

# Learning Divisive Normalization in Primary Visual Cortex

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**Manuscript Source:** <https://www.biorxiv.org/content/10.1101/767285v5>

**Manuscript Authors:** Max F. Burg, Santiago A. Cadena, George H. Denfield, Edgar Y. Walker, Andreas S. Tolias, Matthias Bethge & Alexander S. Ecker

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### Research Paper Sections:

The sections of the research paper input text parsed in this audit.

[illegible]

Title      **Learning Divisive Normalization in Primary Visual Cortex**

**S1 [001]      Abstract**

**S1 [002]**      Divisive normalization (DN) is a prominent computational building block in the brain that has been proposed as a canonical cortical operation.

Divisive normalization ...  
... (DN) ...  
... is a prominent computational building block ...  
... in the brain ...  
... that has been proposed ...  
... as a canonical cortical operation.

**S1 [003]**      Numerous experimental studies have verified its importance for capturing nonlinear neural response properties to simple, artificial stimuli, and computational studies suggest that DN is also an important component for processing natural stimuli.

Numerous experimental studies have verified its importance ...  
... for capturing nonlinear neural response properties ...  
... to simple, ...  
... artificial stimuli, ...  
... and computational studies suggest ...  
... that DN is also an important component ...  
... for processing natural stimuli.

**S1 [004]**      However, we lack quantitative models of DN that are directly informed by measurements of spiking responses in the brain and applicable to arbitrary stimuli.

However, ...  
... we lack quantitative models ...  
... of DN ...  
... that are directly informed ...  
... by measurements ...  
... of spiking responses ...  
... in the brain ...  
... and applicable ...  
... to arbitrary stimuli.

**S1 [005]**      Here, we propose a DN model that is applicable to arbitrary input images.

Here, ...  
... we propose a DN model ...  
... that is applicable ...  
... to arbitrary input images.

- S1 [006]** We test its ability to predict how neurons in macaque primary visual cortex (V1) respond to natural images, with a focus on nonlinear response properties within the classical receptive field.
- We test its ability ...  
... to predict how neurons ...  
... in macaque primary visual cortex ...  
... (V1) ...  
... respond ...  
... to natural images, ...  
... with a focus ...  
... on nonlinear response properties ...  
... within the classical receptive field.
- S1 [007]** Our model consists of one layer of subunits followed by learned orientation-specific DN.
- Our model consists ...  
... of one layer ...  
... of subunits followed by learned orientation-specific DN.
- S1 [008]** It outperforms linear-nonlinear and wavelet-based feature representations and makes a significant step towards the performance of state-of-the-art convolutional neural network (CNN) models.
- It outperforms linear-nonlinear ...  
... and wavelet-based feature representations ...  
... and makes a significant step towards the performance ...  
... of state-of-the-art convolutional neural network ...  
... (CNN) ...  
... models.
- S1 [009]** Unlike deep CNNs, our compact DN model offers a direct interpretation of the nature of normalization.
- Unlike deep CNNs, ...  
... our compact DN model offers a direct interpretation ...  
... of the nature ...  
... of normalization.
- S1 [010]** By inspecting the learned normalization pool of our model, we gained insights into a long-standing question about the tuning properties of DN that update the current textbook description: we found that within the receptive field oriented features were normalized preferentially by features with similar orientation rather than non-specifically as currently assumed.
- By inspecting the learned normalization pool ...  
... of our model, ...  
... we gained insights ...  
... into a long-standing question ...  
... about the tuning properties ...  
... of DN ...  
... that update the current textbook description: ...  
... we found ...  
... that ...

... within the receptive field oriented features were normalized preferentially ...  
... by features ...  
... with similar orientation rather than non-specifically ...  
... as currently assumed.

**S1 [011]** Author summary Divisive normalization (DN) is a computational building block throughout sensory processing in the brain.

Author summary Divisive normalization ...  
... (DN) ...  
... is a computational building block ...  
... throughout sensory processing ...  
... in the brain.

**S1 [012]** We currently lack an understanding of what role this normalization mechanism plays when processing complex stimuli like natural images.

We currently lack an understanding ...  
... of what role this normalization mechanism plays ...  
... when processing complex stimuli like natural images.

**S1 [013]** Here, we use modern machine learning methods to build a general DN model that is directly informed by data from primary visual cortex (V1).

Here, ...  
... we use modern machine learning methods ...  
... to build a general DN model ...  
... that is directly informed ...  
... by data ...  
... from primary visual cortex ...  
... (V1).

**S1 [014]** Contrary to high-predictive deep learning models, our DN-based model's parameters offer a straightforward interpretation of the nature of normalization.

Contrary ...  
... to high-predictive deep learning models, ...  
... our DN-based model's parameters offer a straightforward interpretation ...  
... of the nature ...  
... of normalization.

**S1 [015]** Within the receptive field, we found that neurons responding strongly to a specific orientation are preferentially normalized by other neurons that are highly active for similar orientations, rather than being normalized by all neurons as it is currently assumed by textbook models.

Within the receptive field, ...  
... we found ...  
... that neurons responding strongly ...  
... to a specific orientation are preferentially normalized ...  
... by other neurons ...  
... that are highly active ...  
... for similar orientations, ...  
... rather than being normalized ...

... by all neurons ...  
... as it is currently assumed ...  
... by textbook models.

## **S2 [016] 1 Introduction**

**S2 [017]** A crucial step towards understanding the visual system is to build models that predict neural responses to arbitrary stimuli with high accuracy (Carandini et al., 2005).

A crucial step towards understanding the visual system is ...  
... to build models ...  
... that predict neural responses ...  
... to arbitrary stimuli ...  
... with high accuracy ...  
... (Carandini et al., 2005).

**S2 [018]** The classical standard models of primary visual cortex (V1) are based on linear-nonlinear models (Simoncelli et al., 2004), energy models (Adelson and Bergen, 1985) and subunit (LN-LN) models (Rust et al., 2005; Touryan et al., 2005; Willmore et al., 2008; Butts et al., 2011; McFarland et al., 2013; Vintch et al., 2015).

The classical standard models ...  
... of primary visual cortex ...  
... (V1) ...  
... are based ...  
... on linear-nonlinear models ...  
... (Simoncelli et al., 2004), ...  
... energy models ...  
... (Adelson ...  
... and Bergen, 1985) ...  
... and subunit ...  
... (LN-LN) ...  
... models ...  
... (Rust et al., 2005; ...  
... Touryan et al., 2005; ...  
... Willmore et al., 2008; ...  
... Butts et al., 2011; ...  
... McFarland et al., 2013; ...  
... Vintch et al., 2015).

**S2 [019]** Fueled by advances in machine learning technology, recent studies have shown that multi-layer convolutional neural networks (CNNs) can significantly improve the prediction of neural responses to complex images and videos at several stages of the visual pathway, outperforming classical models (Yamins et al., 2014; Khaligh-Razavi and Kriegeskorte, 2014; McIntosh et al., 2016; Zhang et al., 2019; Cadena et al., 2019; Kindel et al., 2019; Walker et al., 2019; Sinz et al., 2018).

Fueled ...  
... by advances ...  
... in machine learning technology, ...

## **End of Sample Audit**

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