

Characterizing surround suppression with dynamic natural scenes

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Surround suppression refers to the reduction in perceptual sensitivity to a central stimulus caused by its surrounding context. Previous studies have examined this phenomenon mainly with simple stimuli varying only in low-level visual features, leaving it unclear whether the same principles apply to natural scenes. To address this, we investigated surround suppression in complex and dynamic scenes by systematically manipulating categorical similarity and motion congruence between the center and surrounding scenes. Categorical similarity was examined across four levels: identical exemplars, different exemplars of the same basic-level category, different basic-level categories, and different superordinate categories. Motion direction was manipulated by center and surround drifting either in the same or opposite directions. In two experiments, we measured contrast sensitivity for the center scene during a categorization task. We found that the suppression increased as the categorical similarity between the center and the surround decreased, with the strongest suppression observed for different superordinate categories. This finding contrasts with results for simple stimuli, where increasing center-surround similarity increases suppression. Yet, consistent with the findings from simple stimuli, suppression was stronger when the center and surround moved in the same direction. These findings show that contextual modulation in natural vision is governed not only by low-level feature similarity but also by high-level categorical structure. Context-dependent suppression may therefore help the

visual system to prioritize coherent, task-relevant information while filtering incongruent input.

Introduction

Visual perception is inherently context dependent. The appearance and detectability of a stimulus can be significantly influenced by surrounding visual information (Tadin, Lappin, Gilroy, & Blake, 2003). A well-known form of such contextual influence is surround modulation, in which the presence of surrounding stimuli alters perceptual sensitivity to a central target. This modulation can manifest as either suppression (*surround suppression*) or facilitation (*surround facilitation*) depending on the spatial and feature relationships between center and surround (Petrov, Carandini, & McKee, 2005; Xing & Heeger, 2001). For example, perceptual thresholds increase when a center grating is surrounded by iso-oriented high-contrast stimuli, indicating suppression (Er, Pamir, & Boyaci, 2020; Petrov et al., 2005; Schallmo et al., 2018; Xing & Heeger, 2001), whereas thresholds can decrease, reflecting facilitation, when the stimuli are of intermediate size and have low contrast (Er et al., 2020; Mareschal & Shapley, 2004; Schallmo et al., 2018).

To systematically characterize these effects, surround modulation has been extensively studied using simple

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stimuli, such as static or drifting gratings, and has been observed to depend on low-level features, including contrast, orientation, and motion direction (Angelucci et al., 2017; Cavanaugh, Bair, & Movshon, 2002b; Er et al., 2020; Kiniklioglu & Boyaci, 2022; Tadin, 2015; Schallmo et al., 2018; Turkozer, Pamir, & Boyaci, 2016). Suppression is strongest when the center and surround share similar features, but it weakens or even reverses to facilitation when they differ. For example, iso-oriented surrounds typically suppress both neural responses and perceptual sensitivity to a central stimulus, whereas orthogonal surrounds can lead to facilitation (Cavanaugh, Bair, & Movshon, 2002a; DeAngelis, Freeman, & Ohzawa, 1994; Flevaris & Murray, 2015; Schallmo, Grant, Burton, & Olman, 2016; Serrano-Pedraza, Grady, & Read, 2012; Shushruth et al., 2012; Walker, Ohzawa, & Freeman, 1999). A similar pattern is observed with motion direction: when center and surround gratings drift in opposite directions, suppression is reduced compared with when they move in the same direction (Allman, Miezin, & McGuinness, 1985; Born & Tootell, 1992; Cavanaugh et al., 2002b; Kastner, Nothdurft, & Pigarev, 1995; Kiniklioglu & Boyaci, 2022; Kiniklioglu & Boyaci, 2025; Lamme, 1995; Paffen, Alais, & Verstraten, 2005; Paffen, van der Smagt, te Pas, & Verstraten, 2005).

Although the characteristics of surround suppression for simple stimuli are well-established, both behaviorally and neurally, it remains unclear how surround suppression influences the processing of more complex, naturalistic stimuli. Studies in animals using ecologically relevant visual stimuli indicate that surround modulation extends beyond simple gratings to naturalistic stimuli. Coen-Cagli, Kohn, and Schwartz (2015) reported stronger neural suppression in the macaque primary visual cortex when the center and surround consisted of homogeneous natural images. In contrast, Onat, Jancke, and König (2013) found that in natural scene videos, surround patterns that perceptually complete the central stimulus elicit facilitation in the cat's primary visual cortex. Extending these findings, a recent preprint by Fu et al., (2024) used convolutional neural networks trained on neural recordings from mouse visual cortex to model center-surround interactions for natural scenes. Their results showed that congruent center-surround pairings yielded excitatory effects, whereas incongruent pairings yielded inhibitory effects. Taken together, these studies demonstrate that center-surround interactions are sensitive to the statistical properties and spatial organization of natural stimuli, yet it remains unclear whether similar modulations occur at the perceptual level in humans and whether they are influenced by higher-level relationships, such as categorical similarity between the center and surround.

Although surround suppression with natural stimuli has not been systematically investigated in humans, high-level contextual influences on perception have

been studied. In particular, the categorical relationship between central and peripheral content, such as whether both belong to the same scene category (e.g., indoor vs. outdoor), has been shown to influence perceptual judgments in scene categorization tasks (Faurite et al., 2024; Lukavský, 2019; Trouilloud et al., 2022; Trouilloud et al., 2020). For example, categorization accuracy declines when the surrounding context belongs to a different category, even when it is unattended (Lukavský, 2019). Such categorical congruency effects interact with physical stimulus characteristics: Peripheral low spatial frequency information facilitates central scene categorization when it is categorically congruent (Faurite et al., 2024). In contrast, incongruent peripheral scenes impair performance, especially when central and peripheral scenes share similar physical properties, such as amplitude spectrum and spatial configuration. Notably, even categorically congruent surrounds can impair central scene categorization when they are physically dissimilar from the center (Peyrin et al., 2021). Taken together, studies on scene congruency effects suggest an interplay of high-level characteristics and low-level visual attributes. This raises an important question: Does surround suppression for natural stimuli follow the same principles observed with low-level visual stimuli, or is it governed by fundamentally different mechanisms, potentially driven by high-level stimulus characteristics?

To address this question, we investigated whether surround suppression in dynamic natural scenes is modulated by high-level categorical context. To do so, we measured contrast sensitivity to a central scene while systematically manipulating the categorical similarity between the center and surrounding scenes across four levels: 1) identical exemplar, 2) different exemplar from the same basic-level category, 3) different basic-level categories within the same superordinate category, and 4) different superordinate categories. This design allowed us to assess how increasing categorical distance influences the perceptual strength of suppression. Additionally, we manipulated the motion congruency between the center and surround, specifically whether they drifted in the same or opposite directions, to test whether established low-level motion effects observed with simple stimuli generalize to more naturalistic stimuli. By jointly manipulating categorical similarity and motion congruence, our study characterizes how high- and low-level contextual factors shape surround suppression in dynamic natural scenes.

Experiment 1

In **Experiment 1**, we investigated whether categorical similarity between a central scene and its surrounding context influences contrast sensitivity for the central

scene. Participants performed a scene categorization task in which the contrast of both the central and surrounding scenes was adjusted adaptively. This allowed us to estimate contrast sensitivity under varying contextual conditions, comparing performance across four levels of categorical similarity (identical exemplar, different exemplar, different basic-level category, and different superordinate category) and two motion congruency conditions (same direction and opposite direction).

Methods

Participants

Twenty-two volunteers (11 male, mean age, 27.6 years), participated in [Experiment 1](#). All participants reported normal or corrected-to-normal vision. They gave written informed consent before the experiment and received monetary compensation for their participation. The study was approved by the Ethics Committee of Justus Liebig University Giessen. All experimental protocols were in accordance with the Declaration of Helsinki.

Stimuli

The stimuli consisted of panoramic videos created by moving static scene images behind a circular occluder (520×400 pixels, 3 pixels per frame). The scene images were obtained from publicly available online sources via Google Images. The center images were displayed through a 1.9° -diameter aperture, and the surrounding images were presented through an annular aperture ranging from 2.5° to 10.4° in diameter. To separate the center and surrounding scenes, the area between 1.9° and 2.5° remained unstimulated, creating a gap between the center and annular stimuli. To ensure smooth transitions and minimize sharp contrast differences at the aperture edges, a cosine envelope was applied to smooth the boundaries between the center and surround, as well as between the outermost edge of the surround and the background. All images were converted to grayscale by averaging the three color channels, and the mean luminance was matched using the SHINE toolbox ([Willenbockel et al., 2010](#)).

The center scenes were always presented with a surrounding scene, except in the baseline block, where the central stimulus was shown alone. Scene images were selected from two superordinate categories: indoor (restaurants and museums) and outdoor (parks and residential areas), each featuring two basic-level categories, with two exemplars per basic-level category. The center-surround stimuli depicted natural scenes with varied categorical relationships between the center and surround ([Figure 1](#)). Specifically, we devised four conditions: 1) identical exemplar condition, where the

center and surround images were identical; 2) different exemplar condition, where the center and surround images belonged to the same basic-level category (e.g., museums) but were not identical; 3) different basic-level category condition, where the center and surround images belonged to the same superordinate category (e.g., indoor) but were from different basic-level categories; and 4) different superordinate category condition, where the center and surround images belonged to different superordinate categories.

To assess whether the observed effects could be explained by low-level image properties, we conducted a control analysis quantifying low-level visual similarity between center and surround stimuli. Following prior work using hierarchical models of early visual processing ([Riesenhuber & Poggio, 1999](#)), we used an HMAX-based representation to characterize low-level visual structure. For each image, responses were summarized into a fixed-length feature vector, and pairwise cosine similarity between L2-normalized C1 feature vectors was computed for all center-surround image pairs. Similarity values were then averaged within each categorical condition used in the experiment (identical exemplar, different exemplar, different basic-level category, and different superordinate category). The control analysis quantifying low-level visual similarity between center and surround stimuli showed that the mean low-level similarity did not differ reliably across category levels (identical exemplar: $M = 1$; different exemplar: $M = 0.93$; different basic-level: $M = 0.91$; different superordinate: $M = 0.90$), and a permutation test revealed no significant effect of categorical condition on similarity ($p = 0.12$).

The center-surround stimuli were presented in a single *Center-Surround* block. In one-half of the trials, the center and surround moved in the same direction; in the other one-half, they moved in opposite directions. The four category conditions (identical exemplar, different exemplar, different basic-level category, and different superordinate category) and two motion direction conditions (same direction and opposite direction) were presented in randomized order.

Additionally, a separate *Center-Only* block was included as a baseline, in which the central stimulus was presented alone without a surrounding scene. This baseline block allowed us to quantify the suppressive effect of adding the surround to the central stimulus.

Procedure

Stimuli were presented using the Psychophysics toolbox ([Brainard, 1997](#)) with MATLAB R2022b (MathWorks, Natick, MA) on an AORUS FI32Q monitor (resolution $2,560 \times 1,440$, refresh rate 120 Hz). Participants were seated in a dark room with their heads stabilized using a chin rest at a distance of 60 cm from the monitor. The stimuli were presented foveally on a mid-gray background (128 RGB luminance).

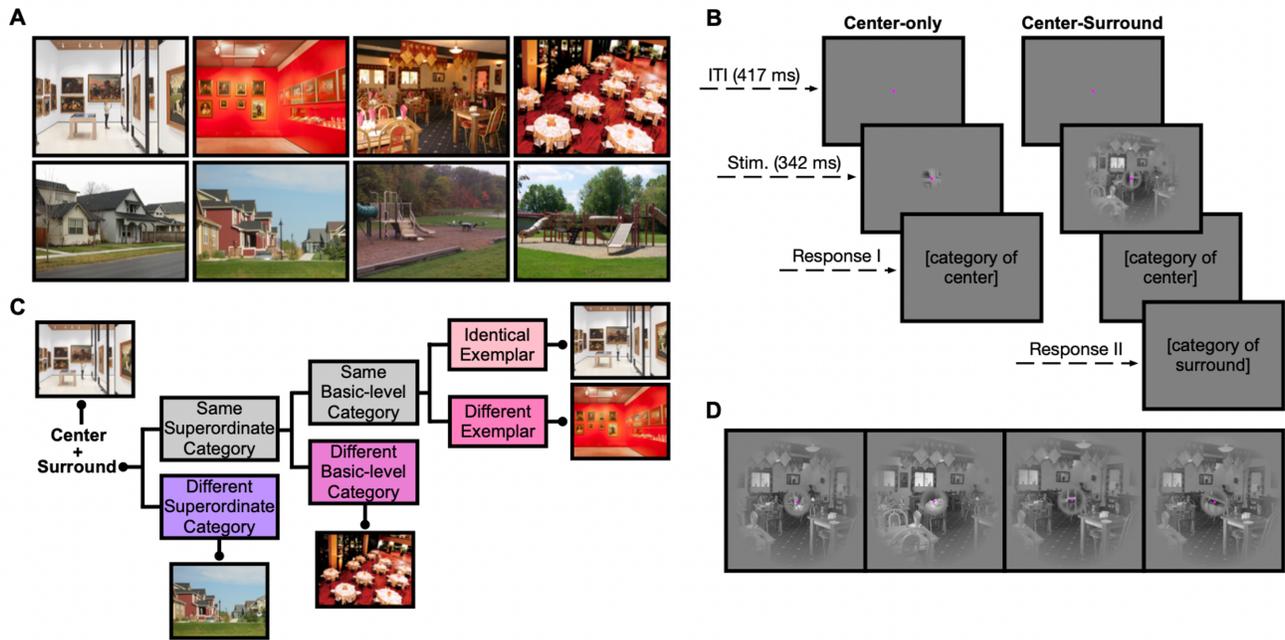


Figure 1. Stimuli and paradigm. (A) The natural scene images used to create the stimuli, drawn from two superordinate categories (indoor and outdoor) and two basic-level categories within each (restaurants, museums, parks, and residential areas), with two exemplars per basic-level category. (B) Experimental design for the Center-Only and Center+Surround blocks. Each trial began with a fixation point, followed by stimulus presentation, with the contrast level adjusted using a one-up three-down staircase. In the Center-Only block, participants reported the superordinate category of the central scene. In the Center+Surround block, they first reported the category of the center scene, then the category of the surrounding scene. (C) Center-surround stimuli were created for four conditions: 1) Identical Exemplar, where center and surround images were identical; 2) Different Exemplar, where images were from the same basic-level category but not identical; 3) Different Basic-Level Category, where images were from different basic-level categories within the same superordinate category; and 4) Different Superordinate Category, where images were from different superordinate categories (e.g., indoor vs. outdoor). (D) Example stimuli for each category condition, shown from left to right: Identical Exemplar, Different Exemplar, Different Basic-Level Category, and Different Superordinate Category.

Responses were collected via a standard computer keyboard.

The experiment began with a practice session to allow participants to familiarize themselves with the task, followed by two main blocks: a Center-Only block and a Center+Surround block. The full session lasted approximately 100 minutes. Short breaks were provided during the experiment.

Participants were instructed to keep their eyes on a fixation point throughout the trial. On each trial, participants viewed foveally presented scene videos and performed a scene categorization task via keypress. Each trial began with a 416.6-ms fixation point followed by the presentation of the stimulus for 341.7 ms. In the Center-Only block, participants were asked to report the superordinate category of the central scene (i.e., indoor vs. outdoor). In the Center+Surround block, participants were instructed to attend to both the center and surrounding scenes. They first reported the category of the center scene, then reported the category of the surrounding scene. The second task was included to ensure that

participants attended to both the center and the surround.

In all conditions, the Michelson contrast of the scenes was adjusted using an adaptive staircase procedure. In the Center-Only block, the contrast of the central scenes was adjusted using two interleaved one-up, three-down staircases, based on participants' categorization judgments of the center scene. Importantly, two separate staircases were used: one starting from a very low contrast level (10%), making the task relatively difficult, and the other starting from a very high contrast level (90%), making the task relatively easy. Each staircase contained 160 trials, resulting in a total of 320 trials per participant for the baseline block.

In the Center+Surround block, the contrast of both the center and surrounding scenes was adjusted using independent one-up, three-down staircases, based on participants' judgments of the center scene category. However, judgments about the surrounding scene category were not used for the contrast adjustment; they were used solely to direct attention to both center and surround. Importantly, the Center+Surround

block always followed the Center-Only block, as the contrast threshold obtained from the baseline block was used as the starting point for the adaptive staircase procedure in the Center+Surround block. One adaptive staircase was used for each condition, yielding eight staircases (4 category conditions \times 2 motion directions). Each staircase included 160 trials, for a total of 1,280 trials per participant in the Center+Surround block.

Data analysis

The contrast thresholds (corresponding with a 79% accuracy rate) were calculated for each participant and experimental condition by fitting a Gumbel psychometric function to the responses using the Palamedes toolbox (Kingdom & Prins, 2010) in MATLAB R2022b (MathWorks, Natick, MA). In cases where the psychometric fit failed to converge or yielded unreliable estimates (e.g., parameter values exceeded acceptable limits), thresholds were computed as the mean of the final six staircase reversals (Supplementary Table S1). This alternative method provides a robust approximation, as the reversal points tend to cluster around the observer's threshold (Levitt, 1971).

Using these thresholds (Supplementary Figures S1 and S2 for plots), we computed a suppression index (SI) to quantify the strength of surround suppression:

$$SI = \frac{T_{C+S} - T_C}{T_C}, \quad (1)$$

where T_C and T_{C+S} are the contrast thresholds for the center-only and center+surround conditions, respectively. Positive SI values indicate suppression, negative values indicate facilitation, and an SI of zero indicates no contextual influence.

SI values exceeding ± 2.5 standard deviations from the mean of the group were excluded from the analysis (1.1% of SI values in total). Surround modulation was assessed by testing SI values against zero using two-tailed one-sample t -tests, with the false discovery rate (FDR) correction applied for multiple comparisons.

To examine whether the suppression strength was influenced by the categorical similarity between center and surround scenes across different direction conditions, we ran linear mixed-effects models (LMMs), with SI values as the dependent variable. Categorical similarity (four levels: identical exemplar, different exemplar, different basic-level category, and different superordinate category), motion-direction congruence (two levels: same direction and opposite direction), and their interaction were included as fixed effects, while between-subject variability was modeled using a random intercept.

All analyses were performed with custom MATLAB R2022b scripts (MathWorks, Natick, MA), except for

the linear mixed-effects analysis, which was conducted in SPSS Statistics Version 25 (IBM Corp., Armonk, NY).

Results

Figure 2 shows suppression indices (SI, Methods) derived from contrast thresholds. In Experiment 1, the presence and characteristics of the surround altered the perceived contrast of the central stimulus. A linear mixed-effects model revealed significant main effects of category, $F(3,166) = 11.19$, $p < 0.001$, and motion direction, $F(1,166) = 9.33$, $p = 0.003$. However, the interaction between category and direction was not significant, $F(3,166) = 0.16$, $p = 0.92$.

These results indicate that surround suppression was modulated by the motion direction of the surrounding stimuli. Consistent with previous findings (Kiniklioglu & Boyaci, 2022; Paffen, Alais et al., 2005; Paffen, van der Smagt et al., 2005), suppression was stronger when the center and surround moved in the same direction compared to opposite directions.

More important, across both motion conditions, suppression strength increased as categorical similarity between the center and surround decreased, with the strongest suppression observed when the center and surround belonged to different superordinate

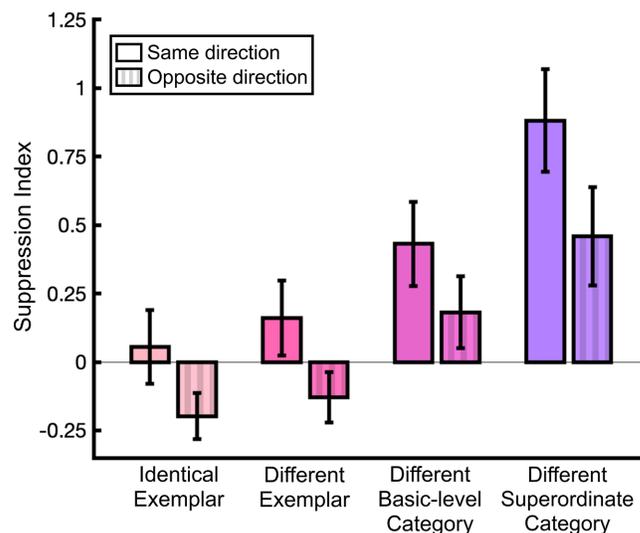


Figure 2. Suppression Index (SI) values from Experiment 1. SI values were computed for each participant across four category conditions (identical exemplar, different exemplar, different basic-level category, and different superordinate category) and two motion direction conditions (same and opposite direction). Higher SI values indicate stronger surround suppression, and negative SI values reflect surround facilitation. Error bars represent the standard error of the mean.

categories. Post hoc paired-sample t -tests with FDR correction confirmed that suppression was significantly greater in the different superordinate category condition than in all other category conditions, all $t(21) > 2.69$, $ps < 0.02$. Similarly, suppression was significantly stronger for different basic-level category condition than in the different exemplar and identical exemplar conditions, all $t(21) > 2.80$, $ps < 0.02$. In contrast, suppression strength did not differ between the identical and different exemplar conditions, $t(21) = 1.34$, $p = 0.20$.

Moreover, SI values were significantly greater than zero in the different superordinate category conditions for both same- and opposite-direction trials, as well as in the different basic-level category conditions for same-direction trials ($ps < 0.05$). These findings show that surround suppression is evident in dynamic natural scenes, particularly when the center and surround belong to different categories, and that suppression becomes stronger as categorical similarity decreases.

Experiment 2

The results of [Experiment 1](#) showed that the suppressive effect of the surround increased as the categorical similarity between the center and surround scenes decreased. One potential explanation for the relatively weak suppression in conditions with higher Center-Surround similarity is a possible order effect resulting from presenting the Center-Only block before the Center+Surround block. Although such an effect is unlikely to alter the overall pattern across conditions, it could bias the SI values toward facilitation. Additionally, presenting Center-Only and Center+Surround trials in separate blocks may have introduced confounds related to spatial attention. To address these concerns, [Experiment 2](#) was designed to replicate [Experiment 1](#) while eliminating potential confounding factors. To this end, we presented the Center-Only and Center+Surround trials together in a single mixed block with randomized trial order.

Methods

Participants

Twenty-five volunteers (7 male, mean age = 28.7 years) participated in [Experiment 2](#). All participants provided written informed consent and received monetary compensation for their participation.

Stimuli and procedure

The apparatus, stimuli, and overall setup were identical to those used in [Experiment 1](#). The key change in [Experiment 2](#) was the inclusion of Center-Only trials within the Center+Surround block. Specifically, Center-Only and Center+Surround trials were randomly presented within a single Mixed block to control for potential order effects and attentional confounds introduced by separate block presentations.

The general procedure remained the same as in [Experiment 1](#). The experiment began with a brief practice session, followed by a separate Center-Only block used to determine the starting values for the adaptive staircases. This was followed by the Mixed block. In the Mixed block, participants were instructed to report only the center scene category on Center-Only trials and to report the center category first, followed by the surround category, on Center+Surround trials. Participants were informed in advance that both trial types (Center-Only and Center+Surround trials) would appear in randomized order within the same block.

In the Mixed block, stimulus contrast for both center and surround images was adjusted using one-up, three-down staircases based on responses to the center scene category. One adaptive staircase was used per condition, resulting in a total of nine staircases (four category conditions \times two motion directions plus one for the Center-Only trials). Each staircase started at the threshold value obtained from the initial Center-Only block.

Data analysis

As in [Experiment 1](#), contrast thresholds corresponding with 79% accuracy were estimated. When the psychometric fit failed to converge or yielded unreliable estimates, thresholds were computed as the mean of the final six staircase reversals (Supplementary Table S1).

SI values were calculated separately using two different baselines: 1) Center-Only trials from the Center-Only block and 2) Center-Only trials from the Mixed block ([Experiment 1](#) Methods for details). SI values were computed for each participant and condition using both baselines. Further statistical tests were performed on the SI values. SI values exceeding ± 2.5 standard deviations from the mean of the group were excluded from the analysis (3.5% of SI values in total).

We compared SI values against zero using one-sample, two-tailed Student's t -tests, with FDR correction applied for multiple comparisons. Next, we analyzed the effects of categorical similarity and motion-direction congruence on suppression strength using linear mixed-effects models (LMMs), with SI values as the dependent variable. Categorical similarity,

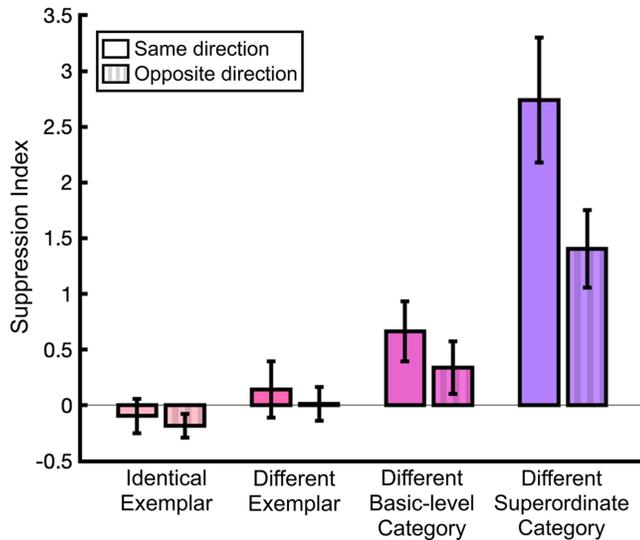


Figure 3. SI values from [Experiment 2](#), calculated using center-only trials from the Center-Only block. SI values were computed for each participant across four category conditions (identical exemplar, different exemplar, different basic-level category, and different superordinate category) and two motion direction conditions (same- and opposite-direction). Higher SI values indicate stronger surround suppression, while negative SI values reflect surround facilitation. Error bars represent the standard error of the mean (SEM).

motion direction, and their interaction were included as fixed effects, while between-subject variability was modeled using a random intercept.

Additionally, to confirm that block structure did not influence baseline sensitivity, we compared contrast thresholds for center-only trials between the Center-only block and the Mixed block using a paired-sample *t*-test.

Results

[Figure 3](#) shows suppression indices (*SI*; Methods) calculated with center-only trials from the initial Center-only block. As in [Experiment 1](#), the presence and the characteristics of the surround altered the perceived contrast of the central stimulus. Linear mixed-effects model results showed a significant main effect of category, $F(3,185) = 22.82$, $p < 0.001$, and a significant main effect of motion direction, $F(1,185) = 5.01$, $p = 0.03$. However, the interaction between category and motion direction was not significant, $F(3,185) = 1.97$, $p = 0.12$.

As in [Experiment 1](#), surround suppression was stronger when the center and surround moved in the same direction. Moreover, across both motion directions, SI values increased as categorical similarity

between center and surround scenes decreased, replicating the pattern observed in [Experiment 1](#). Post hoc paired-sample *t*-tests with FDR correction confirmed that suppression was significantly greater for the different superordinate category condition compared with other category conditions, all $t(24) > 3.91$, $ps < 0.001$. Likewise, suppression was significantly stronger in the different basic-level category condition than in the identical exemplar condition, $t(24) = 4.32$ all $p < 0.001$, and marginally stronger than in the different exemplar condition, $t(24) = 2.06$ all $p = 0.06$. In contrast, suppression strength did not differ between the identical and different exemplar conditions, $t(24) = 1.45$, $p = 0.16$. Moreover, SI values were significantly greater than zero in the different superordinate category conditions for both same- and opposite-direction trials, as well as in the different basic-level category conditions for same-direction trials ($ps < 0.05$).

To assess whether block order influenced baseline sensitivity, we compared contrast thresholds from Center-Only trials in the Center-Only and Mixed blocks. The threshold values were slightly higher in the Mixed block ($M = 0.19$, $SD = 0.13$) compared with the Center-Only block ($M = 0.18$, $SD = 0.17$). However, a paired-sample *t* test showed no significant difference between blocks, $t(24) = -0.20$, $p = 0.84$. Thresholds in the two blocks were moderately correlated across participants ($r = 0.48$, $p < 0.05$). These results suggest that baseline contrast sensitivity was relatively stable across blocks, although small differences might still influence the SI values.

Therefore, we recalculated SI values using center-only trials from the Mixed block ([Figure 4](#)) and reran the linear mixed effect model to assess whether the pattern observed in [Experiment 1](#) remained. Results again showed a significant main effect of category, $F(3,185) = 26.29$, $p < 0.001$, and a significant main effect of motion direction, $F(1,185) = 4.74$, $p = 0.03$. The interaction between category and motion direction was not significant, $F(3,185) = 1.08$, $p = 0.36$.

Taken together, these findings confirm that the effects of categorical similarity and motion congruence on surround suppression were robust across both experiments and were not driven by block structure or attentional confounds. The replication of the effects across block types suggests that the well-established influence of motion congruence on suppression, previously demonstrated with simple stimuli, also generalizes to complex naturalistic scenes. However, while physical similarity typically leads to stronger suppression with low-level stimuli ([Cavanaugh et al., 2002a](#); [Flevaris & Murray, 2015](#); [Serrano-Pedraza et al., 2012](#); [Shushruth et al., 2012](#)), this was not the case for naturalistic stimuli. Instead, categorical dissimilarity between the center and surround produced stronger suppression, highlighting a key difference between

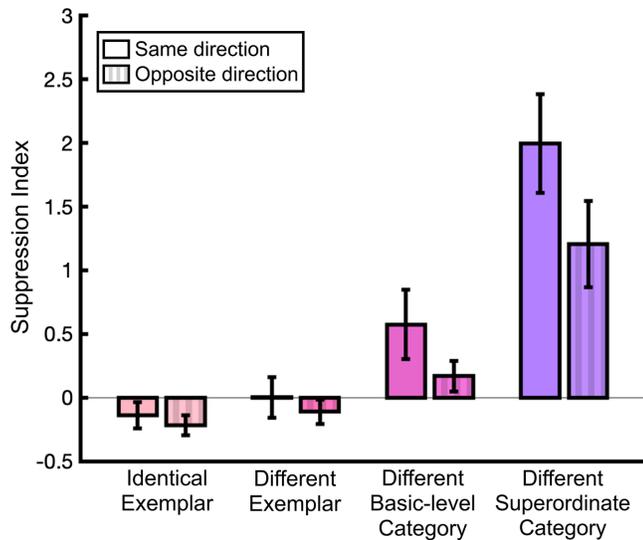


Figure 4. SI values from [Experiment 2](#), calculated using center-only trials from Mixed block. SI values were computed for each participant across four category conditions (identical exemplar, different exemplar, different basic-level category, and different superordinate category) and two motion direction conditions (same and opposite direction). Higher SI values indicate stronger surround suppression, while negative SI values reflect surround facilitation. Error bars represent the standard error of the mean.

suppression mechanisms for highly simplified versus naturalistic stimuli.

Discussion

The current study investigated how motion congruence and categorical similarity between central and surrounding stimuli shape surround modulation during natural scene perception. Across two experiments, we measured contrast thresholds for categorizing foveally presented natural scenes while systematically varying the relationship between the center and surround across four levels of categorical similarity (identical exemplar, different exemplar, different basic-level category, different superordinate category) and two levels of motion congruence (same vs. opposite direction). We found that contrast sensitivity for the central scene was significantly modulated by the presence and characteristics of the surrounding scene. Surround suppression was strongest when the surround moved in the same direction as the center, replicating classic motion congruence effects found with simple stimuli ([Allman et al., 1985](#); [Cavanaugh et al., 2002b](#); [Kastner et al., 1995](#); [Kiniklioglu & Boyaci, 2022](#); [Kiniklioglu & Boyaci, 2025](#); [Lamme, 1995](#); [Paffen et al., 2005](#); [Paffen et al., 2005](#)). Importantly, we also found

that suppression increased as the center and surround became more categorically dissimilar, with the strongest suppression occurring when they belonged to different superordinate categories (e.g., indoor vs. outdoor).

These results provide the first behavioral evidence of surround suppression in human perception using dynamic natural scenes. Although suppression effects have been widely documented with simple stimuli such as gratings, both behaviorally and neurally, ([Cavanaugh et al., 2002b](#); [Schallmo et al., 2018](#); [Tadin et al., 2003](#)), their role in processing complex ecologically valid visual stimuli in humans has remained unclear. A few animal studies using naturalistic stimuli have reported that Center-Surround interactions are sensitive to the statistical properties and spatial organization of natural stimuli. Recent behavioral work has begun to extend surround suppression research beyond simple grating stimuli to images with more complex visual statistics. For example, a recent preprint by [Pokorny, Weldon, and Olman \(2024\)](#) demonstrated robust surround suppression for broadband images using low-level perceptual judgments, showing that suppression generalizes to stimuli with richer spatial frequency content than gratings. The present study complements this work by further extending surround suppression to fully naturalistic, dynamic scenes and by examining its effects during a higher-level semantic categorization task. Our results show that surrounding scene context systematically reduces sensitivity to a central scene, establishing that surround suppression also occurs with naturalistic stimuli in human scene perception.

This suppression effect gets weaker, or may even disappear entirely, when the center and surround move in opposite directions. This has been shown in both neurophysiology studies ([Allman et al., 1985](#); [Born & Tootell, 1992](#); [Cavanaugh et al., 2002b](#); [Kastner et al., 1995](#); [Lamme, 1995](#)) and behavioral studies ([Kiniklioglu & Boyaci, 2022](#); [Paffen et al., 2005](#); [Paffen et al., 2005](#)). Consistent with these findings, we observed stronger suppression when the center and surround moved in the same direction compared to when they moved in opposite directions. This effect was robust across all category conditions, suggesting that motion congruence modulates suppression even with complex, naturalistic stimuli. Motion-based Center-Surround interactions have been linked to inhibitory mechanisms in motion-selective cortex, particularly area MT (MT hypothesis; see [Tadin et al., 2003](#)), where neural responses are reduced when stimulation extends beyond the classical receptive field ([Cavanaugh et al., 2002b](#); [Shushruth et al., 2013](#)). The present behavioral results parallel these neural findings and are consistent with the MT hypothesis, although they do not provide direct evidence about the underlying neural mechanisms. Although neural surround modulation is often considered a candidate mechanism

underlying perceptual suppression (Angelucci et al., 2017; Nurminen & Angelucci, 2014; Tadin, 2015), additional factors, including neural variability, task demands, and attentional modulation, may also shape the resulting perceptual effects. Nevertheless, our findings demonstrate that motion-based surround suppression is preserved under ecologically more valid conditions involving dynamic natural scenes.

In both experiments, suppression strength increased as the categorical distance between center and surround increased. Surrounds that belonged to different superordinate categories (e.g., indoor vs. outdoor) produced the strongest suppression, whereas scenes from the same basic-level category (e.g., two museums) produced weaker or no suppression. These results suggest that categorical similarity plays a critical role in contextual modulation: the more categorically dissimilar the surround, the more it interferes with the perception of the central scene. This pattern contrasts with findings from studies using low-level stimuli, where perceptual sensitivity typically decreases with center-surround similarity in features like orientation or spatial frequency (Petrov et al., 2005; Schallmo et al., 2016; Serrano-Pedraza et al., 2012; Tadin et al., 2003; Xing & Heeger, 2001). For example, the strongest suppression is observed when the center and surround are physically identical. In our study, however, no suppression was observed when the center and surround scenes were drawn from the same exemplar; instead, suppression increased with the greater categorical dissimilarity. This divergence from classical findings may reflect differences in task demands and representational level. Importantly, although many classical surround suppression studies focus on low-level perceptual judgments such as contrast detection, motion, or orientation discrimination (Er et al., 2020; Kiniklioglu & Boyaci, 2022; Schallmo et al., 2018; Tadin et al., 2003; Turkozer et al., 2016), our task involved the semantic categorization of dynamic natural scenes. Accordingly, the observed effects likely reflect contextual modulation at a higher representational level, rather than suppression driven primarily by basic visual features. In this context, perceptual sensitivity is influenced not only by lower-level visual properties but also by categorical relationships between the center and surround. In line with this interpretation, our findings align with animal studies using natural stimuli, which show that perceptually similar surround stimuli facilitate neural responses in the cat visual cortex, whereas dissimilar surrounds lead to suppression (Fu et al., 2024; Onat et al., 2013). Taken together, our results suggest that, in natural vision, suppression is not solely driven by low-level feature similarity, but is also influenced by a higher-level categorical structure.

A control analysis of low-level visual similarity indicated that similarity between center and surround did not differ reliably across categorical conditions. This makes it unlikely that the observed modulation of suppression by categorical distance can be attributed to differences in low-level orientation or spatial-frequency content. Instead, the results suggest that contextual modulation in natural scene perception reflects processing beyond basic visual features, potentially involving higher-level representations of scene category and contextual coherence.

Our findings also align with previous research showing that categorical incongruence between center and surround scenes impairs scene categorization accuracy (Faurite et al., 2024; Lukavský, 2019; Trouilloud et al., 2022). Critically, we extend these findings by demonstrating that such categorical congruency effects also modulate low-level perceptual sensitivity, as reflected in contrast thresholds, even when the task involves high-level scene categorization. Moreover, Peyrin et al. (2021) showed that even when central and peripheral scenes are categorically congruent (e.g., two man-made scenes), physical dissimilarities between the scenes (e.g., buildings vs. streets) lead to decreased central scene categorization accuracy. Consistent with this, we found suppression effects even when the center and surround belonged to the same task-relevant superordinate category (e.g., two indoor scenes), but differed at the basic level (e.g., restaurant vs. museum).

Furthermore, there was no interaction between motion congruence and categorical similarity. This finding suggests that these two types of contextual information modulate suppression independently. One possibility is that suppression arises from multiple stages of processing, with earlier visual areas primarily sensitive to basic features like contrast and motion (Angelucci et al., 2017), whereas higher-level perceptual systems contribute additional modulation based on categorical information. Together, our results suggest that traditional models of surround suppression, which have focused primarily on low-level features such as contrast, orientation, and motion (Angelucci et al., 2017), should be expanded to incorporate the influence of higher-level contextual factors. In this regard, our recent functional magnetic resonance imaging (fMRI) preprint provides an initial neural investigation of contextual modulation using similar stimuli and design (Kiniklioglu, Pitcher, & Kaiser, 2025). Specifically, we found that neural surround modulation during natural scene perception varies systematically across the visual hierarchy, with motion-dependent effects in hMT+ and category-dependent modulation in scene-selective cortex, providing complementary neural context for the present behavioral findings.

In real-world environments, scenes generally follow consistent categorical structures (e.g., a kitchen

containing related objects such as appliances, utensils, and cabinets, all organized within a coherent spatial layout). To process such environments efficiently, the visual system integrates spatial and semantic context across multiple levels (Bar, 2004; Kaiser, Quek, Cichy, & Peelen, 2019; Vö, 2021). Numerous studies have shown that coherent scene structure facilitates or speeds scene and object processing (Chen, Cichy, & Kaiser, 2022; Davenport & Potter, 2004; Kaiser & Peelen, 2018; Kaiser et al., 2019; Kaiser, Häberle, & Cichy, 2020; Kaiser, Häberle, & Cichy, 2021; Vö & Wolfe, 2013). Predictive coding and contextual modulation frameworks propose that perceptual efficiency is supported by suppressing predictable or redundant input (Angelucci & Bressloff, 2006; Gilbert & Li, 2013; Rao & Ballard, 1999). In early visual areas, surrounds that share similar low-level features with a central stimulus often suppress neural responses, an effect commonly interpreted as reducing statistical redundancy and improving the encoding of task-relevant features (Angelucci et al., 2017; Coen-Cagli, Dayan, & Schwartz, 2012; Nurminen & Angelucci, 2014; Schwartz & Simoncelli, 2001; Vinje & Gallant, 2000). Importantly, efficient-coding accounts suggest that this form of neural suppression does not necessarily entail impaired behavioral performance and is frequently associated with enhanced perceptual sensitivity (Coen-Cagli et al., 2012).

Our findings are consistent with the possibility that contextual modulation operates differently at higher, semantic levels of processing. Incongruent surrounds at both the basic and superordinate categorical levels led to behavioral suppression, whereas congruent surrounds did not. In natural scenes, redundancy may therefore be defined at a semantic or categorical level rather than in terms of low-level feature similarity: information that violates scene expectations may fail to provide useful predictive context and be effectively down weighted. Under this interpretation, the functional role of contextual modulation may shift across the visual hierarchy, such that while low-level neural suppression reduces redundancy in predictable sensory input, effects observed at higher levels could reflect reduced contextual integration or interference from incongruent information. In this view, both forms of modulation may support perceptual efficiency by prioritizing task-relevant input through distinct mechanisms at different stages of processing.

A common concern in studies of contextual modulation is the potential influence of spatial attention. To address this, we used both blocked (Experiment 1) and mixed (Experiment 2) designs to control for possible order effects and attentional biases. The consistency of results across both designs suggests that the observed suppression effects cannot be attributed to block order or attentional strategies.

One might also argue that the suppression effects observed in natural scenes reflect the increased cognitive demands of the second task. However, if task difficulty were the primary factor, suppression strength should not differ between same- and opposite-direction trials. Instead, our results consistently show stronger suppression under the same-direction condition. Together, these findings support the interpretation that suppression in our paradigm reflects active, stimulus-driven contextual inhibition, rather than passive attentional withdrawal or task-related artifacts.

It is also possible that the Center+Surround trials required participants to divide attention between the center and surround stimuli, potentially making them more demanding than the Center-Only trials. Although attending to both stimuli may modestly increase task demands, several aspects of our design and results argue against attentional load as the primary explanation for the observed effects. If divided attention were driving the difference between Center-Only and Center+Surround conditions, we would expect a general reduction in performance (e.g., uniformly increased thresholds) across all Center+Surround conditions. However, our results show selective modulation as a function of surround category rather than a general decrease in performance, suggesting that the observed differences are unlikely to reflect attentional capacity limits. Moreover, because Center-Only and Center+Surround trials were interleaved in Experiment 2 and were unpredictable at trial onset, participants had to maintain a comparable attentional scope throughout the session, thereby minimizing systematic differences in attentional strategy.

We also considered the possibility that incongruent Center+Surround trials may impose greater working memory or response selection demands, because participants may have needed to maintain two categorical responses. However, maintaining two responses falls well within established working memory capacity limits. Critically, if working memory demands were the primary driver of the observed effects, we would expect thresholds to be selectively increased in the different superordinate category condition, where two distinct responses must be held in memory (e.g., center = indoor, surround = outdoor), and minimal suppression in the remaining category conditions, where center and surround share the same response. However, this pattern did not emerge. Instead, suppression increased systematically with categorical distance, and reliable suppression was observed even in the different basic-level category condition, where the required response for the center and surround was identical. Together, these findings suggest that the reported effects are unlikely to be explained solely by divided attention, response selection, or working memory demands.

Having ruled out these alternative accounts, we next assessed whether center–surround interactions reflect perceptual-level modulation by computing trial-by-trial correlations between center and surround response accuracies. If surround processing is perceptually modulated by the center, response errors should be more strongly correlated when two stimuli belong to the same category than when they are categorically incongruent. Consistent with this prediction, error correlations were higher for same-category than different-category conditions in both experiments, and correlation strength decreased systematically with categorical similarity (Supplementary Table S2).

Although the present study provides robust evidence for both categorical and motion-based surround suppression in natural vision, several questions remain open for future research. First, although a control analysis indicated that low-level visual similarity did not differ reliably across categorical conditions, we did not explicitly manipulate low-level image properties such as spatial frequency or amplitude spectrum. It therefore remains possible that more specific or localized visual features, not captured by the present analysis, contribute to surround suppression effects (Peyrin et al., 2021). Future studies could independently vary such physical image properties and categorical coherence to better disentangle their influences. Second, although we observed reliable effects of categorical similarity, the underlying neural mechanisms remain to be clarified. Follow-up studies using neuroimaging methods could further help localize the sources and time course of suppression and determine whether distinct neural circuits mediate motion-based and category-based suppression. Although our stimuli consisted of natural scenes, the applied drifting motion does not fully reflect the complexity of motion in everyday visual experience. Coherent global motion can occur in natural vision, such as during self-motion or smooth pursuit eye movements, when large portions of the visual field move in a common direction, but motion patterns in natural environments are much richer than that. Thus, our stimuli provide a first controlled approximation of naturalistic motion, and future work should extend this approach using natural videos with more complex and unconstrained dynamics. Finally, in our experiments, participants performed a categorization task on a relatively narrow range of scene categories. Future work using a larger and more diverse set of scene exemplars will be important for assessing the generality of these effects across images and categories. It remains an open question whether similar suppression effects would generalize to a broader set of scenes, such as comparisons between natural and man-made environments, and beyond categorization tasks. Together, these directions highlight the need for further research to refine our understanding of

how high-level contextual information shapes visual processing in natural vision.

Conclusions

Our study demonstrates that surround suppression in natural scene perception is shaped by both motion–direction congruence and categorical similarity. Consistent with results with simple stimuli, suppression was stronger when the center and surround moved in the same direction. However, unlike low-level studies, where identical center–surround features typically yield the greatest suppression, we observed no suppression in the identical exemplar condition. Instead, suppression increased as the categorical similarity between center and surround decreased. Thus, in natural vision, contextual modulation is driven not only by low-level feature similarity but also by higher-level categorical structure. These findings advance our understanding of contextual modulation in natural vision, and suggest that context-dependent suppression may help the visual system prioritize coherent, task-relevant information while suppressing incongruent input.

Keywords: scene perception, center–surround interaction, motion perception, surround suppression

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References

- Allman, J., Miezin, F., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (mt). *Perception*, *14*, 105–126, <https://doi.org/10.1068/p140105>.
- Angelucci, A., Bijanzadeh, M., Nurminen, L., Federer, F., Merlin, S., & Bressloff, P. C. (2017). Circuits and mechanisms for surround modulation in visual cortex. *Annual Review of Neuroscience*, *40*, 425–451, <https://doi.org/10.1146/annurevneuro-072116-031418>.
- Angelucci, A., & Bressloff, P. C. (2006). The contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate V1 neurons. *Progress in Brain Research*, *154*, 93–120, [https://doi.org/10.1016/S0079-6123\(06\)54005-1](https://doi.org/10.1016/S0079-6123(06)54005-1).
- Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, *5*(8), 617–629, <https://doi.org/10.1038/nrn1476>.
- Born, R. T., & Tootell, R. B. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature*, *357*, 497–499, <https://doi.org/10.1038/357497a0>.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436.
- Cavanaugh, J. R., Bair, W., & Movshon, J. A. (2002a). Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *Journal of Neurophysiology*, *88*(4), 2530–2546, <https://doi.org/10.1152/jn.00692.2001>.
- Cavanaugh, J. R., Bair, W., & Movshon, J. A. (2002b). Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons. *Journal of Neurophysiology*, *88*, 2547–2556, <https://doi.org/10.1152/jn.00693.2001>.
- Chen, L., Cichy, R. M., & Kaiser, D. (2022). Semantic scene-object consistency modulates n300/400 EEG components, but does not automatically facilitate object representations. *Cerebral Cortex*, *32*(16), 3553–3567, <https://doi.org/10.1093/cercor/bhab433>.
- Coen-Cagli, R., Dayan, P., & Schwartz, O. (2012). Cortical surround interactions and perceptual salience via natural scene statistics. *PLoS Computational Biology*, *8*(3), e1002405, <https://doi.org/10.1371/journal.pcbi.1002405>.
- Coen-Cagli, R., Kohn, A., & Schwartz, O. (2015). Flexible gating of contextual influences in natural vision. *Nature Neuroscience*, *18*(11), 1648–1655, <https://doi.org/10.1038/nn.4128>.
- Davenport, J. L., & Potter, M. C. (2004). Scene consistency in object and background perception. *Psychological Science*, *15*(8), 559–564, <https://doi.org/10.1111/j.0956-7976.2004.00719.x>.
- DeAngelis, G. C., Freeman, R. D., & Ohzawa, I. (1994). Length and width tuning of neurons in the cat's primary visual cortex. *Journal of Neurophysiology*, *71*(1), 347–374, <https://doi.org/10.1152/jn.1994.71.1.347>.
- Er, G., Pamir, Z., & Boyaci, H. (2020). Distinct patterns of surround modulation in V1 and HMT+. *NeuroImage*, *220*, 117084, <https://doi.org/10.1016/j.neuroimage.2020.117084>.
- Faurite, C., Aprile, E., Kauffmann, L., Mermillod, M., Gallice, M., Chiquet, C., ... Peyrin, C. (2024). Interaction between central and peripheral vision: Influence of distance and spatial frequencies. *Journal of Vision*, *24*(1), 3, <https://doi.org/10.1167/jov.24.1.3>.
- Flevaris, A. V., & Murray, S. O. (2015). Attention determines contextual enhancement versus suppression in human primary visual cortex. *Journal of Neuroscience*, *35*(35), 12273–12280, <https://doi.org/10.1523/JNEUROSCI.1409-15.2015>.
- Fu, J., Shrinivasan, S., Baroni, L., Ding, Z., Fahey, P. G., Pierzchlewicz, P., ... Franke, K. (2024). Pattern completion and disruption characterize contextual modulation in the visual cortex [Preprint]. bioRxiv. <https://doi.org/10.1101/2023.03.13.532473>.
- Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*(5), 350–363, <https://doi.org/10.1038/nrn3476>.
- Kaiser, D., Häberle, G., & Cichy, R. M. (2020). Cortical sensitivity to natural scene structure. *Human Brain Mapping*, *41*(5), 1286–1295, <https://doi.org/10.1002/hbm.24875>.
- Kaiser, D., Häberle, G., & Cichy, R. M. (2021). Coherent natural scene structure facilitates the extraction of task-relevant object information in visual cortex. *NeuroImage*, *240*, 118365, <https://doi.org/10.1016/j.neuroimage.2021.118365>.
- Kaiser, D., & Peelen, M. V. (2018). Transformation from independent to integrative coding of multi-object arrangements in human visual cortex. *NeuroImage*, *169*, 334–341, <https://doi.org/10.1016/j.neuroimage.2017.12.065>.
- Kaiser, D., Quek, G. L., Cichy, R. M., & Peelen, M. V. (2019). Object vision in a structured world. *Trends in Cognitive Sciences*, *23*(8), 672–685, <https://doi.org/10.1016/j.tics.2019.04.013>.

- Kastner, S., Nothdurft, H. C., & Pigarev, I. N. (1995). Neuronal correlates of pop-out in cat striate cortex. *Vision Research*, *37*, 371–376, [https://doi.org/10.1016/S0042-6989\(96\)00184-8](https://doi.org/10.1016/S0042-6989(96)00184-8).
- Kingdom, F. A. A., & Prins, N. (2010). *Psychophysics: A practical introduction*. New York: Academic Press.
- Kiniklioglu, M., & Boyaci, H. (2025). Hmt+ activity predicts the effect of spatial attention on surround suppression. *Journal of Vision*, *25*(4), 12, <https://doi.org/10.1167/jov.25.4.12>.
- Kiniklioglu, M., & Boyaci, H. (2022). Increasing the spatial extent of attention strengthens surround suppression. *Vision Research*, *199*, 108074, <https://doi.org/10.1016/j.visres.2022.108074>.
- Kiniklioglu, M., Pitcher, D., & Kaiser, D. (2025). Distinct mechanisms of surround modulation for dynamic natural scenes in motion-and scene-selective cortex [Preprint]. bioRxiv. <https://doi.org/10.1101/2025.11.06.686956>.
- Lamme, V. A. F. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *Journal of Neuroscience*, *15*, 1605–1616, <https://doi.org/10.1523/JNEUROSCI.15-02-01605.1995>.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, *49*(2B), 467–477, <https://doi.org/10.1121/1.1912375>.
- Lukavský, J. (2019). Scene categorization in the presence of a distractor. *Journal of Vision*, *19*(2), 6, <https://doi.org/10.1167/19.2.6>.
- Mareschal, I., & Shapley, R. M. (2004). Effects of contrast and size on orientation discrimination. *Vision Research*, *44*(1), 57–67, <https://doi.org/10.1016/j.visres.2003.07.009>.
- Nurminen, L., & Angelucci, A. (2014). Multiple components of surround modulation in primary visual cortex: Multiple neural circuits with multiple functions? *Vision Research*, *104*, 47–56, <https://doi.org/10.1016/j.visres.2014.08.018>.
- Onat, S., Jancke, D., & König, P. (2013). Cortical long-range interactions embed statistical knowledge of natural sensory input: A voltage-sensitive dye imaging study. *F1000Research*, *2*, 51, <https://doi.org/10.12688/f1000research.2-51.v2>.
- Paffen, C. L. E., Alais, D., & Verstraten, F. A. J. (2005). Center-surround inhibition deepens binocular rivalry suppression. *Vision Research*, *45*(20), 2642–2649, <https://doi.org/10.1016/j.visres.2005.04.018>.
- Paffen, C. L. E., van der Smagt, M. J., te Pas, S. F., & Verstraten, F. A. J. (2005). Center-surround inhibition and facilitation as a function of size and contrast at multiple levels of visual motion processing. *Journal of Vision*, *5*(6), 571–578, <https://doi.org/10.1167/5.6.8>.
- Petrov, Y., Carandini, M., & McKee, S. (2005). Two distinct mechanisms of suppression in human vision. *Journal of Neuroscience*, *25*(38), 8704–8707, <https://doi.org/10.1523/JNEUROSCI.2871-05.2005>.
- Peyrin, C., Roux-Sibilon, A., Trouilloud, A., Khazaz, S., Joly, M., Pichat, C., . . . Kauffmann, L. (2021). Semantic and physical properties of peripheral vision are used for scene categorization in central vision. *Journal of Cognitive Neuroscience*, *33*(5), 799–813, <https://doi.org/10.1162/jocn.a.01689>.
- Pokorny, V. J., Weldon, K. B., & Olman, C. A. (2024). Surround suppression of broadband images [preprint]. bioRxiv. <https://doi.org/10.1101/2024.05.15.594329>.
- Rao, R., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*, 79–87, <https://doi.org/10.1038/4580>.
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, *2*(11), 1019–1025, <https://doi.org/10.1038/14819>.
- Schallmo, M.-P., Grant, A. N., Burton, P. C., & Olman, C. A. (2016). The effects of orientation and attention during surround suppression of small image features: A 7 tesla fMRI study. *Journal of Vision*, *16*(10), 19, <https://doi.org/10.1167/16.10.19>.
- Schallmo, M.-P., Kale, A. M., Flevaris, A. V., Brkanac, Z., Edden, R. A., Bernier, R. A., . . . Murray, S. O. (2018). Suppression and facilitation of human neural responses. *eLife*, *7*, 1–23, <https://doi.org/10.7554/eLife.30334.001>.
- Schwartz, O., & Simoncelli, E. P. (2001). Natural signal statistics and sensory gain control. *Nature Neuroscience*, *4*(8), 819–825, <https://doi.org/10.1038/90526>.
- Serrano-Pedraza, I., Grady, J. P., & Read, J. C. A. (2012). Spatial frequency bandwidth of surround suppression tuning curves. *Journal of Vision*, *12*(6), 24, <https://doi.org/10.1167/12.6.24>.
- Shushruth, S., Mangapathy, P., Ichida, J.M., Bressloff, P. C., Schwabe, L., & Angelucci, A. (2012). Strong recurrent networks compute the orientation tuning of surround modulation in the primate primary visual cortex. *Journal of Neuroscience*, *32*, 308–321, <https://doi.org/10.1523/JNEUROSCI.3789-11.2012>.
- Shushruth, S., Nurminen, L., Bijanzadeh, M., Ichida, J. M., Vanni, S., & Angelucci, A. (2013). Different orientation tuning of near- and far-surround

- suppression in macaque primary visual cortex mirrors their tuning in human perception. *Journal of Neuroscience*, 33(1), 106–119, <https://doi.org/10.1523/JNEUROSCI.2518-12.2013>.
- Tadin, D. (2015). Suppressive mechanisms in visual motion processing: From perception to intelligence. *Vision Research*, 115, 58–70, <https://doi.org/10.1016/j.visres.2015.08.005>.
- Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature*, 424, 312–315, <https://doi.org/10.1038/nature01800>.
- Trouilloud, A., Kauffmann, L., Roux-Sibilon, A., Rossel, P., Boucart, M., Mermillod, M., . . . Peyrin, C. (2020). Rapid scene categorization: From coarse peripheral vision to fine central vision. *Vision Research*, 170, 60–72, <https://doi.org/10.1016/j.visres.2020.02.008>.
- Trouilloud, A., Rossel, P., Faurite, C., Roux-Sibilon, A., Kauffmann, L., & Peyrin, C. (2022). Influence of physical features from peripheral vision on scene categorization in central vision. *Visual Cognition*, 30(6), 425–442, <https://doi.org/10.1080/13506285.2022.2087814>.
- Turkozer, H. B., Pamir, Z., & Boyaci, H. (2016). Contrast affects fMRI activity in middle temporal cortex related to center-surround interaction in motion perception. *Frontiers in Psychology*, 7, 1–8, <https://doi.org/10.3389/fpsyg.2016.00454>.
- Vinje, W. E., & Gallant, J. L. (2000). Sparse coding and decorrelation in primary visual cortex during natural vision. *Science*, 287(5456), 1273–1276, <https://doi.org/10.1126/science.287.5456.1273>.
- Võ, M. L.-H. (2021). The meaning and structure of scenes. *Vision Research*, 181, 10–20, <https://doi.org/10.1016/j.visres.2020.11.003>.
- Võ, M. L.-H., & Wolfe, J. M. (2013). Differential electrophysiological signatures of semantic and syntactic scene processing. *Psychological Science*, 24(9), 1816–1823, <https://doi.org/10.1177/0956797613476955>.
- Walker, G. A., Ohzawa, I., & Freeman, R. D. (1999). Asymmetric suppression outside the classical receptive field of the visual cortex. *Journal of Neuroscience*, 19(23), 10536–10553, <https://doi.org/10.1523/JNEUROSCI.19-23-10536.1999>.
- Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods*, 42(3), 671–684, <https://doi.org/10.3758/BRM.42.3.671>.
- Xing, J., & Heeger, D. J. (2001). Measurement and modeling of center-surround suppression and enhancement. *Vision Research*, 41, 571–583, [https://doi.org/10.1016/S0042-6989\(00\)00270-4](https://doi.org/10.1016/S0042-6989(00)00270-4).