kramer, and M. R. Cohen, "Task interference as a neuronal basis for the cost of cognitive flexibility." *bioRxiv*, p. 2024.03.04.583375, Mar. 06, 2024. doi: 10.1101/2024.03.04.583375.
- [49] P. R. Roelfsema, P. S. Khayat, and H. Spekreijse, "Subtask sequencing in the primary visual cortex," *Proceedings of the National Academy of Sciences*, vol. 100, no. 9, pp. 5467–5472, Apr. 2003, doi: 10.1073/pnas.0431051100.
- [50] S. I. Moro, M. Tolboom, P. S. Khayat, and P. R. Roelfsema, "Neuronal Activity in the Visual Cortex Reveals the Temporal Order of Cognitive Operations," *J Neurosci*, vol. 30, no. 48, pp. 16293–16303, Dec. 2010, doi: 10.1523/JNEUROSCI.1256-10.2010.
- [51] A. T. Morgan, L. S. Petro, and L. Muckli, "Scene Representations Conveyed by Cortical Feedback to Early Visual Cortex Can Be Described by Line Drawings," *J. Neurosci.*, vol. 39, no. 47, pp. 9410–9423, Nov. 2019, doi: 10.1523/JNEUROSCI.0852-19.2019.
- [52] F. W. Smith and L. Muckli, "Nonstimulated early visual areas carry information about surrounding context," *Proceedings of the National Academy of Sciences*, vol. 107, no. 46, pp. 20099–20103, Nov. 2010, doi: 10.1073/pnas.1000233107.
- [53] L. Muckli *et al.*, "Contextual Feedback to Superficial Layers of V1," *Curr Biol*, vol. 25, no. 20, pp. 2690–2695, Oct. 2015, doi: 10.1016/j.cub.2015.08.057.
- [54] P. Papale *et al.*, "The representation of occluded image regions in area V1 of monkeys and humans," *Current Biology*, vol. 33, no. 18, pp. 3865–3871.e3, Sep. 2023, doi: 10.1016/j.cub.2023.08.010.
- [55] M. M. Murray, A. Thelen, G. Thut, V. Romei, R. Martuzzi, and P. J. Matusz, "The multisensory function of the human primary visual cortex," *Neuropsychologia*, vol. 83, pp. 161–169, Mar. 2016, doi: 10.1016/j.neuropsychologia.2015.08.011.
- [56] P. Vetter, F. W. Smith, and L. Muckli, "Decoding sound and imagery content in early visual cortex," *Curr Biol*, vol. 24, no. 11, pp. 1256–1262, Jun. 2014, doi: 10.1016/j.cub.2014.04.020.
- [57] L. S. Petro, A. T. Paton, and L. Muckli, "Contextual modulation of primary visual cortex by auditory signals," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 372, no. 1714, p. 20160104, Feb. 2017, doi: 10.1098/rstb.2016.0104.
- [58] A. B. Saleem, A. Ayaz, K. J. Jeffery, K. D. Harris, and M. Carandini, "Integration of visual motion and locomotion in mouse visual cortex," *Nat Neurosci*, vol. 16, no. 12, pp. 1864–1869, Dec. 2013, doi: 10.1038/nn.3567.
- [59] C. M. Niell and M. P. Stryker, "Modulation of visual responses by behavioral state in mouse visual cortex," *Neuron*, vol. 65, no. 4, pp. 472–479, Feb. 2010, doi: 10.1016/j.neuron.2010.01.033.
- [60] G. B. Keller, T. Bonhoeffer, and M. Hübener, "Sensorimotor Mismatch Signals in Primary Visual Cortex of the Behaving Mouse," *Neuron*, vol. 74, no. 5, pp. 809–815, Jun. 2012, doi: 10.1016/j.neuron.2012.03.040.
- [61] J. P. Liska *et al.*, "Running modulates primate and rodent visual cortex differently," *eLife*, vol. 12, Jul. 2023, doi: 10.7554/eLife.87736.1.
- [62] B. C. Talluri *et al.*, "Activity in primate visual cortex is minimally driven by spontaneous movements," *Nat Neurosci*, vol. 26, no. 11, pp. 1953–1959, Nov. 2023, doi: 10.1038/s41593-023-01459-5.
- [63] A. V. Askham, "Monkey studies throw wrench into decade-old idea about movement's effect on visual cortex," *The Transmitter: Neuroscience News and Perspectives*. Accessed: Mar. 11, 2024. [Online]. Available: <https://www.thetransmitter.org/animal-models/monkey-studies-throw-wrench-into-decade-old-idea-about-movements-effect-on-visual-cortex/>