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Nonlinear convergence preserves information

Gabrielle J. Gutierrez[1,✉], **Fred Rieke**[2], **and Eric Shea-Brown**[1]

[1]Department of Applied Mathematics, University of Washington, Seattle, WA
[2]Department of Physiology and Biophysics, University of Washington, Seattle, WA

Neural circuits are structured in layers of converging and diverging nonlinear neurons with selectivities and preferences. These components have the potential to hamper an efficient encoding of the circuit inputs. Past computational studies have optimized the nonlinearities of single neurons, or the weights matrices of networks, to maximize encoded information yet none have grappled with simultaneously optimizing circuit structure and neuron response functions for efficient coding. Rather than an explicit optimization of that kind, our approach is to compare circuit configurations with different combinations of these suboptimal components to discover how the interactions of these components affect the efficient coding of the neural circuit. We construct computational model circuits with different configurations and we compute and compare their response entropies. We find that the circuit configuration with divergence, convergence, and nonlinear subunits preserves the most information despite the compressive loss induced by both the convergence and the nonlinearities individually. These results show that the combination of selective nonlinearities and a compressive architecture - both elements that induce lossy compression - can promote efficient coding in tandem.

Correspondence: ***ellag9@uw.edu***

Introduction

Sensory systems by necessity compress a wealth of information gathered by receptors into the smaller amount of information needed to guide behavior. This compression occurs via common circuit motifs - namely convergence of multiple inputs onto a single output neuron and divergence of inputs to multiple parallel pathways (Jeanne and Wilson, 2015). Here we investigate how these motifs work together to dictate how much and what information is retained in compressive neural circuits.

These issues are particularly approachable in the retina, because the bottleneck provided by the optic nerve means that considerable compression occurs prior to transmission of signals to central targets (Zhaoping, 2006; Nirenberg, et al., 2001). Receptive field subunits are a key feature of the retina's compressive circuitry. Multiple bipolar cells converge onto a single ganglion cell - forming functional subunits within the receptive field of the ganglion cell (Demb and Singer, 2015; Enroth-Cugell and Robson, 1966). Ganglion cell responses can often be modeled as a linear sum of a population of nonlinear subunits. These subunit models have been used to investigate center-surround interactions (Enroth-Cugell and Freeman, 1987; Hochstein and Shapley, 1976; Barlow, 1953) and to determine how cells integrate spatial inputs (Enroth-Cugell and Robson, 1966; Turner and Rieke, 2016; Hartline, 1940; Freed and Sterling, 1988).

While it is clear that subunit coding imposes a compressive circuit architecture, it is not known whether this architecture subserves an efficient code. Since the 1950s, information theory has been used to quantify the amount of information that neurons encode. The efficient coding hypothesis proposes that the distribution of neural responses should be one that is maximally informative about the inputs (Attneave, 1954; Barlow, 1961). Inherent in these studies is the use of Shannon's entropy (Shannon and Weaver, 1998; Cover and Thomas, 2006) as a measure of information in the neural code.

In this paper, we explore how a combination of divergence of inputs into multiple parallel pathways and convergence in each pathway via nonlinear receptive field subunits impacts coding efficiency. We find that the convergence of nonlinear subunits minimizes the loss of information despite the selectivity of the nonlinearities.

Results

We start by quantifying the effect of common signaling motifs, alone and in combination, on coding efficiency. We then explore, geometrically, how nonlinear subunits shape the response distribution to gain intuition as to how they can enhance information retention. Finally, we explore the implications of nonlinear subunits for which stimulus properties are encoded.

Common circuit components are lossy or inefficient. Our goal is to understand how the convergence and divergence of nonlinear subunits impacts the retina's ability to efficiently encode spatial inputs. The retina is organized in layers that converge and diverge (Fig. 1A), ultimately leading to the compression and re-formatting of a high-dimensional visual input into a lower dimensional neural code that can be interpreted by the brain. In addition, nonlinear responses abound in the neurons that compose these layers. These mechanisms complicate the ability of the circuit to retain information. We use entropy to describe the maximum amount of information that a distribution of responses could contain about its inputs. Specifically, we use discrete entropy to compare the information content of (continuous) distributions of responses generated by different circuits. Although the discrete entropy depends on the resolution of the discretization (see methods), our qualitative conclusions are the same regardless of the resolution of this discretization.

Two converging inputs can result in ambiguities. The ability to distinguish the stimulus combinations that sum to the same value is lost, making linear convergence a form of lossy compression in this case. (Fig. 1B). The entropy of the full two-dimensional stimulus (Fig. 1B, top) is 19.85 bits - meaning

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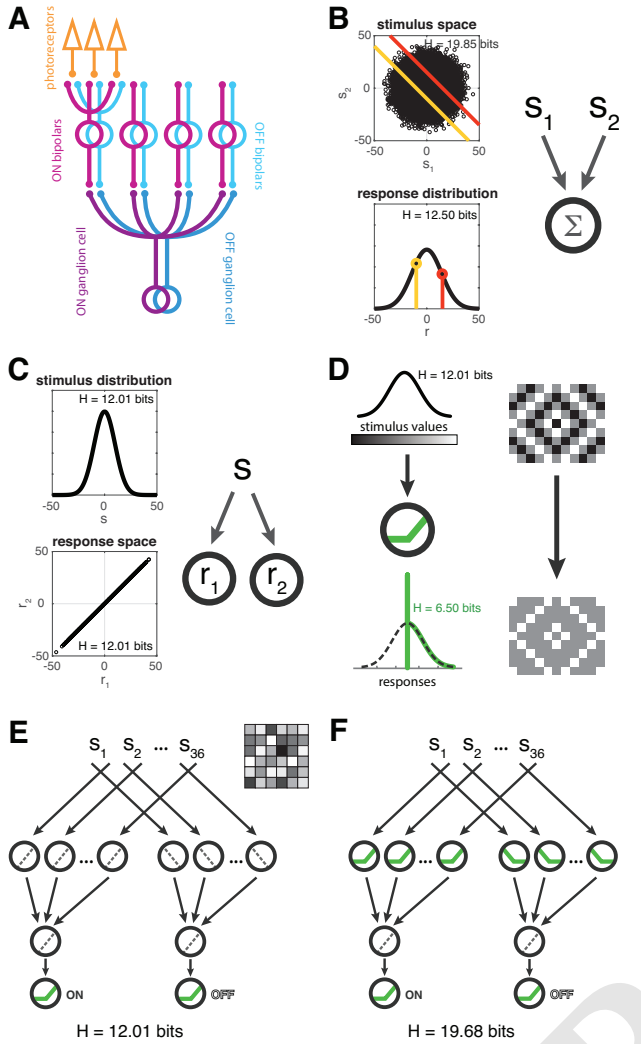

Fig. 1. Neural circuits are composed of inherently lossy components. (A) schematic of retina circuit with its convergent and divergent structure. (B) Converging two inputs results in ambiguities. A 2D stimulus space is reduced to a 1D response space in which one response represents all stimuli along an isoline where s1 + s2 = constant. (C) Diverging to two outputs can produce redundancies. (D) Nonlinear transformation of a gaussian distributed input with a ReLU can distort the distribution, producing a compressed response in which some portion of the stimulus information is discarded. (E-F) Convergent, divergent circuits with (E) nonlinear outputs, or (F) nonlinear subunits. Subunit responses are weighted by $1/\sqrt{36}$. Example stimulus image is shown.

that it would take 19.85 bits to convey a distinction between any two points in the stimulus space with our choice of bin size (see methods). The entropy of the convergent response is smaller (12.50 bits; Fig. 1B, bottom).

Diverging motifs are another common neural circuit construction. In the example shown in Figure 1C, the divergent responses are identical and the entropy of the 2-dimensional response space (H = 12.01 bits) is the same as the entropy of the 1-dimensional stimulus distribution shown in the top plot (H = 12.01 bits). Diverging an input into two neurons may produce an inefficient neural architecture by producing redundant signals.

Similarly to convergence, nonlinear transformations can lead to loss of information by introducing ambiguities. Take the example of a rectified-linear transformation that is thresholded at zero (Fig. 1D). It is a non-invertible nonlinearity where half of the stimulus distribution is encoded by one response. Therefore, this nonlinearity induces lossy compression because the information that would distinguish these stimuli has been irretrievably discarded. The entropy of the rectified-linear (ReLU) response (H = 6.50 bits) is nearly half of that for the stimulus distribution (H = 12.01 bits).

Each of the common circuit motifs described above is inefficient or discards information when considered in isolation (Figs. 1A-D). How much information can a neural circuit with all of these components retain? We sought functional architectures that cause minimal information loss given the constraint of compression. We constructed a model circuit that compresses a high-dimensional input into a low-dimensional output. It has a 36-dimensional input structure that diverges along two pathways, an ON and an OFF pathway, each culminating in a single output neuron. The inputs to each output neuron come from a layer of subunits - neural units that define the receptive field structure of the output neuron. Each subunit receives input from one of the N stimulus inputs that compose a stimulus image where each pixel is independently drawn from a gaussian distribution. Within each pathway, the normalized subunit responses linearly sum at the output neuron and are then rectified.

The ON and OFF output responses are embedded in a 2-dimensional space that corresponds to a low-dimensional representation of the N-dimensional input. The entropy of the 2-dimensional output response is computed after showing many stimulus samples to the circuit. The circuit in Figure 1E has linear subunits. Its output has 12.01 bits of entropy. The circuit in Figure 1F applies nonlinearities to the subunits and its output response has 19.68 bits of entropy. The greater entropy of the nonlinear subunit circuit is counterintuitive because the nonlinear elements considered in isolation lead to a loss of information (Fig. 1D). This motivated us to investigate smaller motifs and to gradually build up to these full circuits to understand how each component or structure interacts with the other components. We next investigate how convergence interacts with subunit nonlinearities.

Lossy nonlinear subunits benefit from convergence. To understand how nonlinear subunits interact with a convergent architecture to increase encoded information, we examined circuit configurations with a single pathway, i.e. no divergence (Fig. 2). All stimuli that sum to the same value (as highlighted in the top plot of Fig. 2) are represented by the same response in the circuit pathway with linear subunits because the subunits do not transform or scale the inputs (Fig. 2, left, 3rd and 4th rows). The nonlinear subunits transform the stimulus space such that all points are compressed into a single quadrant (Fig. 2 right, 2nd row). When the subunits are summed (Fig. 2, right, 3rd row), this allows the ambiguous stimuli to have a more distributed representation in the output response - meaning that they are represented more distinctly by the nonlinear subunits pathway than the pathway with linear subunits.

If there were only a single subunit, the linear and nonlinear subunits circuits would have identical output responses so

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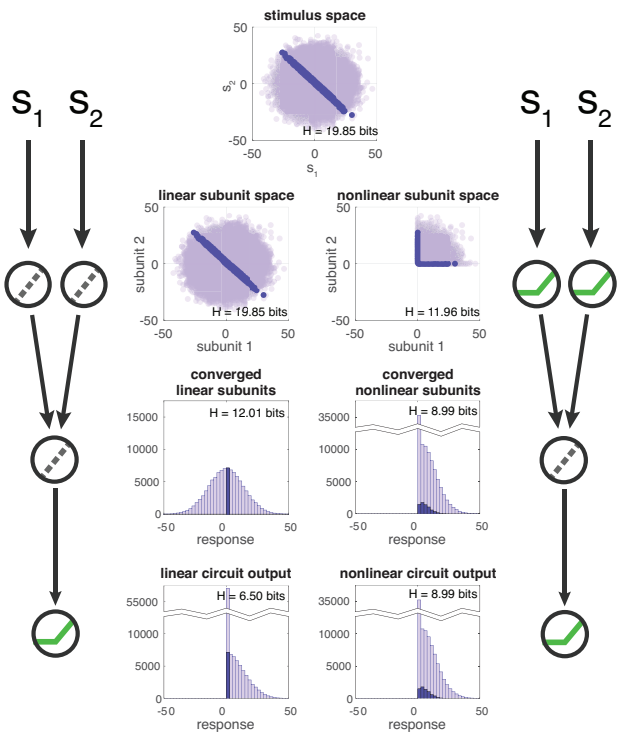

Fig. 2. The encoding of the stimulus space (top) within each circuit layer (subunits, 2nd row; linearly summed response, 3rd row; nonlinear output response, 4th row) of a 2-subunit pathway configuration without divergence. Left, linear subunits pathway; right, nonlinear subunits pathway. The output nonlinearity does not have an additional effect on the summed nonlinear subunits without noise.

long as there remained an output nonlinearity. The 2-subunit example in Figure 2 showed improved information transmission in the case of two nonlinear subunits, and prompted us to ask whether there would be a continued improvement with additional nonlinear subunits. We computed the entropy of the output responses for the linear and nonlinear subunit configurations for a range of subunit dimensions. With increasing subunit dimension, more subunit responses are compressed into the output response. To observe a relative change in entropy, the subunits were normalized. Consequently, for the linear subunits configuration, the output response distribution is invariant to the number of subunits (Fig. 3A). The distribution of output responses for the nonlinear subunits pathway, however, qualitatively changes with the number of subunits (Fig. 3B). With few subunits, the output response distribution resembles the truncated gaussian seen for the rectified output response in Figures 1D and 3A. With increasing numbers of subunits, the output response distribution approximates a gaussian (due to the central limit theorem) with a mean that shifts towards more positive values (Fig. 3B). The mean shift is relevant because summing the nonlinear subunits allows the output distribution to escape the most detrimental part of the subunit nonlinearity. In other words, each nonlinear subunit is negatively impacted by its own threshold, but collectively, they pull the output response distribution away from the rectification that each one is individually responsible for.

The entropy for the nonlinear subunits pathway is the only one that increases with increasing subunit dimension (Fig. 3C). It saturates before reaching the entropy of the fully linear pathway - which is to say that, although convergence improves the information retention of nonlinear subunits, the convergence of linear subunits still contains more information about the stimulus than any single pathway configuration that includes nonlinearities.

Figures 2 and 3 show that convergence reduces the impact of the subunit nonlinearity on the entropy of the circuit. Furthermore, the nonlinear subunits circuit encodes different parts of the full stimulus distribution than the linear subunits circuit. These results only partially explain why the divergent nonlinear subunits circuit in Figure 1F has higher entropy than the divergent linear subunits circuit (Fig. 1E). Recall, those circuits had two complementary, diverging pathways - an ON and an OFF pathway while Figure 3C considers only a single pathway. The divergent ON and OFF linear subunits circuit with output nonlinearities (as in Figure 1F) encodes complementary aspects of the stimuli - i.e. those that sum to positive or negative values. Because the OFF pathway encodes the stimuli that are discarded by the ON pathway and vice versa, one might expect this circuit to perform as well as, if not better than, the divergent circuit with nonlinear subunits - yet it does not. Hence we next explore the impact of divergence on information coding with nonlinear subunits.

Divergent circuit structure leverages selectivity of nonlinear subunits. Although divergence improves the information retention of both circuits, it is not enough to allow the linear subunits circuit to surpass the entropy of the nonlinear subunits circuit. We present a geometrical exploration of the transformations that take place in the different layers of the circuit configurations with two divergent output pathways. Our demonstration uses circuits with two input dimensions to facilitate the visualization of the stimulus and subunit spaces. Figure 4 shows a 2-dimensional stimulus space that displays each stimulus quadrant in a different color (top, Figs. 4A,D). The points in all subsequent plots are color-coded by the stimulus quadrant from which they originate. The linear ON subunit space (Fig. 4A, 2nd row, left) is identical to the stimulus space because no transformation or compression has taken place through the linear subunits. The OFF subunits receive a negative copy of the same stimulus that the ON subunits receive which rotates the stimuli by 180 degrees (Fig. 4A, 2nd row, right). When the linear subunits are converged within their respective pathways, the ON and OFF responses are compressed onto a diagonal line because they are anti-correlated (Fig. 4B). When the output nonlinearities are applied, this linear manifold is folded into an L-shape (Fig. 4C).

The entropy for the output response of the linear subunits circuit with diverging pathways (H = 12.01 bits) is higher than it was with just a single pathway (H = 6.50 bits, Fig. 3C, black). However, it is only increased enough to match the entropy of a single pathway response without any nonlinearities in either the subunits or the output (H = 12.01 bits, Fig. 3C, grey dashed). In other words, the OFF pathway in the linear subunits circuit with output nonlinearities (Fig. 4C) is indeed encoding the information discarded by the ON pathway, but

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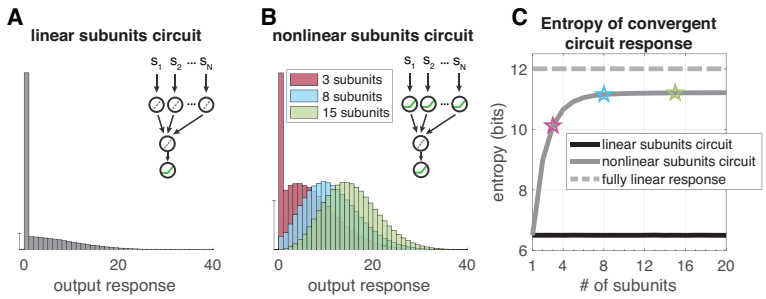

Fig. 3. Compression with increasing numbers of converging subunits. The subunit to output weights are normalized so that each subunit has a weight of $1/\sqrt{N}$. The inputs [s1,s2,...,sN] are independently drawn from a gaussian distribution. (A,B) Histograms of the output response. The response distribution for the linear subunits configuration (A) does not depend on the number of subunits due to the normalization. Response histograms for the nonlinear subunits configurations are shown for 3, 10, and 25 subunits (B). (C) Entropy of output response as a function of number of subunits where subunits are normalized (black solid, entropy of nonlinear output response from linear subunits circuit; gray solid, entropy of nonlinear output response from nonlinear subunits circuit; gray dashed, entropy of the linear summation of linear subunits). Stars correspond to their respective distributions in (B).

it does not enable the full divergent circuit to do any better than an ON pathway alone with no nonlinearities anywhere.

To understand how the nonlinear subunits produce an additional advantage, observe how the nonlinear subunits transform the inputs (Fig. 4D). Unlike the linear subunits, the nonlinear subunits actually compress the subunit space, but they do so in complementary ways for the ON and OFF subunits. When these subunits are converged in their respective pathways (Fig. 4E), the output response has some similarities to that for the linear subunits circuit (Fig. 4C). The L-shaped manifold is still present, but the points representing the stimulus inputs with mixed sign have been projected off of it. By virtue of having these points leave the manifold and fill out the response space, entropy is increased. In fact, as more nonlinear subunits are converged in a divergent circuit, the entropy continues to increase until saturation (Fig. 4F). It even increases beyond that of the fully linear response (shown in Fig. 4B) where there are no nonlinearities anywhere.

The output nonlinearities have the effect of decorrelating the ON/OFF output response in the linear subunits circuit, while for the nonlinear subunits circuit, it is the nonlinear subunits themselves that decorrelate the output response and by about the same amount (correlation coefficients: linear response = -1, linear subunits, nonlinear output circuit = -0.4670, nonlinear subunits circuit = -0.4669). Indeed, although the output nonlinearity decorrelates the ON/OFF outputs of the linear subunits circuit, this decorrelation does not produce any gains in entropy relative to the linear subunits circuit before output nonlinearities are applied. Furthermore, the ON/OFF responses of the nonlinear subunits circuit are as decorrelated as for the linear subunits circuit, however, it experiences an entropy gain over the fully linear response unlike the linear subunits circuit. The additional entropy conferred by divergence for the nonlinear subunits circuit is due to how the nonlinear subunits decorrelate the ON and OFF pathways before convergence, and not merely the fact that those outputs have been decorrelated. It is this step that pulls responses off of the linear manifold in the output response space leading to an increase in response entropy.

Increased response entropy quantifies the fact that a circuit encodes additional information about the stimulus, but does not convey anything about which aspects of the stimulus are encoded - only that the encoding has the potential to convey more distinct states. For example, in principle it is possible for increased entropy to simply relate an increase in the encoding resolution of a single stimulus feature, rather than the encoding of additional stimulus features. We next show that this is not the case here. Nonlinear subunits lead to the encoding of additional stimulus features.

Nonlinear subunits circuit encodes both mean and contrast information. To determine whether increases in entropy accompany an encoding of new stimulus features, we once again did a visualization of the stimulus and response spaces for the two circuit configurations. The stimulus inputs are assumed to represent relative luminance values and the distributions are the same as before. We chose two basic features of visual stimuli to investigate: mean relative luminance and contrast. In Figure 5A, the stimulus space is color-coded by bands of mean luminance levels. In both of the response spaces in Figure 5A, a banded structure is preserved, indicating that there is a separation of the mean luminance levels within the response spaces for the circuits with linear subunits and with nonlinear subunits. This is emphasized by the separation of the red square and red circle (which occupy different bands in the stimulus space) in the response spaces. However, note that the red and cyan squares overlap each other in the output response space for the linear subunits circuit (Fig. 5A, middle). These two symbols represent stimuli with the same mean luminance but different contrasts. Only the nonlinear subunits circuit represents these stimuli with distinct output responses.

The nonlinear subunits circuit encodes stimulus contrast. The bottom row explicitly shows how contrast is encoded by the different circuits (Fig. 5B). The stimulus space is color-coded for three contrast levels (Fig. 5B, left). The highest contrast areas of the space are in the mixed sign quadrants. The representations for low, medium, and high contrast stimuli overlap each other in the output response space of the linear subunits circuits (Fig. 5B, middle). However, there is separation of these contrast levels in the output response space of the nonlinear subunits circuit (Fig. 5B, right). The nonlinear subunits circuit encodes both mean and contrast information whereas the linear subunits circuit only encodes mean luminance.

Discussion

We set out to understand how common neuron and circuit properties impact information retention. We asked how much stimulus information a compressive circuit could preserve if it also has selective nonlinear subunits. To answer this question, we built a circuit model and compared the entropy of lin-

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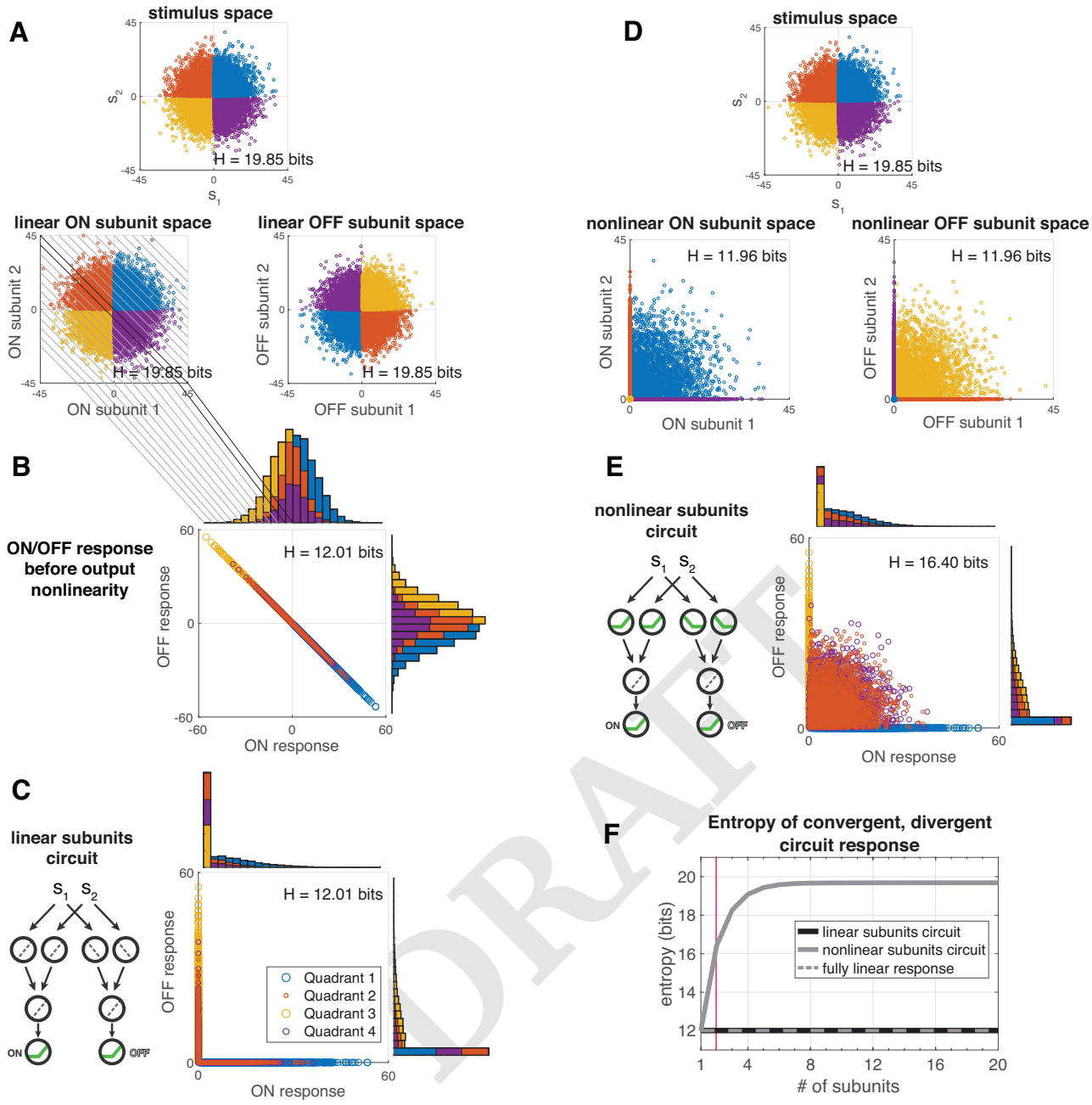

Fig. 4. Visualization of stimulus/response mappings at each level of a convergent, divergent circuit with two inputs, two subunits for each pathway (ON and OFF pathways), and a nonlinear output neuron for each pathway. (A) The spaces are color-coded according to the 4 stimulus quadrants (top). The 2D stimulus space maps onto a 2D linear subunit space for each pathway (second row, left: ON; right: OFF). The subunit spaces are shown before subunit normalization. (B) The response space is shown for the linear sum of subunits before the nonlinearity is applied and (C) after the nonlinear output response. (D) The 2D stimulus space maps onto a 2D nonlinear subunit space for each pathway (second row, left: ON; right: OFF). (E) The output response space for the nonlinear subunits circuit. Note that the output response before the output nonlinearity is applied is the same as when the output nonlinearity is applied for the circuit with nonlinear subunits. (F) Entropy of the output response for convergent, divergent circuits with increasing input and subunit dimension (subunits are normalized as before).

ear and nonlinear subunit configurations. We found that the circuit with nonlinear subunits preserves more information than the circuit with linear subunits despite the fact that the nonlinear subunits, due to their selectivity, are compressive themselves. Divergence, convergence, and non-invertible nonlinear signal transformations each have a negative impact on efficiency or information individually. However, when arranged together they can mitigate the loss of information and encoding capacity that is imposed by the reduction in dimension from inputs to outputs.

Implications for artificial neural networks. Artificial neural networks (ANNs) were inspired by the layered organization of biological neural networks. Practitioners of ANNs are fond of the ReLU activation function which rectifies inputs before propagating outputs to subsequent layers. The ReLU frequently has the best performance among other nonlinear activation functions (Glorot et al., 2011; LeCun et al., 2015) in tasks ranging from the discrimination of handwritten digits to restricted Boltzmann machines (Nair and Hinton, 2010). It is a typical choice because it preserves the lin-

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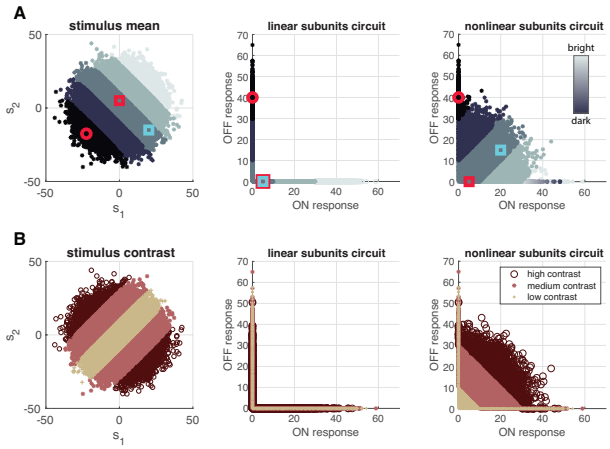

Fig. 5. Mean and contrast encoding of convergent, divergent circuits from Figure 4 (2 subunits, ON and OFF output). (A) Visualization of the stimulus mean representation and response spaces. The red square is an arbitrary reference point. In the stimulus space, the cyan square has the same mean luminance as the red square but a different contrast, while the red circle has the same contrast as the red square but a different mean luminance. (B) Visualization of the stimulus contrast representation and response spaces.

ear properties that make optimizing with gradient-descent as easy as for a regular linear function (LeCun et al., 2015). The geometrical interpretation presented here of the information preserving capabilities of the ReLU within an architecture that is reminiscent of a generic feedforward ANN may be relevant to the field of machine learning. The separation of stimulus features in the response space (Fig. 5) suggests that the task of categorization using linear boundaries (i.e. a linear decoder) is made easier with nonlinear hidden units than with linear hidden units. Furthermore, it eliminates the need to expand the dimension of the output in order to make the feature representations linearly separable.

Selectivity versus efficiency. Nonlinearities can have different functions in a neuron. Nonlinear transformations can induce selectivity in that they can cause a neuron to encode a very particular aspect of the stimulus or its inputs (Gollisch, 2013; Gollisch and Meister, 2010). Otherwise, nonlinearities can optimize efficiency by maximizing the entropy of the response distribution (Laughlin, 1981). The rectified linear nonlinearity that we used does not maximize the response entropy of the single neuron that receives gaussian-distributed inputs, but it does enforce a strict selectivity for inputs above threshold. Selectivity, however, is in conflict with efficient coding in that discarding information is a poor way to maximize it. The selective coding of features is often conflated with redundancy reduction, but it is important to make a distinction in the context of efficient coding - where a redundancy reducing code is reversible and is expected to maximize information about the stimulus (Barlow, 2001). Selectivity indicates that some stimulus information will be irreversibly discarded.

The existence of selective cell types that compute different aspects of the visual scene appears to confound an efficient coding framework (Pitkow and Meister, 2012). Yet, properties of selectivity are crucial to the functions of a diverse array of cell types, such as object-selective cells in medial temporal lobe (Ison, et al., 2011), face-selective cells in the inferior temporal cortex (Eifuku et al., 2004; Hasselmo, et al., 1989), and direction-selective cells, orientation-selective cells, and edge detector cells in the retina (Sanes and Masland, 2015). Furthermore, many cell types in the retina and other circuits have both an ON and an OFF variant (Gjorgjieva et al., 2014). In our study, rather than optimizing the nonlinearities for information maximization, we chose non-invertible nonlinearities that exhibit generic selectivity (ON or OFF) and that induce lossy compression of stimuli with no inherent statistical redundancy to exploit. Despite those properties, we found that, within a convergent, divergent circuit architecture, selective nonlinearities produced the most information. This increase comes from a reformatting of the stimulus distribution in a manner that reduces the ambiguities produced by the convergence of multiple inputs (Fig. 2). This reformatting facilitates the encoding of multiple stimulus features in Figure 5. Thus, in the circuits we study here, true efficient coding can be achieved with selective nonlinear components.

Contribution of divergence to information maximization. Past work (Brinkman et al., 2016; Gjorgjieva et al., 2014; Kastner et al., 2015) has explored the optimal nonlinearities and configurations of divergent circuits - though none have explicitly explored convergence or nonlinear compression as we did. Brinkman, et al, found that the optimal nonlinearities are highly dependant on the placement and magnitude of noise in the circuit. Our study did not include noise; however, for low noise conditions, they found that the optimal sigmoidal nonlinearities cross at the lower bend which is similar to the crossing at threshold for the nonlinearities in our study. In their study, noise had the effect of changing the optimal nonlinearities, but it is unclear whether changing the convergence or divergence in a circuit structure like ours would be more effective for maximizing information than changing the properties of the nonlinearity. Our future studies will investigate how noise impacts the efficiency of a nonlinear subunit code.

A key finding in our work is that the efficiency of divergent circuits is enhanced by nonlinearities that decorrelate the outputs (Gjorgjieva, et al., 2014; Kastner, et al., 2015). Indeed, our findings show that divergence resulted in efficiency gains for both the linear and nonlinear subunits circuits (compare the entropies in the solid lines for the single pathway configurations in Figure 3C to those for the corresponding divergent circuits in Figure 4F). Our findings also show that nonlinearities facilitate decorrelation among the ON and OFF outputs when looking across divergent circuits (compare the fully linear circuit in Figure 4B (corr coef = -1) to the other circuits in Figure 4C and 4E (corr coeff = -0.467 for both)). Despite achieving the same amount of decorrelation, any efficiency gains are dependent on the manner in which this decorrelation is achieved. For the linear subunits circuit, the output nonlinearities induced decorrelations among the outputs but did not result in an increase in entropy beyond that for the fully linear response. The decorrelations due to the nonlinear subunits did, however, lead to an increase in entropy relative to the fully linear response.

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Nonlinearities are known to have a special role in decorrelating and separating signals. Pitkow and Meister (2012) show that nonlinear responses in ganglion cells have more of an effect on decorrelating their responses than their center-surround receptive field properties. However, as they point out, weak correlation is not necessarily weak dependence. In the divergent, convergent circuits in Figure 4, putting nonlinearities in either the outputs or the subunits decorrelates the outputs by the same amount relative to the response without any nonlinearities where the outputs are perfectly anti-correlated. However, only by placing the nonlinearities in the subunits does a gain in entropy result relative to the scenario in which there are no nonlinearities in the circuit. Bell and Sejnowski (1995) showed that nonlinearities have the effect of reducing redundancy between output neurons by separating statistically independent parts of the inputs. Following that, it was shown that the efficient encoding of natural signals is facilitated by a nonlinear decomposition whose implementation is similar to the nonlinear behaviors observed in neural circuits through divisive normalization (Schwartz and Simoncelli, 2001). Our study contributes to this body of work by showing how nonlinear processing contributes to a more informative representation that has lower dimension than the inputs.

Materials and Methods

We used Shannon's entropy (Shannon and Weaver, 1998) to quantify the information retention of our model circuits because it quantifies how many distinct neural responses are possible given a particular stimulus distribution, and this relates to the specificity of encoding even though it does not indicate which specific stimulus features are encoded. Since there was no noise anywhere in the circuit, the mutual information between the stimulus and the response reduces to the entropy of the response. Mutual information is defined as $MI = H[r] - \langle H[r|s] \rangle$ (Cover and Thomas, 2006). In our study, there is a deterministic relationship between the response and the stimulus due to the lack of noise. The second term of the MI goes to zero and one is left with the entropy of the response. We were careful to avoid any effects that could distort the interpretation of the entropy. The ReLU was ideal here because it compresses the input signal without necessarily scaling it, so the compression was entirely derived from the non-invertibility of the nonlinearity and not a linear gain factor.

The convergent structure of the retina reduces the dimension of the high-resolution visual input it receives, placing an upper bound on the amount of information that is possible to transmit through the optic nerve. The data compression implemented by the circuit architecture may perform lossless or lossy compression or some combination. In this study, we focus on lossy compression. By using images of random pixels (i.e. no redundant structure), we place the inputs into a regime where lossless compression is impossible or assumed to have already taken place. Therefore, the circuit configuration that experiences less lossy compression has a higher entropy than that which experiences more lossy compression. We consider higher entropy to be an indication of better performance.

Model simulations and visualizations. All simulations, visualizations, and entropy computations were done in Matlab. The dimension of the stimulus always matches the dimension of the subunits within a pathway, and a stimulus consists of N stimulus inputs. For example, if there are 5 subunits in each of the ON and OFF pathways, then the stimulus has 5 stimulus inputs (sometimes referred to as pixels). Each stimulus input was independently drawn from a gaussian distribution with arbitrary units and a standard deviation of 10 ($\mu = 0, \sigma^2 = 100$). Each subunit receives input from one stimulus input. For all figures in this paper, linear subunits did not transform or scale stimulus inputs and therefore the ON linear subunit response was equivalent to the stimulus input and the OFF linear subunit response was the negative of the stimulus input.

All weights were uniform with unit weights from stimulus inputs to subunits and normalized weights from subunits to outputs. The subunits were normalized so that the variance of the linear sum of subunits is maintained. With N subunits, each subunit weight is $1/\sqrt{N}$. This normalization facilitated a comparison between circuit configurations with linear and nonlinear subunits. All circuit configurations are subject to the same uniform weighting and subunit normalization here and throughout the paper.

Each nonlinear unit applied a ReLU thresholded at zero with unit slope to the stimulus input - effectively a positive-pass filter for ON subunits, $R_{ON\ subunit\ i}$, and a negative-pass filter for OFF subunits, $R_{OFF\ subunit\ i}$,. The output neuron linearly sums the subunit responses in its pathway and then applies the nonlinearity. The output response, $R_{ON\ output}$ or $R_{OFF\ output}$, to a given stimulus image, Υ, was a single value that represents a steady state response, as this model did not have temporal dynamics.

$$R_{ON\ subunit\ i}(s_i) = \begin{cases} s_i, & \text{if } s_i > 0 \\ 0, & \text{otherwise} \end{cases} \quad \textbf{(1)}$$

$$R_{OFF\ subunit\ i}(s_i) = \begin{cases} -s_i, & \text{if } s_i < 0 \\ 0, & \text{otherwise} \end{cases} \quad \textbf{(2)}$$

$$R_{ON\ output}(\vec{R}_{ON\ subunit}) = \quad \textbf{(3)}$$

$$\begin{cases} \sum_i^N R_{ON\ subunit\ i}, & \text{if } \sum_i^N R_{ON\ subunit\ i} > 0 \\ 0, & \text{otherwise} \end{cases} \quad \textbf{(4)}$$

$$R_{OFF\ output}(\vec{R}_{OFF\ subunit}) = \quad \textbf{(5)}$$

$$\begin{cases} \sum_i^N R_{OFF\ subunit\ i}, & \text{if } \sum_i^N R_{OFF\ subunit\ i} > 0 \\ 0, & \text{otherwise} \end{cases} \quad \textbf{(6)}$$

Visualizations in stimulus, subunit, and response spaces. Each quadrant was color-coded such that: $s_1 > 0, s_2 > 0 : blue, s_1 > 0, s_2 < 0 : purple$, etc. Output response histograms in Figure 4 are also color-coded in this way to show which response bins represent which stimuli. For mean luminance and contrast visualization, spaces were color-coded to indicate evenly spaced bands

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of mean stimulus luminances, M, and stimulus contrasts, Λ. Each stimulus image, Υ, consists of N stimulus inputs, $\Upsilon = [s_1, s_2, ..., s_N]$. In Figures 4 and 5, $N = 2$.

$$M(\Upsilon) = \frac{s_1 + s_2 + ... + s_N}{N} \tag{7}$$

$$\Lambda(\Upsilon) = \left| \sqrt{\frac{1}{2} \sum_i (s_i - \langle s \rangle)^2} \right| \tag{8}$$

Entropy calculations. Information entropy is defined as $H = -\sum P[r] log P[r]$. Discrete entropy was used even though stimulus and response distributions were continuous. Because stimuli that fall into the same bin are ambiguous, the discretization has a similar effect as noise. A consistent bin width of 0.01 was used for all entropy calculations to facilitate comparison. This bin width was used for all dimensions. For example, in a 2D response space, bins would be boxes that are 0.01 x 0.01. Entropy computations were done by simulating the circuit responses to batches of 10^5 stimulus samples, binning the responses, and computing response probabilities to enter into the entropy equation. The entropy quantities presented come from the average over five batches.

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