Published in final edited form as:

*Neurocomputing*. 2003 June ; 52-54: 671–676. doi:10.1016/s0925-2312(02)00863-9.

# Layer 4C in monkey V1 may linearize the output of the LGN

**M. Brandon Westover**[*], **Charles H. Anderson**

Department of Anatomy and Neurobiology, School of Medicine, Washington University, 4496 Maryland Avenue 1-8, St Louis, MO 63110, USA

## Abstract

In primates, most LGN fibers terminate in cortical layer 4C, an anatomically prominent structure of unexplained function. We hypothesize that the enormous number of cells in layer 4C of monkey primate visual cortex functions as a neural network "hidden layer" that inverts distortions introduced by transmitting visual signals through the LGN. This hypothesis helps explain how simple cells respond (quasi-) linearly to visual inputs in spite of nonlinearities present in LGN responses. Linearization averts prematurely discarding visual information, in keeping with the role of primary visual cortex as *the* source of raw visual information to the rest of the brain.

### Keywords

Layer 4; Visual cortex; Nonlinearity; Distortion

The transfer of sensory information to the visual cortex occurs primarily at the interface between afferents from the LGN and a large population of tiny, densely packed "spiny stellate" cells in cortical layer 4C. There is an enormous mismatch between the number of incoming LGN fibers and the number of recipient 4C neurons, leading to the estimate that each LGN fiber branches to connect with 30–100 4C neurons [2,5]. Layer 4C also serves as the primary source of visual input to the simple cell population in cortical layer 2/3, each simple cell receiving inputs from numerous 4C cells.

It would appear that layer 4C is strategically situated to perform some kind of conditioning of visual signals before "turning them over" for further analysis by the other cortical layers. However, the function of layer 4C has been hard to decipher. For example, at other stages in the visual hierarchy, new computations are reflected in a progressively more complex selectivity of cellular responses for features of the visual input. On the other hand, layer 4C cells appear to simply inherit the receptive fields of their LGN drivers.

There have been two main previous hypotheses. First, based on the large fanout of incoming LGN fibers, Horace Barlow suggested that layer 4C might serve as an "interpolating grid" [2]. Image samples conveyed by LGN afferents would be interpolated by the more numerous, densely packed 4C cells, and this higher resolution neural image would serve as the readout underlying visual hyperacuity. In another hypothesis, Anderson and Van Essen proposed that layer 4C serves as a grid for rescaling and rerouting visual information, as part

---

[*] Corresponding author. westovem@medicine.wustl.edu (M.B. Westover).

of the operation of a “shifter circuit” [1]. Subsequent experimental work has failed to validate key predictions of either proposal (c.f. [3]).

In this paper we outline a new proposal for the function of layer 4C. To motivate our proposal, we first discuss in detail an often overlooked problem encountered in early visual processing, namely, that visual signals undergo *nonlinear distortion* during transmission from retina to cortex. This fact at first appears inconsistent with the well-known observation that simple cells show an essentially *linear* dependence on visual inputs. By what mechanism is linearity achieved, and why? *We propose that layer 4C functions to reverse the distortion, and by doing so, prevents the loss of visual information.* We provide illustrations from computer simulations to demonstrate the principles of our proposal, and highlight ways in which our hypothesis may help to explain the experimentally observed linearity of simple cell physiology.

The early stages of visual processing admit a straightforward computational description: In response to images projected on the retina, the firing rates of ganglion-, lateral geniculate-, spiny stellate-, and simple cells are well predicted using models which compute the inner product (spatial integral of the product) of a linear filter with the incoming image, and pass the result through a static nonlinear function. We use the notation $\mathscr{I}$, $\mathscr{F}$, and $g$ for the image, linear filter, and static nonlinearity, respectively. Then we express a neural firing rate in terms of the input image as

$$r(\mathscr{I}) = g[\langle \mathscr{I}, \mathscr{F} \rangle - \theta]$$

where $\theta$ is a threshold, and $\langle , \rangle$ denotes the inner product. Here we have neglected the effects of noise, but will discuss these later. For simple cells, the underlying linear filter is usually described as a Gaussian-weighted sine wave, i.e. a Gabor function. Current evidence suggests that these receptive fields arise basically in a feedforward fashion from alternating stripes of ON and OFF centers of LGN receptive fields, as originally proposed by Hubel and Wiesel [4]. However, completely explaining the linear behavior of simple cells with the Hubel and Wiesel model is complicated by the presence of the static nonlinearity in the retinal ganglion and LGN cells, $g$. The essential features of the LGN nonlinearity are saturation at high contrasts, and nonnegativity (firing rates are positive quantities). We can conveniently model this nonlinearity using the sigmoid function $g(x) = kx^2 = (\sigma + x^2)$, where $k$ and $\sigma$ are constants determining the maximum firing rate and half saturation level.

The essential problem introduced by saturation is illustrated in Fig. 1. Consider a time-varying sinusoidal signal transmitted down the retinogeniculate pathway by pairs of ON and OFF RGCs and LGN RCs. As shown on the left in Fig. 1, the ON and OFF responses can be combined (by taking the difference) to capture both the positive and negative components of the visual signal. Using this combined representation highlights the effects of saturation. Saturation at high signal amplitudes produces a compressed sinewave as the output of RGCs, and the effect is cascaded through the LGN to produce more pronounced distortion in the output of the ON/OFF pair of LGN cells. In the following paragraphs we first explain how layer 4C can “linearize” the overall transfer of signals from the retina to simple cells by reversing the effects of saturation. We postpone addressing the *benefits* of linearization to allow us to frame the discussion in the context of the hypothetical question, “what if layer 4C did not exist?”

The implementation of our hypothesis is simple. As stated above, each LGN cell arborizes to contact 30–100 layer 4C cells. Due to this direct feedforward connection, each spiny stellate cell will inherit the basic ON or OFF, difference-of-Gaussians-shaped receptive field of its presynaptic LGN afferent. Suppose, however, that there is moderate diversity amongst either the form of the static nonlinearities $g$ for the cells, e.g. different maximum firing rates, or some scatter among the thresholds $\theta_i$. Then by taking an appropriate synaptically weighted sum of ON and OFF spiny stellate cell inputs to a simple cell, the overall amplitude transfer function characterizing the relay LGN to the simple cell input can be made to approximate the inverse of the preceding distortion function, achieving an overall linear transfer of the visual signal to the target simple cell. In other words, we propose that layer 4C serves as a “hidden layer”, in which the response curves of its neurons serve as basis functions with which the inverse of the RGC/LGN amplitude transfer function is computed. For our example, we have used 30 ON and 30 OFF neurons, and have computed weights $w_i$ by the method of least squares, i.e. by minimizing

$$E(\{w_i\})\left\langle\left\|g^{-1}(x)-\sum_i w_i a_i(x)\right\|^2\right\rangle_x,$$

where $a_i$ are the response functions ($''g's''$) for layer 4 cells, $x=\langle\mathscr{I},\mathscr{F}\rangle$, and $\langle,\rangle x$ indicates an average over the ensemble of possible scalar inputs $x$ to the cells, which for simplicity we assumed as uniform. In this case, the simple cell response will not show evidence of the distortion, but will have a linear response, consistent with experimental observations.

We now discuss the benefits of removing distortions, which we refer to as “linearization”. The most immediate benefit is that linearization reformats LGN signals in such a way that the responses of simple cells saturate less. The consequence is that simple cell responses provide more information about the initial retinal input than if they were directly fed the LGN output. To qualitatively illustrate this point, we performed the following numerical experiments: Suppose that the visual input to the static nonlinearity $g$ of a single ON/OFF pair of RGC is a scalar valued, zero-mean random variable $x$, with variance $\sigma^2$; i.e., $x\sim\mathscr{N}\left(0,\sigma^2\right)$. The variance is chosen so that the RGC and LGN responses occasionally saturate. Also, assume that at each synapse, the signal is corrupted by additive Gaussian noise, where the noise sources at each stage are independent. The firing rate of an “antiphase pair” of simple cells (obtained by taking the difference of the responses of the simple cells in Fig. 2) is then a (non-Gaussian) random variable $y$ (Fig. 3).

We produced 1,000,000 random sample input/output pairs ($x$, $y$) and used these to form Monte-Carlo histogram estimates of the probability densities $p(y)$ and $p(y/x)$. We used these histograms and the assumed pdf for $x$, $p(x)$, to compute the Shannon information (mutual information) between the visual signals and the firing rates of the model simple cell pair, given by

$$I(y;x) = \sum_{x,y} p(x)p(y|x)\log\frac{p(y|x)}{p(y)}.$$

We repeated these experiments for two cases: with and without the layer 4C “inverter”, for several different noise levels. We find generally that so long as the noise involved in the inversion process is small compared to the noise already present in the incoming signals, linearization by layer 4C produces substantial improvements in the overall information transfer $I(y; x)$. Notice that the benefits will be greatest for simple cells responding to low spatial frequency information. This is because these simple cells suppress the noise.

More speculatively, we suppose that distortion inversion for low spatial frequency information is important for visual perception. Most of the information in natural images resides in the low spatial frequency bands; residual distortions would be noticeable if not inverted.

We have outlined a novel computational hypothesis for the function of layer 4C in primate visual cortex. A testable prediction of our hypothesis is that there exists a diversity of neural response curves in layer 4C. To our knowledge, the data to confirm of refute this prediction does not yet exist.

A final interesting related question for further study is whether a similar operation takes place in cats, which lack the densely packed layer 4C found in primates [3]. Instead, a similar though less dramatic fanout (1→4–10 in cats vs. 1→30–100 in primates) occurs in cat LGN. We hypothesize that this fanout in cat LGN may serve the same purpose as we have hypothesized for layer 4C in primates.

## References

[1]. Anderson CH, Van Essen DC, Shifter circuits: a computational strategy for dynamic aspects of visual processing, PNAS 84 (1987) 6297–6301. [PubMed: 3114747]

[2]. Barlow HB, Critical limiting factors in the design of the eye and visual cortex. The Ferrier Lecture, 1980, Proc. R. Soc. London Ser. B 212 (1981) 1–34. [PubMed: 6115386]

[3]. Edelman S, Weiss Y, Vision: Hyperacuity, in: Arbib M (Ed.), The Handbook of Brain Theory and Neural Networks, MIT Press, Cambridge, MA, 1998.

[4]. Ferster D, Miller KD, Neural mechanisms of orientation selectivity in the visual cortex, Ann. Rev. Neurosci 23 (2000) 441–471. [PubMed: 10845071]

[5]. Lund JS, Local circuit neurons of Macaque monkey striate cortex: I. Neurons of Laminae 4C and 5A, J. Comp. Neuol 257 (1987) 60–92.

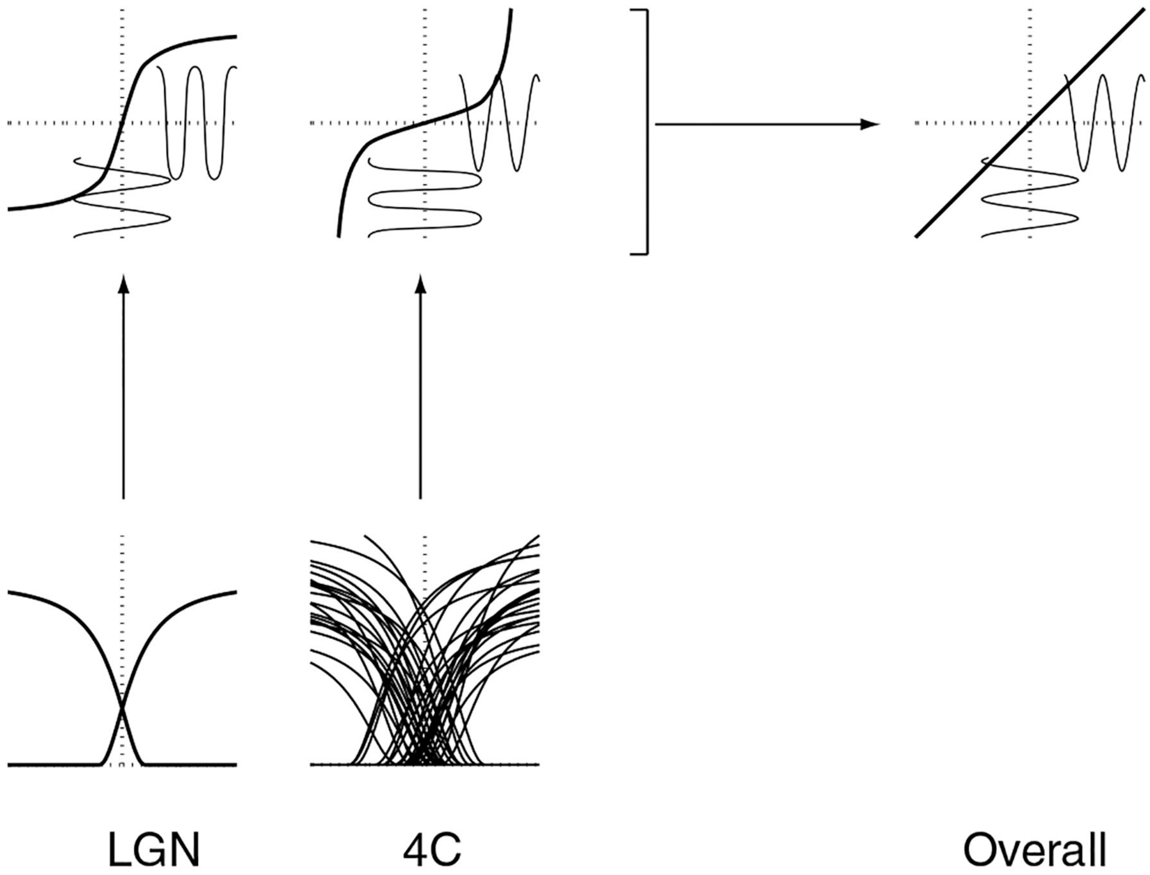

**Fig. 1.**

Bottom: Response curves for an ON/OFF pair of LGN relay neurons (left) and their postsynaptic layer 4C targets. Top: Amplitude transfer function for visual signals using responses of the ON/OFF pair (left), and using layer 4C as a distortion inverter (middle). Combining these in tandem yields an overall linear transfer (right).

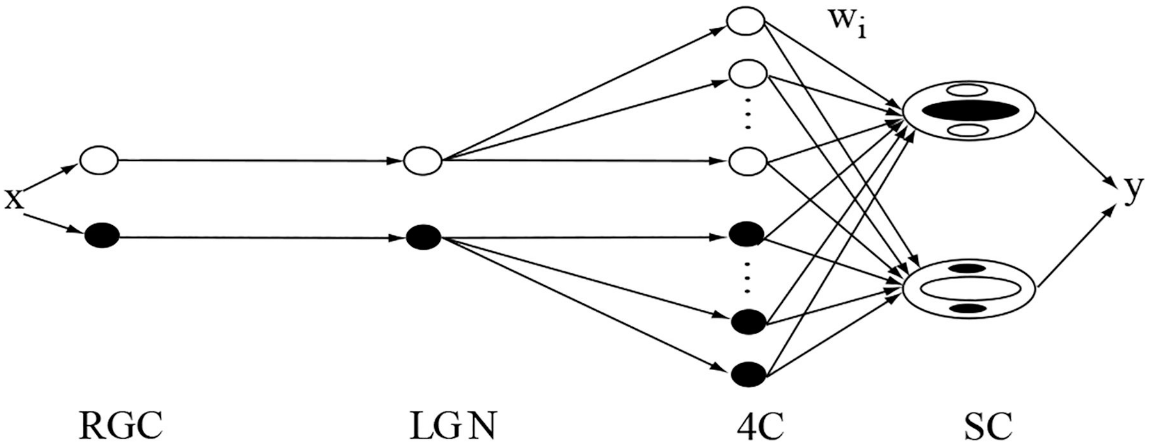

**Fig. 2.**
Schematic of the feedforward neuronal implementation of our proposal. Pairs of neurons are used to represent both positive and negative signal components.

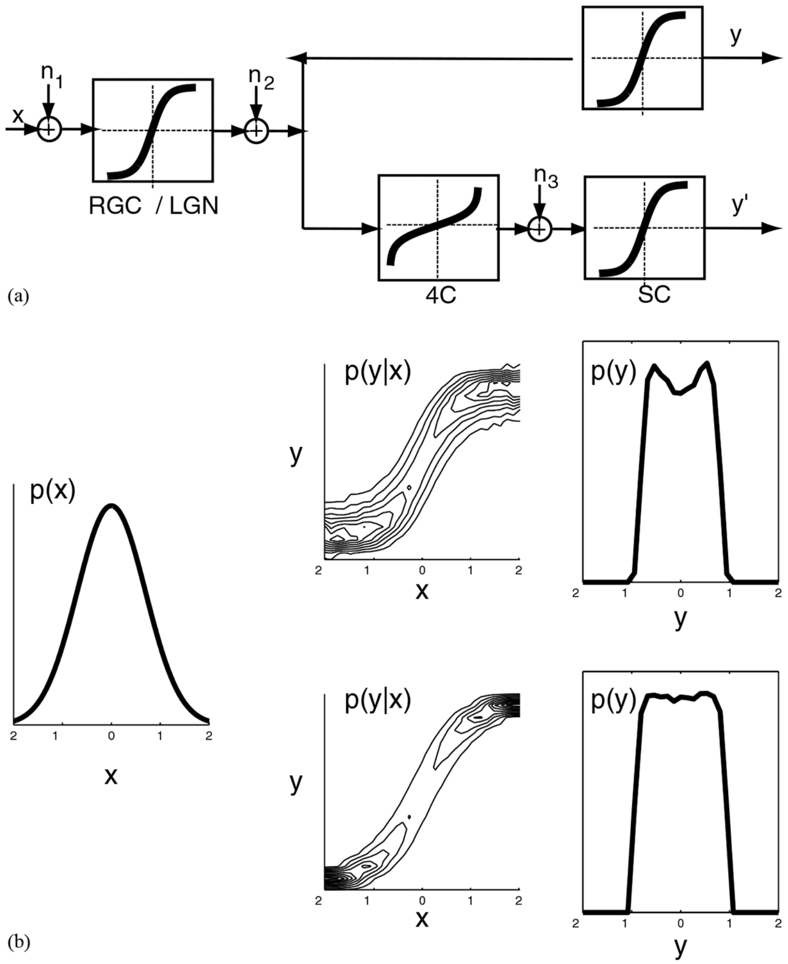

**Fig. 3.**

Top: Block diagram for the numerical experiments described in the text. Top pathway, without layer 4C; bottom pathway, layer 4C acting as distortion inverter. Bottom: Plots and contour plots for estimated pdf’s (see text).