The effect of color tuning on priming in neuronal circuits of the visual cortex

Applied Data Science Master Thesis

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Abstract

This thesis explores the influence of color stimuli on the priming effects and neuronal response patterns within the visual cortex of macaque monkeys. Using multi-unit activity (MUA) data from 38 recording sessions, the study investigates how different neurons in the V4 area of the visual cortex respond to red and green stimuli. By examining the feature tuning index (FTI) and the priming effects for each electrode site, the research aims to uncover the relationship between a neuron's color preference and its response to primed stimuli. Additionally based on obtained FTI and neuronal preference clustering is conducted to see if different neuronal populations can be distinguished based on those values.

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1. Introduction

1.1 Motivation and context

This thesis embarks on a journey to examine the effect of color tuning on priming on neuronal circuits in the visual cortex. The greatest emphasis will be on feature selection's impact on neuronal behavior. Neuroscience is a continuously expanding field with the goal of finding patterns and schemas in the brain's actions. Conducting research on human brains is often much more complex and time-consuming than obtaining representable results by examining other primates' brains, such as monkeys (Kaas, 2008; Orban et al., 2004). Therefore, in this thesis, the analyzed dataset was collected from two macaque' monkeys' brains, which can serve as a model to understand how priming also works in human brains (Van Essen et al., 2001; Nassi & Callaway, 2009).

The main research question of this thesis is as follows:

How does the preferred color tuning of neurons in area V4 influence the priming effects when exposed to specific color stimuli?

In other words, this thesis aims to determine the neuronal priming effects for each of the neuronal groups when exposed to their preferred stimuli vs. their non-preferred stimuli. The hypothesis behind this research question is that in the form of priming called repetition suppression, neuronal responses decrease, indicating more efficient processing, as Desimone (1996) stated. To answer the above question and confirm the hypothesis, two supporting research questions were constructed, firstly:

How is every analyzed neuronal group tuned in terms of color?

This first sub-question will serve as a starting point of analysis. Each neuronal group must be classified as red-tuned, neutral, or green-tuned. Classification will be made based on the Feature Tuning Index, explained in detail in the "Methods" section. Secondly:

What is the priming effect for each of the colors of stimuli?

The second sub-question is strictly connected to answering the main research question. It focuses on quantifying differences in neural response to red and green stimuli for each neuronal group. This calculation's core is comparing baseline trial neuronal response (for the first picture shown in the block of trials) to neuronal response in succeeding trials.

The next part of the Introduction chapter explains all the paradigms mentioned in the research questions in detail.

1.1.1 Priming

To understand the data structure and the purpose of the analysis presented in further chapters, the reader must be introduced to the term Priming. Priming can be described as a nonconscious impact of previous experience on current performance or behavior (Schacter and Buckner, 1998). In other words, it is a phenomenon that influences the interpretation of the situation by the brain based on the similarities from the past. Changes that occur because of priming influence the speed of interpretation, bias, and accuracy (Henson, 2003). The measurement of priming can consist of comparing neuronal action potentials between the initial presentation of a stimulus and repeated ones.

Priming can be classified into different types based on the nature of stimuli and the processes involved. Three main types can be distinguished, namely: perceptual, conceptual, and repetition priming. Perceptual priming takes place when the priming effect depends on the physical form of the stimulus. For example, it occurs when the subject better identifies a word when previously exposed to this word. Thus, it can be said that the word's physical form has been primed. Unlike perceptual priming, conceptual priming is not related to the physical form of the stimuli but rather to its meaning and semantics. Such priming phenomenon happens when the subject is better at generating words related to a previously studied category. Finally, repetition priming refers to the priming effect originating from repeatedly exposing the subject to the same stimuli, leading to faster and more accurate responses over time (Maljkovic and Nakayama, 1994). Priming analyzed in this thesis falls into two categories: perceptual and repetition priming, as stimuli' physical form is a crucial factor, and subjects are exposed repeatedly to these stimuli.

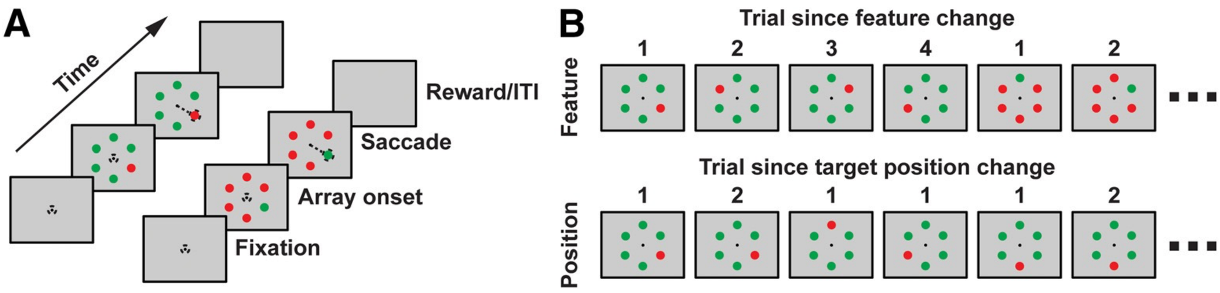
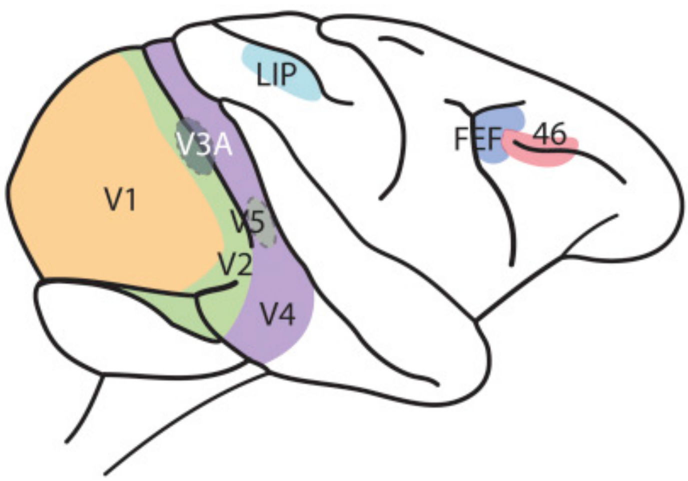


Figure 1. Pop-out priming experiment schema

Datasets used to answer this thesis' research question were obtained by placing electrodes in macaque monkeys' brains. As described by Westerberg et al. (2020) – creators of the experiment, monkeys were exposed to pop-out visual search tasks presented on monitors in front of them. In the pop-out visual search task, subjects are exposed to an array of objects, among which one item stands out, or "pops-out", due to its distinct feature compared to other items; in this thesis, this feature is color. The task was done correctly only if monkeys could direct their sight within 1000 ms to one stimulus of a different color than 5 other items. For each correctly completed trial, monkeys got the reward in the form of juice. There were two colors selected for the experiment: red and green.

1.1.2 Architecture of the visual cortex

It is crucial to introduce the reader to the structure of the visual cortex in the monkey's brain.



[1]

Figure 2. Macaque monkey visual cortex

[1] Source: Chapter 6 - Interareal Connections of the Macaque Cortex: How Neocortex Talks to Itself

As shown in Figure 2, the visual cortex of the macaque monkey consists of the primary visual cortex ("V1") and higher visual areas such as V2, V3, V4, and V5 (Vanni S et al., 2020). Within V1, monkeys exhibit retinotopic map. Extensive feedforward and feedback connections between areas in the visual cortex facilitate complex visual processing.

V4, which is the main focus of this thesis, holds a significant role in the analysis of features of objects, such as their shape and color. Since the color and shape of objects highly differentiate the visual information, this area is specialized in detecting this kind of information. This is mandatory for color discrimination and visual attention. The functional organization of V4 includes neurons that are selectively tuned to different colors and orientations that mediate the monkey's ability to perceive and differentiate objects based on these visual features.

1.1.3 Neuronal Circuits

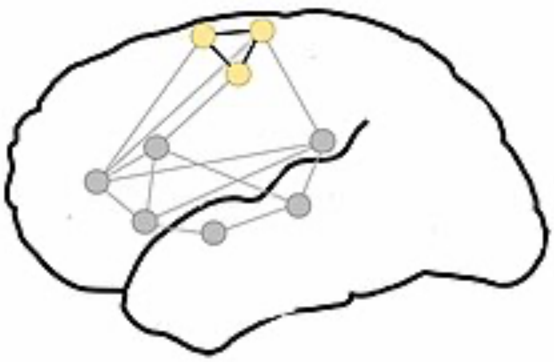

[2]

Figure 3. Neuronal circuits schema

Networks of interconnected neurons form neural circuits that use synaptic connections to transmit and process information. Several circuits are needed to get the ability to take in sensory inputs to call up suitable reactions. These circuits also allow an organism to take in and comprehend the visual world in the visual cortex. The attention mechanisms include the top-down or cognitive-driven mechanisms and the bottom-up or sensory-driven ones to increase or allow the perception of relevant inputs. These processes depend critically on brain networks such as the ventral stream, which is involved in object recognition, and the dorsal stream, which

J.C. Anderson, K.A.C. Martin. https://doi.org/10.1016/B978-0-12-801393-9.00006-2

[2] Source: https://www.physio-pedia.com/index.php?title=Neuroplasticity_After_Stroke&veaction=edit&section=4

is involved in spatial attention (Vanni et al., 2020). Electrophysiology and neuroimaging work validate these circuits' specialized and interconnected nature.

1.1.4 Feature tuning

In the context of neurobiology, feature tuning term can be translated as a single neuron or neuronal circuit preference for a certain property. This property can be either shape, orientation, or color for the visual cortex. To quantify this preference, neuronal responses must be measured separately for each distinct stimuli type within a category. Only then can those categories be compared so that neuronal groups can be classified based on their preference. In the setting of this thesis, feature tuning is calculated based on two different stimuli colors: red and green. Thus, this analysis is oriented around color property preference for each neuronal group.

2. Data

2.1 Introduction

Data concludes probes readings from 38 sessions. Thirty-one sessions were done on one macaque monkey and seven on the other one. For each session, the probe was placed in a different area of V4. Therefore, there are 570 total recording sites, and on each probe, there were 15 electrode sites. For this thesis, two datasets will be used: *MUA_array* (Multiunit activation) and *task.csv*. The multiunit activation ("MUA") dataset contains neuronal activation values collected while performing the priming tasks. The task file is a CSV that will serve as a supporting table that contains information about each trial within the session, especially the color of the stimuli. Both tables will be joined together in order to determine the feature tuning of each examined neuronal group.

contact	**position_from_top_mm**	**position_from_L4_boundary_mm**	**layer_category**
1	0	1	upper
2	0.1	0.9	upper
3	0.2	0.8	upper
4	0.3	0.7	upper
5	0.4	0.6	upper
0	0.5	0.5	middle
7	0.6	0.4	middle
0	0.7	0.3	middle
9	0.8	0.2	middle
10	0.9	0.1	middle
11	1	0	deep
12	1.1	-0.1	deep
13	1.2	-0.2	deep
14	1.3	-0.3	deep
15	1.4	-0.4	deep

Figure 4. Electrodes position

The MUA dataset has three dimensions. The first dimension corresponds to the electrode number, as shown in Figure 5. There are 15 electrode sites placed within the V4 area of the visual cortex. The second dimension translates to timestamps. Finally, the third dimension coincides with the trial number.

Before conducting any further analysis on the impact of the color of stimuli on priming tasks on neuronal circuits, it is crucial to decide on feature tuning for each neuronal group. Each electrode site represents a group of neurons in either the upper, middle, or deep layer (Figure 5.) of the V4 area in the visual cortex. For those groups of neurons, exploration will consist of calculating the average MUA signal value for each target color separately. It will allow for an initial assessment of the probe's tuning.

2.2 Data preprocessing

Before conducting any exploration or analysis steps, data has to be transformed and preprocessed to a suitable form. Neural spiking data in the MUA dataset was recorded with 24kHz resolution. Therefore, 5 filtering and preprocessing steps, were conducted to obtain data in the desired format (Westerberg et al., 2020):

1. Band-pass filter at 3kHz
2. Full-wave rectified
3. High-pass filter at 300 Hz
4. Low-pass filter at 150 Hz
5. Z-score normalization

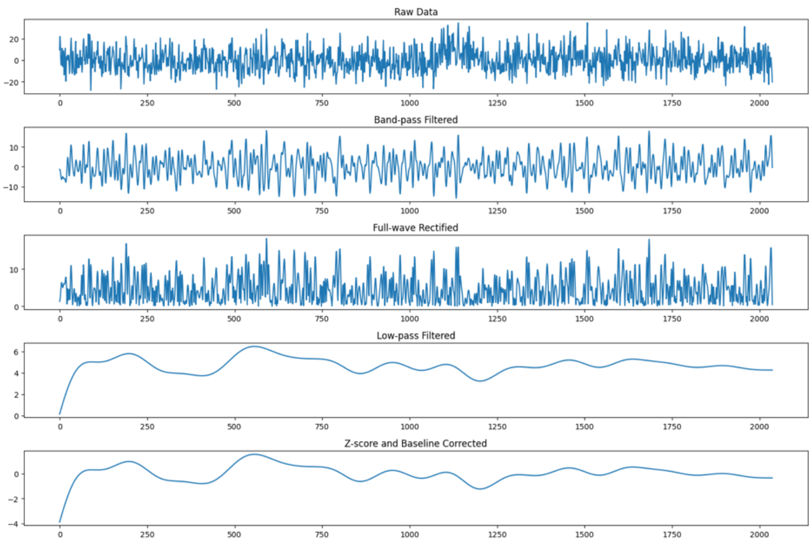


Figure 5. Data filtering

Four applied filters served the purpose of eliminating the noise in the dataset. As presented in Figure 6, neural spiking data is smooth and ready for analysis after filtering the application. Z-score normalization was the last step of preprocessing, where each time point activity was standardized based on the mean and standard deviation of the baseline period using the formula (Westerberg et al., 2020):

$$z_t = \frac{x_t - \text{mean}(x_{\text{baseline}(c1,c2)})}{s_{(\text{baseline}(c1,c2))}}.$$

Using z-score normalization allows for meaningful comparisons of neuronal responses across different conditions by accounting for baseline variability.

2.3 Data exploration

Understanding and revealing the characteristics of the dataset is vital for further analysis. This subsection will explore two values: firing rates for red and green stimuli and the average MUA signal for each session and electrode site across different time points.

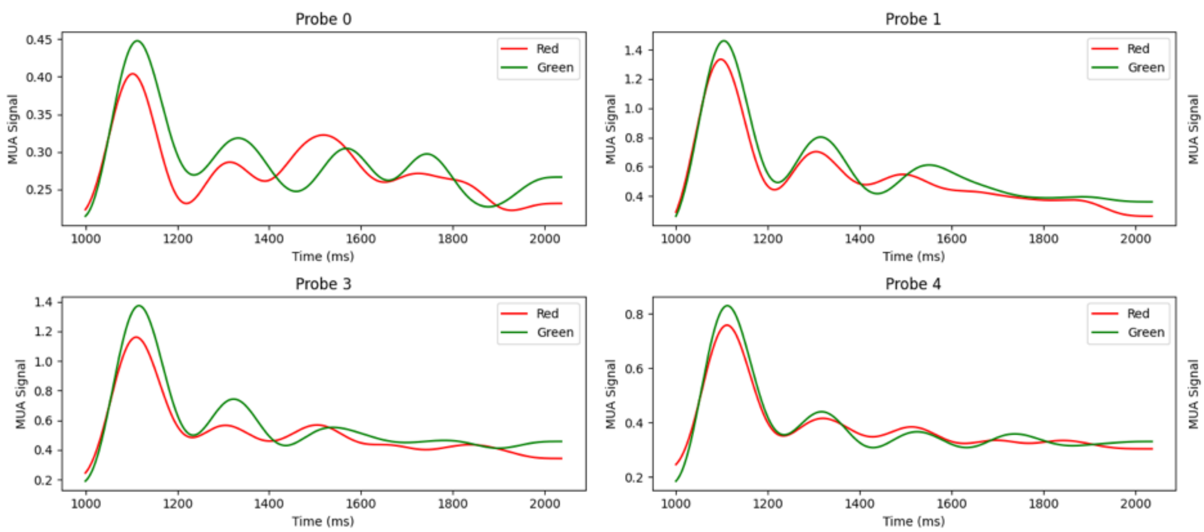


Figure 6. Average MUA signal for 4 electrode sites across one session

Figure 7 shows the average MUA signal for 4 electrode sites (this serves as an example – the same calculation was performed for each of the 570 electrode sites) within one session, with a distinction made based on the color of the stimuli. The time window for these plots starts from 1000 ms to 2000 ms, capturing the period immediately after the picture was shown to the monkeys. The responses to red and green stimuli differ significantly. For green stimuli, the peak values of the MUA signal often appear higher, while for the red stimuli, the responses usually seem to keep higher rates throughout the trial altogether. These plots illustrate the preferential responses of neurons to different colors, suggesting color-tuning effects in the visual cortex.

3 Methods

3.1 Introduction

This chapter outlines the methodological approach used to address the research question: *"*How does the preferred color tuning of neurons in area V4 influence the priming effects when exposed to specific color stimuli?". This chapter's methods include feature tuning index calculation and priming effect analysis. Moreover, after calculating features, the outcomes will be used to perform clustering analysis to answer the Data Science Research Question:

Can clustering based on feature tuning and priming effects reveal distinct neuronal populations?

3.2 Models and formulas

Each method used in this chapter will answer a separate research sub-question to address the main research question. This subchapter will be divided into three sections organized chronologically, each describing a different method and corresponding research question.

3.2.1 Feature tuning index

The first point of the analysis is to classify each of the 570 neuronal groups into being either red or green-tuned. These calculations will be used to answer the following research sub-question:

How is every analyzed neuronal group tuned in terms of color?

The Feature Tuning Index ("FTI") formula has been developed to assess the tuning of each neuronal group. For each electrode site, the average response from the MUA signal is calculated to red and green stimuli:

$$\mathrm{FTI} = \frac{\text{Average MUA}_{\text{green}} - \text{Average MUA}_{\text{red}}}{\text{Average MUA}_{\text{green}} + \text{Average MUA}_{\text{red}}}$$

FTI ranges from -1 to 1, where positive values indicate a preference for red, negative values indicate a preference for green, and values around zero indicate no strong preference. The threshold for classifying neurons as neutral ranges is calculated as 0.5 times the standard deviation.

3.2.2 Priming Effect

Calculating the priming effect is the second step in the analysis. It will allow to answer the following research sub-question:

What is the priming effect for each of the colors of stimuli?

The priming effect is calculated as the difference in neuronal response between primed and unprimed trials. Primed trials are identified as consecutive trials with the same target color, while unprimed trials are those where the target color changes – the first trial in the block.

$$\text{Priming Effect} = \text{mean response to primed} - \text{mean response to unprimed}$$

Firstly, priming effects were aggregated for preferred and non-preferred stimuli for each neuronal group. T-tests were performed to decide whether the priming effect differs between preferred and non-preferred colors for each of the tuning of the neuronal groups.

3.2.3 Clustering

Clustering is a critical step in this analysis since it identifies subpopulations of neurons based on feature tuning and priming effects. By grouping neurons with similar response patterns, we can obtain insight into the underlying neural mechanisms and potentially identify discrete functional groupings within the visual cortex. One of the reasons behind performing such analysis is to see whether there are differences between the initial division of the neuronal groups into layers (upper, middle, deep) and their group assignment based on clustering. The hypothesis for clustering analysis is that cluster assignments for neuronal groups based on FTI and priming effects will align with the initial classification of electrode sites.

The first step in the clustering workflow is to create a feature matrix that combines FTI and the priming effect for each electrode site. This matrix will serve as the input for clustering algorithms.

The selected clustering algorithm is K-Means. K-means is a widely used clustering algorithm that splits data into K clusters. The reason for choosing this algorithm originates from the objective of the whole analysis and structure of the data. Clusters should be compared to the initial categories of neuronal layers, and the number of clusters should be specified based on this knowledge. Thus, K = 3 for comparison purposes.

3.2.4 Sampling

Due to high dimensionality and computation power limitations, datasets must be sampled before conducting analysis. The structure of the dataset and the goal of the analysis require maintaining statistical properties to obtain valid results. Thus, stratified random sampling is the best solution to adequately represent each group, i.e., different stimuli colors and priming conditions.

[3]
Figure 7. Stratified random sampling schema

[3] Source: Chapter 7 - Best practices when conducting and reporting a meta-analysis. Fernanda S. Tonin, Aline F. Bonetti , Fernando Fernandez-Llimo. https://doi.org/10.1016/B978-0-323-91888-6.00028-4

4 Results

4.1 Feature tuning index

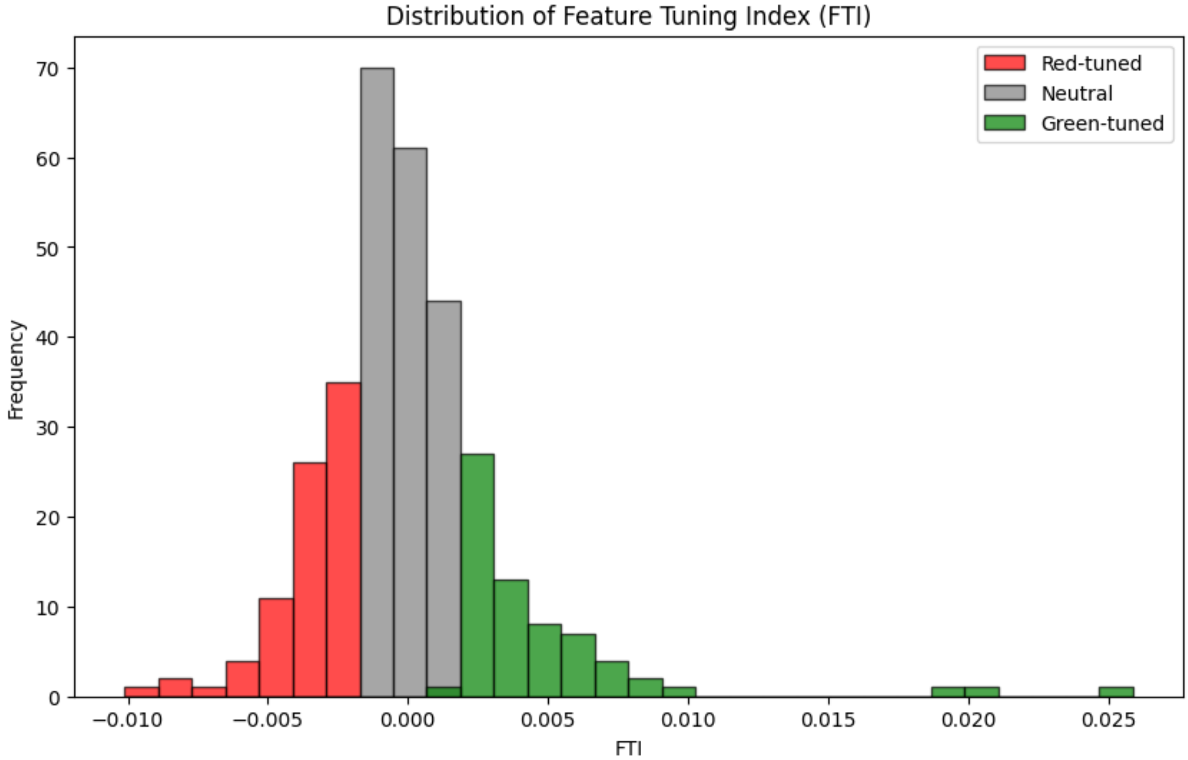


Figure 8. Distribution of FTI

The histogram represents the distribution of the Feature Tuning Index (FTI) across the neuronal population. These results suggest that neurons, on average, were almost neutrally tuned (M = 0.00118, SD = 0.004, Mdn = -0.0002), with a slight tendency toward positive FTI values. The standard deviation indicates that most neurons are very close to the mean, but there are some outliers.

The percentiles provide an overview of the spread and skewness of the FTI distribution: the 25th percentile is -0.00748, the 50th percentile (median) is 0.00104, and the 75th percentile is 0.00872. These values highlight a slightly positive median, indicating a skew towards green-tuned neurons. This is evidenced by the histogram, with the majority of neurons having their FTI values classifying them as neutral: 54% of neuronal sites classified as neutral, 20% as green-tuned, and 26% as red-tuned. The number of green-tuned neurons is also slightly higher compared to the red-tuned ones, with more neurons having their FTI values above zero. The feature tuning index value distribution of red-tuned neurons is spread over a larger range on the x-axis compared to green-tuned neurons.

The overall analysis of FTI values shows that the macaque monkey visual cortex distribution is close to Gaussian with a slight skew toward green tuning: most neurons are neutral, and a large fraction tips toward a stronger preference for green over red stimuli. The standard deviation and percentiles, respectively, detail the spread and variability within the neuronal response.

This distribution now becomes a major reference point for comparing the response of tuned neurons under different stimulation conditions, particularly when looking at priming effects. Such priming measurements and their statistical significance emerge inferences about how neuronal tuning and attention are modulated in the visual cortex, either explaining or shedding light on the neural processes subserving vision.

4.2 Priming Effect

The results of the priming effect analysis indicate a subtle but measurable impact on neuronal responses in the visual cortex. On average, neuronal efficiency is slightly increased when exposed to repeated stimuli ($M = 0.0003$). The interquartile range, with the 25th percentile at −0.00158 and the 75th percentile at 0.00216, further underscores that while the majority of neurons exhibit a small positive priming effect, a significant proportion experiences either negligible or slightly negative effects.

A paired t-test was conducted to analyze the red-tuned neurons' response to red and green stimuli, comparing the priming effect between the two conditions. The results revealed a statistically significant difference, with a $t(14)$ value of 2.20 and $p = 0.045$. The positive t-statistic suggests an increased priming effect for red stimuli, significantly different from green stimuli. The p-value indicates statistical significance, confirming a substantial disparity in priming effect for red-tuned neurons in relation to their preferred and non-preferred stimuli.

Additionally, a paired t-test was performed for the green-tuned neurons to assess the priming effect when exposed to green and red stimuli. The findings demonstrated a marginally significant distinction between the two scenarios, with a $t(14)$ value of 2.08 and $p = 0.056$. The positive t-statistic suggests a slightly higher priming effect from green stimuli compared to red stimuli in these neurons. The p-value, though close to the threshold for significance, suggests a trend towards a substantial variance in the priming effect for green-tuned neurons when encountering their preferred and non-preferred stimuli.

4.3 Clustering

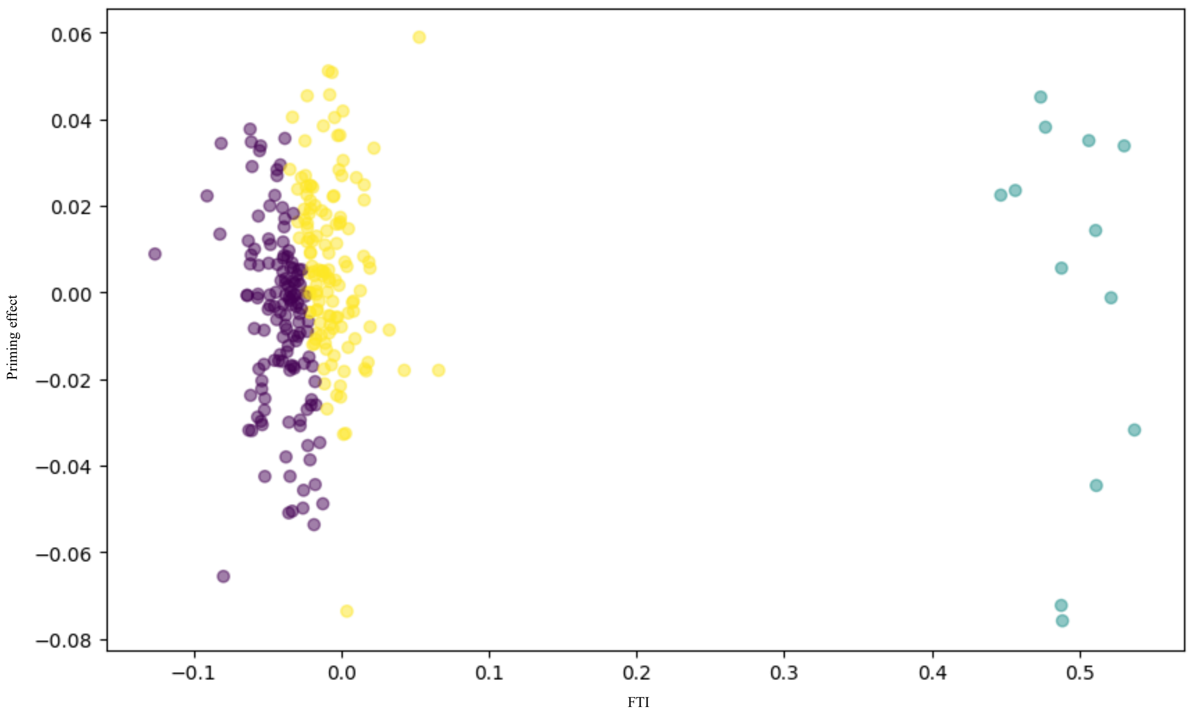


Figure 9. Clustering of neuronal groups based on FTI and priming effects

The provided plot illustrates the clustering of neurons based on their feature tuning index and priming effects. Data has been reduced to two dimensions using principal component analysis for visualization purposes. Color-coding represents different clusters obtained using K-means.

The plot defines three distinct clusters: cluster 0, in purple; cluster 1, in yellow; and cluster 2, in cyan. Most of the neurons are contained in cluster 0, which appears relatively homogeneous with respect to their FTI and priming effect. Cluster 1 has neurons that spread along the PCA Component 2 axis, which means that these neurons had a different priming effect. Cluster 2 disperses more along principal component 1, showing a strong variation of FTI values.

Along the axis of PCA, component 1 tends to be a spread for Cluster 2, accounting for the variation in FTI values. PCA component 2 appears to account for the effects of priming by spreading more on Clusters 0 and 1.

Cluster 0 consisted of neurons with moderate FTI and large priming effects, hence having balanced tuning and priming characteristics. In cluster 1, there were neurons with larger variations of priming effects but very consistent FTI values. Cluster 2 consisted of neurons with marked FTI values but variable priming effects.

Clustering revealed that the neuronal group's placement in terms of depth in V4 does not influence its FTI and priming effects values. Neuronal groups from different layers (deep, middle, upper) are evenly distributed among 3 clusters based on FTI and priming effects, not showing any correlation within layers.

This clustering analysis has, quite successfully, grouped neurons into distinct categories with regard to their feature tuning and priming responses. The results show that some neurons are highly tuned to specific features, while others display strong priming effects.

5 Conclusion

In this study, the authors asked whether color tuning of neurons in V4 and other visual areas affects priming results under conditions where cells respond to specific colors. We analyzed electrophysiological data from macaque monkeys doing a visual search task using red and green stimuli.

Feature tuning index (FTI) measures neurons' tuning preferences. FTIs were used to classify neurons as red-tuned, green-tuned, or neutral. Responses on primed and unprimed trials were compared to assess the magnitude of these residual or carry-over effects and their overall vs. stimulus-specific nature.

Critically, priming reduced neuronal activity, thus supporting the notion of repetition suppression. This shows repetition suppression is real, based on Desimone's (1996) hypothesis that neuronal responses decrease when the same stimulus keeps getting repeated. Within green-tuned neurons, responses evoked by favored stimuli were more suppressed than unfavored ones; the effect was reversed in red-tuned neurons. These results are consistent with those showing that attending to specific features, such as color, facilitates reactivity in the V4 region of neurons and increases precision for detection and processing (Driver & Dolan 2002). Clustering analysis revealed that neurons with distinct FTI properties and priming effects were prominent, illustrating the heterogeneity of V4 area neuronal responses.

The Color-tuned neurons exhibit a spectrum of priming effects, resulting in greater suppression by preferred stimuli. This is consistent with the results of Maunsell and Treue (2006), showing that feature-based attention increases the responses to attended features, irrespective of spatial location. It is possible that shape or orientation as a whole provides this priming behavior and neuronal tuning. Surveying the role and interplay of different cortical areas may provide further information about visual attention and priming at a neural level.

This thesis emphasizes the complex connection between feature adjustment and priming in the visual cortex, providing understanding of the neural processes involved in visual attention and perception. The findings also corroborate the review on "Neural Mechanism of Priming in Visual Search" (Westerberg et al., 2020) which highlighted that repeated exposure to specific features increases neural efficiency in areas like V4 and the frontal eye fields (FEF), thereby reducing errors and processing time in visual search tasks.

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