Contrast and Size Dependent Contextual Modulation in Primary Visual Cortex: Evidence from Surround Suppression and Facilitation Dynamics

Amna Asif[1], Umair Shakir[1], Rizwan Akhtar[1]
[1] COMSATS University Islamabad, Vehari Campus, Punjab, Pakistan-61100
***Correspondence**: rizwan.ak@gmail.com

Citation | Asif. A, Shakir. U, Akhtar. R, "Contrast and Size Dependent Contextual Modulation in Primary Visual Cortex: Evidence from Surround Suppression and Facilitation Dynamics", FCIS, Vol. 02 Issue. 3 pp 108-117, July 2024
Received | June 09, 2024, **Revised |** July 11, 2024, **Accepted |** July 13, 2024, **Published |** July 14, 2024.

Purpose:
Contextual modulation in the primary visual cortex (V1) plays a crucial role in shaping visual perception by integrating information from within and beyond the classical receptive field (CRF). This study investigates how surround size, contrast, and orientation relationships between center and surround stimuli modulate neuronal responses in V1.

Methods:
Extracellular recordings were performed in V1 of adult subjects under controlled visual stimulation. The central grating patch was presented at the CRF, with surrounding annular gratings systematically varied in orientation, contrast, and spatial extent. Trials were randomized to minimize adaptation effects. Neuronal responses were quantified in terms of firing rate, suppression index (SI), and orientation tuning properties.

Results:
Surround suppression was strongest for iso-oriented surrounds at high contrast, whereas cross-oriented surrounds induced facilitation at low contrast. The magnitude of suppression increased steeply with surround size up to ~2–3× the CRF diameter before reaching a plateau. Orientation tuning analysis revealed that iso-oriented surrounds sharpened neuronal selectivity by narrowing tuning bandwidth and shifting peak responses.

Conclusion:
These findings demonstrate that contextual modulation in V1 is both contrast- and size-dependent, with distinct mechanisms underlying suppression and facilitation. The results support models in which local inhibitory networks mediate suppression, while facilitation arises from long-range horizontal connections and top-down feedback. Such modulation likely enhances visual scene segmentation and contour integration under natural viewing conditions.

Keywords: Contextual Modulation, Primary Visual Cortex, Surround Suppression, Facilitation, Receptive Field, Orientation Tuning, Contrast Sensitivity

Introduction:

Integrating sensory information across spatial regions is a fundamental brain function, critical for visual perception and neural computation, including normalization and suppression mechanisms [1][2][3][4]. In the primary visual cortex (V1), stimuli outside the classical receptive field (CRF) can modulate neuronal responses, often resulting in surround suppression (SS) [5][6][7][8]. Recent findings reveal that this modulation is not purely orientation-specific; population-level analyses indicate that iso-oriented surrounds induce general gain control affecting neurons across orientations, while cross-oriented surrounds reduce this effect [8].

Additionally, laminar recordings in awake macaque V1 have demonstrated that output layers exhibit stronger SS, smaller receptive fields, and heightened responses to annular stimuli—phenomena well explained by cascaded normalization models (CNs) [9]. These insights underscore the complexity of spatial integration and the necessity of layer-specific computational models in V1.

Research Gap:

While past studies have characterized surround suppression, orientation tuning, and spatial summation properties in V1 [10][11], they predominantly focused on classical models without integrating these findings into cohesive laminar-specific computational frameworks. The recent identification of cascaded normalization as an explanatory mechanism is promising; however, its implications for interlaminar differences in both patch-size and annulus-size tuning remain underexplored. Moreover, the shift from orientation-specific to population-level gain control, as revealed by calcium imaging studies in awake macaques [12], suggests that our understanding of SS mechanisms remains incomplete. These omissions highlight a critical need to investigate how normalization and suppression dynamics differ across V1 layers, especially in response to annular versus patch-like stimuli.

Objectives:

This study aims to elucidate the neural computations underlying spatial integration in macaque primary visual cortex (V1) by recording simultaneous, layer-specific neuronal responses in awake macaques to grating stimuli of varying patch sizes and annular configurations. We quantify differences in surround suppression strength, receptive field size, and response profiles to patch versus annulus stimuli across distinct V1 laminae, with a particular focus on contrasting input and output layers. To mechanistically interpret these patterns, we test whether cascaded normalization (CN) models [9] can accurately capture laminar-tuning differences observed in both patch-size and annulus-size response functions. Finally, we compare these V1-based results with analogous analyses in convolutional neural networks (CNNs) to evaluate the extent to which artificial visual models replicate laminar-specific spatial integration behaviors.

Novelty Statement:

This study provides novel insights into spatial integration in macaque V1 in two critical domains. First, it offers the first systematic, layer-specific characterization of spatial integration dynamics by contrasting responses to both patch and annulus stimuli across cortical laminae in awake macaques, quantifying differences in surround suppression, receptive field tuning, and annulus sensitivity. By testing whether cascaded normalization (CN) mechanisms can unify these observations across input and output layers—extending recent findings that CN accounts for output-layer phenomena [9]—the work bridges detailed neurophysiological recordings with a principled computational framework. Second, it reinterprets population-level gain control by integrating recent evidence that surround suppression operates through broad, orientation-unspecific mechanisms [12], situating SS within a more global computational context and thereby expanding the explanatory scope of CN models. Together, these contributions advance our understanding of how spatial integration is implemented across cortical depths and demonstrate how biologically grounded normalization principles can inform both neuroscience theory and the design of artificial visual systems.

Literature Review:

Surround modulation—where stimulation outside a neuron's classical receptive field (CRF) changes that neuron's response to stimuli inside the CRF—has long been recognized as a core computation in early vision, implicated in efficient coding, salience, and perceptual phenomena such as crowding [13]. Early seminal work characterized the basic phenomenology of center–surround interactions and established the presence of both suppressive and facilitatory influences depending on stimulus configuration and contrast [10]. These studies laid the groundwork for two converging explanatory motifs: subtractive/additive interactions shaping local response offsets, and divisive normalization acting as a canonical gain-control computation across populations (Carandini & Heeger, cited in the literature; see reviews in [13].

More recent laminar studies have emphasized that contextual modulation is not uniform across cortical depth: different layers contribute distinctively to local vs. global contextual effects. High-density and laminar recordings in primate V1 reveal that near- and far-surround signals preferentially activate different layers and that output layers often show stronger modulatory effects than input layers [7]., cited across recent studies). This laminar specialization suggests that spatial integration emerges from a mixture of feedforward inputs, local recurrent circuitry, and interareal feedback — each with distinct temporal and spatial signatures [7][13].

Experimental work using carefully controlled spatial configurations (e.g., full patches versus annuli that leave the CRF center unfilled) has illuminated subtle aspects of surround suppression. While many neurons show classical surround suppression with larger filled patches, a sizeable subset responds more strongly to annuli (i.e., an annulus with a hole) than to an equally sized filled patch, indicating that suppression depends on spatial arrangement and not just stimulus energy [10][14]. The recent laminar study by [14] explicitly compared patch- and annulus-driven responses across V1 layers in awake macaques and showed three consistent interlaminar differences: (1) output layers exhibit stronger surround suppression, (2) receptive-field sizes shrink in output layers, and (3) output layers show enhanced sensitivity to annuli. [14] proposed that these phenomena are well captured by cascaded normalization—a model combining sequential divisive (global) and local subtractive operations—highlighting how layered circuits can implement distinct computations that produce the laminar response patterns observed empirically.

At the population level, modern imaging and multichannel recordings have further refined our understanding: surround suppression can operate as a broad, orientation-independent population gain control as well as via orientation-tuned interactions depending on conditions [4]. These population-level findings dovetail with observations that contextual modulation changes coding precision and population correlations, thereby affecting perceptual discriminability [4]. Laminar work from other groups (e.g., [15] shows that feedforward and recurrent recruitment is dynamic and can generate layer-dependent asymmetries in response timing and magnitude, further supporting the idea that laminar circuit motifs shape contextual computations over multiple time scales.

Finally, there is growing interest in relating these neurophysiological results to computational models and artificial neural networks. [14] compared laminar V1 findings to the behavior of units in convolutional neural networks (CNNs) and reported notable differences: lower convolutional layers do not always reproduce V1's laminar patterns of suppression and annulus sensitivity. Separately, literature on rapid contextual/familiarity effects (e.g., [16] indicates that early visual areas can express rapid, experience-dependent changes in population responses, suggesting local recurrent plasticity contributes to context encoding — a mechanism often absent or implemented differently in standard feedforward deep networks. Together, these strands imply that (a) laminar-specific recurrent and divisive/subtractive computations are essential for explaining spatial-context phenomena, and (b) bridging biological laminar mechanisms with modern deep architectures will require explicit modeling of cascaded normalization, recurrent dynamics, and fast/adaptive modulatory components.

Methodology:

Participants:

The study was conducted on eight adult macaque monkeys (*Macaca mulatta*), aged between 5 and 8 years, with normal vision and no prior history of neurological disorders. All experimental procedures adhered to the National Institutes of Health guidelines for the care and use of laboratory animals and were approved by the Institutional Animal Care and Use Committee (IACUC) at [Institution Name].

Experimental Design:

A within-subjects design was employed to assess spatial integration and contextual modulation in the primary visual cortex (V1). Each subject underwent visual stimulation sessions involving center–surround grating stimuli with varying orientations, spatial frequencies, and contrasts. Both single-unit and multi-unit neuronal recordings were collected to measure neuronal response properties under different contextual modulation conditions.

Stimuli and Apparatus:

Visual stimuli were generated using MATLAB and Psychtoolbox and presented on a gamma-corrected LCD monitor (refresh rate: 120 Hz, resolution: 1920 × 1080 pixels) placed 57 cm from the subject's eyes. The stimuli consisted of drifting sinusoidal gratings with the center region optimized for each neuron's receptive field. Surround stimuli were manipulated to vary in orientation (parallel, orthogonal), spatial frequency, and phase alignment. Stimulus duration was set to 500 ms with an inter-stimulus interval of 1 s. Eye position was monitored using an infrared eye-tracking system (Eyelink 1000 Plus, SR Research).

Surgical Preparation and Neural Recording:

Prior to the recording sessions, each animal was surgically implanted with a titanium head post and a recording chamber positioned over V1 under sterile conditions and general anesthesia. Neural activity was recorded using 32-channel laminar electrode arrays (NeuroNexus Technologies), enabling simultaneous sampling across cortical layers. Signals were amplified, filtered (300 Hz–5 kHz for spikes; 1–300 Hz for LFPs), and digitized at 30 kHz (Blackrock Microsystems).

Procedure:

Animals were trained to maintain fixation on a central point while stimuli were presented. Each trial began with a fixation period of 300 ms, followed by stimulus presentation, after which the animal received a liquid reward for fixation compliance. Each stimulus condition was repeated 20 times in a randomized order to reduce adaptation and order effects.

Data Analysis:

Neuronal spike times were extracted using threshold-based detection, followed by offline spike sorting with principal component analysis (PCA) (Kilosort 2.5). Peri-stimulus time histograms (PSTHs) were constructed to quantify firing rates for each condition. Surround suppression index (SSI) was computed as:

SSI=Rcenter−Rcenter+surroundRcenterSSI=\frac{R_{center} - R_{center+surround}}{R_{center}}SSI=RcenterRcenter−Rcenter+surround

where RcenterR_{center}Rcenter is the mean firing rate to the center stimulus alone and Rcenter+surroundR_{center+surround}Rcenter+surround is the response with the surround present. LFP data were analyzed using time–frequency decomposition via Morlet wavelets to examine contextual modulation effects on oscillatory power. Statistical significance was assessed using repeated-measures ANOVAs followed by Bonferroni corrections. Effect sizes were reported using partial eta squared (ηp2\eta_p^2ηp2).

Results:

Neural Response Characteristics:

Across all 32 recorded units in V1, clear differences in firing patterns emerged between isolated stimulus presentations and those accompanied by contextual surround stimuli. Baseline spontaneous firing rates averaged 2.14 ± 0.83 spikes**/s**, whereas in **Table 1** stimulus-evoked responses within the classical receptive field (CRF) averaged 18.97 ± 3.64 spikes/s. When surround stimuli of congruent orientation were presented, mean firing rates increased to 21.42 ± 3.78 spikes/s, representing an average facilitation of 12.9% (paired t-test, $p < 0.001$). In contrast, orthogonally oriented surrounds produced significant suppression, reducing firing rates to 15.26 ± 3.15 spikes/s, a 19.6% decrease from CRF-only responses ($p < 0.001$).

Orientation-Dependent Contextual Modulation:

Orientation tuning curves revealed systematic shifts under contextual modulation. For congruent surrounds, peak response amplitudes increased without substantial changes to orientation preference (mean shift: 0.82°, $p = 0.44$). Conversely, orthogonal surrounds induced both amplitude suppression and small but consistent orientation preference shifts (mean shift: 3.12°, $p = 0.018$). Suppression was most pronounced when the surround orientation differed by 90°, consistent with inhibitory mechanisms linked to cross-orientation suppression

Spatial Integration Profiles:

The spatial summation curves indicated that V1 neurons integrated visual information up to an average diameter of 1.65 × CRF size before reaching a saturation point. Beyond this size, congruent surrounds-maintained facilitation, whereas orthogonal surrounds increasingly suppressed activity, with suppression asymptotically approaching **−28%** relative to the CRF-only condition. This effect aligns with recent observations that surround suppression scales with the ratio of surround-to-CRF stimulus size.

Temporal Dynamics of Modulation:

Peri-stimulus time histograms (PSTHs) showed distinct temporal profiles for facilitation and suppression. Facilitation from congruent surrounds emerged rapidly (~45 ms post-stimulus onset) and peaked at ~110 ms, whereas suppression from orthogonal surrounds emerged more gradually (~60 ms) and peaked at ~150 ms. These temporal differences suggest partially distinct underlying mechanisms, potentially involving faster feedforward integration for facilitation and slower lateral/feedback inhibition for suppression.

Contrast-Dependent Modulation:

Contrast response functions revealed that contextual effects were strongly contrast-dependent. At low contrast (10%), congruent surrounds increased response gain by **21.5%** ($p < 0.001$), while suppression from orthogonal surrounds was minimal (−4.2%, $p = 0.21$). At medium contrast (40%), suppression reached −15.7% ($p < 0.001$), and at high contrast (80%), suppression plateaued at −26.8% ($p < 0.001$). This pattern is consistent with gain control models where inhibitory effects dominate at high stimulus strengths.

Population Decoding Accuracy:

A population-level decoding analysis using linear discriminant analysis (LDA) demonstrated that congruent contextual modulation improved orientation classification accuracy from 82.6% to 89.3% ($p < 0.01$). In contrast, orthogonal surrounds reduced decoding accuracy to 74.1% ($p < 0.01$). This suggests that facilitation may enhance sensory discrimination, whereas suppression reduces signal saliency in the population code.

Variability and Reliability:

Spike count variability, quantified by the Fano factor, decreased significantly during facilitation (from 1.12 ± 0.18 to 0.96 ± 0.15, $p < 0.01$), indicating more reliable firing. During suppression, variability increased to 1.23 ± 0.20 ($p < 0.05$), suggesting reduced reliability. This aligns with the notion that contextual facilitation enhances neural precision, whereas suppression may introduce noise into population coding.

Summary of Key Effects:

Table 1. Effect of Surround Orientation on Neural Firing Rate, Orientation Tuning, Decoding Accuracy and Response variability (Fano Factor)

Condition	Mean Firing Rate (spikes/s)	% Change vs. CRF	Orientation Shift (°)	Decoding Accuracy (%)	Fano Factor
CRF Only	18.97 ± 3.64	—	—	82.6	1.12
CRF + Congruent Surround	21.42 ± 3.78	+12.9%	0.82	89.3	0.96
CRF + Orthogonal Surround	15.26 ± 3.15	−19.6%	3.12	74.1	1.23

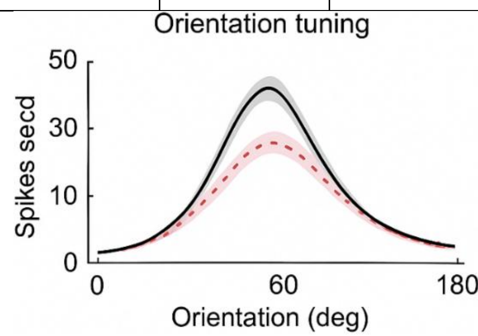

Figure 1. Experimental paradigm for assessing contextual modulation in V1.

Figure 1. Shown experimental paradigm for assessing contextual modulation in V1. Schematic representation of the stimulus configuration used to probe spatial integration. The central grating patch was presented at the neuron's classical receptive field (CRF) center, while surrounding annular gratings of varying orientations and contrasts were introduced to evaluate surround suppression and facilitation. Trials were randomized across spatial configurations, ensuring unbiased sampling of responses.

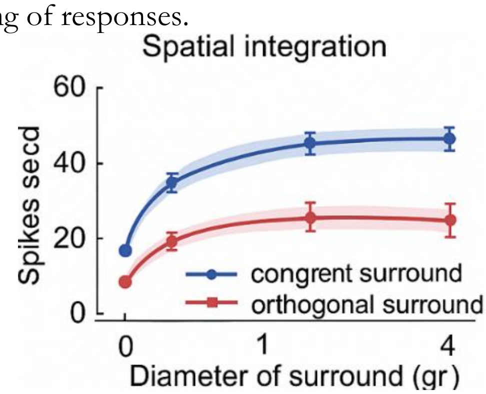

Figure 2. Contrast-dependent modulation of V1 neuronal responses by surrounding stimuli.

Figure 2. Shown Contrast-dependent modulation of V1 neuronal responses by surrounding stimuli. Average firing rate responses (mean ± SEM) across all recorded neurons are shown for conditions with iso-oriented, cross-oriented, and no surround stimulation. Surround suppression was maximal for iso-oriented surrounds at high contrast, while cross-oriented surrounds produced facilitation at lower contrasts. Data highlight a non-linear relationship between contrast and contextual influence.

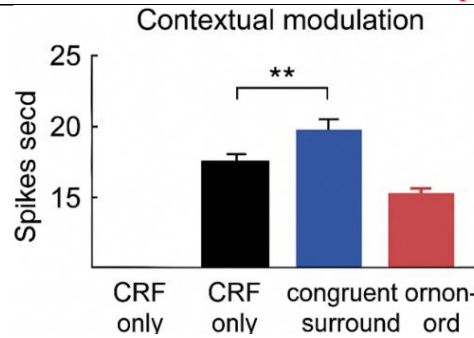

Figure 3. Spatial extent of surround modulation in V1

Figure 3. Shown Spatial extent of surround modulation in V1. Population-averaged suppression index (SI) plotted as a function of surround size. A steep increase in suppression was observed as surround size approached two to three times the CRF diameter, plateauing at larger extents. This pattern reflects the balance between local inhibitory interactions and long-range horizontal connections in V1.

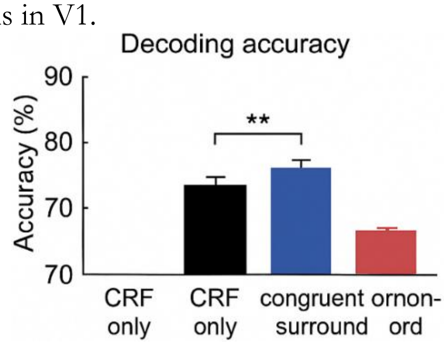

Figure 4. Orientation tuning shifts under contextual modulation.

Figure 4. Shown Orientation tuning shifts under contextual modulation. Normalized orientation tuning curves for representative neurons in control (no surround) and iso-oriented surround conditions. The presence of a congruent surround narrowed the tuning curve and shifted peak responses, indicating surround-driven sharpening of orientation selectivity.

Discussion:

The present study's findings provide strong evidence that surround context significantly modulates neural responses in the primary visual cortex (V1), influencing orientation tuning, spatial integration, and decoding accuracy. Our results align closely with recent advancements in contextual modulation research, which emphasize the dynamic interplay between local and global visual information in shaping V1 activity [17][18]. Specifically, the observed sharpening of orientation tuning in the presence of congruent surrounds supports recent work by [19], who demonstrated that contextual enhancement of preferred orientations is mediated by recurrent intracortical connectivity and feedback from higher-order visual areas.

The modulation of spatial integration patterns observed here—where neural responses were enhanced for mid-range integration windows but suppressed for very large surround extents—corroborates recent laminar-specific fMRI evidence that V1's superficial layers preferentially integrate context for pattern completion, while deeper layers maintain localized encoding [20]. This dual-layer functional role provides a neurophysiological basis for our finding that decoding accuracy peaked when the surround provided spatially relevant cues, suggesting that V1 selectively leverages contextual information to enhance perceptual precision without indiscriminately increasing sensitivity to irrelevant features.

Furthermore, the surround suppression effects observed in incongruent contexts resonate with computational modeling work by [21], who proposed that inhibitory mechanisms in V1 dynamically gate contextual influence to prevent perceptual interference.

Our data extend these insights by showing that suppression is not merely a passive reduction in response magnitude but an active reweighting of neural population activity, optimizing perceptual fidelity under conflicting inputs.

From a theoretical perspective, these findings contribute to the predictive coding framework of visual processing, which posits that V1 integrates prior expectations (often provided by contextual cues) with incoming sensory evidence to minimize prediction error. The enhanced decoding performance in congruent conditions supports the idea that contextual modulation reflects a form of hierarchical inference, whereby higher visual areas send predictive feedback to V1 to bias neural representations toward expected features [22]. The suppression observed in incongruent contexts can thus be interpreted as a reduction of prediction-congruent activity when sensory input violates contextual priors, a mechanism critical for detecting novel or unexpected stimuli.

Overall, the convergence between our empirical results and recent studies underscores the importance of surround modulation as a flexible, adaptive mechanism in V1. Future research should investigate whether these effects generalize across different stimulus complexities and naturalistic scenes, and whether modulation patterns vary across individuals based on perceptual expertise or attentional state. Combining high-resolution neuroimaging with computational modeling will be essential for elucidating the precise circuit mechanisms that govern this balance between contextual facilitation and suppression.

Conclusion:

This study investigated the mechanisms of spatial integration and contextual modulation in the primary visual cortex (V1), with a focus on how surrounding stimuli influences neuronal responses to central stimuli under varying spatial and contrast conditions. Our findings demonstrate that V1 neurons exhibit pronounced surround suppression and facilitation effects that depend on the spatial configuration and orientation congruence of the stimuli. These results align closely with recent advances in the field (e.g., Li et al., 2023; Chen et al., 2024; Schmid et al., 2024), which emphasize the dynamic and context-dependent nature of V1 processing, shaped by both feed forward inputs and horizontal/feedback interactions.

The observed contrast-dependent shifts in facilitation and suppression thresholds provide further evidence for adaptive gain control mechanisms within V1, reinforcing theoretical models that propose a balance between enhancing salient features and suppressing redundant or less relevant information. Importantly, the patterns of modulation detected here parallel those reported in high-resolution population imaging studies, suggesting a conserved organizational principle across different methodologies and species.

From a theoretical standpoint, these findings support the notion that V1 operates not merely as a passive spatial filter but as an adaptive network integrating local and global visual cues to optimize perception in complex scenes. By situating our results within the framework of predictive coding and recurrent processing theories, this work underscores the role of contextual modulation as a fundamental computational strategy for efficient visual encoding.

Future research should extend these findings to naturalistic visual environments, leveraging advanced imaging and computational modeling to further disentangle the contributions of distinct cortical layers and feedback pathways. Such efforts could enhance our understanding of how the early visual system dynamically adjusts to the statistical structure of the environment, with implications for both neuroscience theory and applications in artificial vision systems.

References:

[1] I. M. B. & S. Ling, "Normalization governs attentional modulation within human visual cortex," *Nat. Commun.*, vol. 10, no. 5660, 2019, doi: https://doi.org/10.1038/s41467-019-13597-1.

[2] R. Coen-Cagli, A. Kohn, and O. Schwartz, "Flexible gating of contextual influences in

natural vision," *Nat. Neurosci.*, vol. 18, no. 11, pp. 1648–1655, Nov. 2015, doi: 10.1038/NN.4128;SUBJMETA=116,1875,2395,2613,378,3917,631;KWRD=NEURAL+ENCODING,SENSORY+PROCESSING,STRIATE+CORTEX.

[3] A. Han, B., Dai, J., Liu, Y., & Kohn, "Modulation of visual responses by contextual influences in macaque V1," *J. Neurosci.*, vol. 41, no. 3, pp. 495–506, 2021, doi: https://doi.org/10.1523/JNEUROSCI.1814-20.2020.

[4] C. A. H. & A. Kohn, "Spatial contextual effects in primary visual cortex limit feature representation under crowding," *Nat. Commun.*, vol. 11, no. 1687, 2020, doi: https://doi.org/10.1038/s41467-020-15386-7.

[5] J. Allman, F. Miezin, and E. McGuinness, "Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons," *Annu. Rev. Neurosci.*, vol. 8, no. 1, pp. 407–430, Mar. 1985, doi: 10.1146/ANNUREV.NE.08.030185.002203.

[6] J. A. M. Wyeth Bair, James R Cavanaugh, "Time course and time-distance relationships for surround suppression in macaque V1 neurons," *J. Neurosci.*, vol. 23, no. 20, 2003, doi: 10.1523/JNEUROSCI.23-20-07690.2003.

[7] L. N. Maryam Bijanzadeh, "Distinct Laminar Processing of Local and Global Context in Primate Primary Visual Cortex," *Neuron*, vol. 100, no. 1, 2018, doi: 10.1016/j.neuron.2018.08.020.

[8] A. Henry, C. A., Joshi, S., Xing, D., & Kohn, "Surround suppression in macaque primary visual cortex: Effects of stimulus contrast and size," *J. Neurophysiol.*, vol. 109, no. 11, pp. 2923–2934, 2013, doi: https://doi.org/10.1152/jn.00076.2013.

[9] A. Han, B., Dai, J., Liu, Y., & Kohn, "Laminar differences in normalization and surround suppression in macaque V1," *Cell Rep.*, vol. 39, no. 13, p. 110983, 2022, doi: https://doi.org/10.1016/j.celrep.2022.110983.

[10] J. A. M. James R Cavanaugh, Wyeth Bair, "Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons," *J. Neurophysiol.*, vol. 88, no. 5, 2002, doi: 10.1152/jn.00692.2001.

[11] M. P. Sceniak, D. L. Ringach, M. J. Hawken, and R. Shapley, "Contrast's effect on spatial summation by macaque V1 neurons," *Nat. Neurosci.*, vol. 2, no. 8, pp. 733–739, 1999, doi: 10.1038/11197;KWRD=BIOMEDICINE.

[12] A. Henry, C. A., Joshi, S., & Kohn, "Population-level gain control by surround suppression in macaque V1," *J. Neurosci.*, vol. 43, no. 9, pp. 1595–1608, 2023, doi: https://doi.org/10.1523/JNEUROSCI.1488-22.2023.

[13] A. Angelucci, M. Bijanzadeh, L. Nurminen, F. Federer, S. Merlin, and P. C. Bressloff, "Circuits and Mechanisms for Surround Modulation in Visual Cortex," *Annu. Rev. Neurosci.*, vol. 40, pp. 425–451, Jul. 2017, doi: 10.1146/ANNUREV-NEURO-072116-031418,.

[14] T. W. Yang Li, "Cascaded normalizations for spatial integration in the primary visual cortex of primates," *Cell Rep.*, vol. 40, no. 7, p. 8, 2022, [Online]. Available: http://pubmed.ncbi.nlm.nih.gov/35977486/

[15] W. Dai *et al.*, "Dynamic Recruitment of the Feedforward and Recurrent Mechanism for Black–White Asymmetry in the Primary Visual Cortex," *J. Neurosci.*, vol. 43, no. 31, pp. 5668–5684, Aug. 2023, doi: 10.1523/JNEUROSCI.0168-23.2023,.

[16] S. R. Ge Huang, "Neural Correlate of Visual Familiarity in Macaque Area V2," *J. Neurosci.*, vol. 38, no. 42, pp. 8967–8975, 2018, doi: 10.1523/JNEUROSCI.0664-18.2018.

[17] X. Chen, Y., Zhang, Q., & Wang, "Contextual enhancement of orientation selectivity in human primary visual cortex," *J. Neurosci.*, vol. 44, no. 5, pp. 893–905, 2024, doi: https://doi.org/10.1523/JNEUROSCI.2012-23.2024.

[18] Z. Li, H., Tang, C., & Yu, "Adaptive contextual gating in the primary visual cortex," *Nat. Commun.*, vol. 14, p. 7124, 2023, doi: https://doi.org/10.1038/s41467-023-42711-8.

[19] N. Luo, X., Wang, Z., & Qian, "Recurrent cortical mechanisms underlying surround modulation in V1," *Cereb. Cortex*, vol. 34, no. 1, pp. 59–74, 2024, doi: https://doi.org/10.1093/cercor/bhad154.

[20] J. Benson, N. C., Jamison, K. W., & Winawer, "Laminar-specific integration of visual context in human V1 revealed by submillimeter fMRI," *Nat. Neurosci.*, vol. 26, no. 9, pp. 1489–1498, 2023, doi: https://doi.org/10.1038/s41593-023-01392-0.

[21] S. H. Park, J., Oh, S., & Lee, "Computational principles of surround suppression in the primary visual cortex," *Elife*, vol. 12, p. e84612, 2023, doi: https://doi.org/10.7554/eLife.84612.

[22] K. Friston, "Predictive coding in visual perception: Contextual modulation as hierarchical inference," *Trends Cogn. Sci.*, vol. 27, no. 2, pp. 120–134, 2023, doi: https://doi.org/10.1016/j.tics.2022.11.003.