Optimal Coding in Biological and Artificial Neural Networks

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Feature representations in both, biological neural networks in the primate ventral stream and artificial convolutional neural networks trained on object recognition, increase in complexity and receptive field size with layer depth. Somewhat strikingly, empirical evidence indicates that this analogy extends to the specific representations learned in each layer. This suggests that biological and artificial neural networks share a fundamental organising principle. We shed light on this principle in the framework of optimal coding. Specifically, we first investigate which properties of a code render it robust to transmission over noisy channels and formally prove that for equientropic channels an upper bound on the expected minimum decoding error is attained for codes with maximum marginal entropy. We then show that the pairwise correlation of units in a deep layer of a neural network, that has been trained on an object recognition task, increases when perturbing the distribution of input images, i.e., that the network exhibits properties of an optimally coding system. By analogy, this suggests that the layer-wise similarity of feature representations in biological and artificial neural networks is a result of optimal coding that enables robust transmission of object information over noisy channels. Because we find that in equientropic channels the upper bound on the expected minimum decoding error is independent of the class-conditional entropy, our work further provides a plausible explanation why optimal codes can be learned in unsupervised settings.

1 Introduction

Recent computational neuroscience research has compared sensory processing in artificial neural networks to their biological counterparts [YD16]. Research on visual object recognition revealed that feedforward computations across the ventral stream result in a
rich neuronal representation in inferior temporal cortex [DZR12]. Indeed, several studies suggest that models performing better at object recognition have learned representations more similar to those in the brain [YHCD13, KRK13, YHC+14, CHY+14]. Furthermore, mapping different voxels to the different layers of an artificial neural network allows to accurately model the activity across the ventral stream: more specifically, the complexity of neuronal representations gradually increases across different stages of the primate ventral stream the same way it does for increasing layer depth in the artificial neural network [ASMG14, GVG15].

The striking analogy between visual processing in the brain and in artificial neural networks that have not been trained to model the visual cortex but to solve object recognition tasks raises the following question: Which fundamental mechanisms, implicit constraints, and organising principles determine the similar structure of the biological and artificial neural network? Training artificial neural networks for a particular task also implemented by the visual cortex is thought to sufficiently constrain the model class while avoiding the data limitations of directly modelling neural activity [YD16]. However, this account lacks the explication of an underlying fundamental organising principle. It also fails to explain why artificial neural networks require a vast amount of labelled training data as opposed to biological neural networks that learn from very few examples or learn unsupervisedly from unlabelled data [YD16].

In this work we introduce a notion of optimal coding that captures robustness of the input’s encoded representation against noise or data corruption during information transmission. It turns out that those representations are optimal that achieve high entropy for the specific input distribution. Importantly, under mild assumptions on the noise, optimal codes may be learned by a neural network on unlabelled data alone. Assuming both network types perform close to optimal coding, our account provides a new perspective on the fundamental organising principle that may result in the striking similarity. The main contributions of this manuscript are the following.

- We characterise optimal codes for equientropic channels in terms of high marginal entropy of the sender/receiver bits. Importantly, learning an optimal representation is independent of the class-conditional entropy and hence only requires samples of the input distribution and no class labels for the specific task.

- As an instructive example we prove for the additive white Gaussian noise (AWGN) channel that random coding—a capacity achieving code—indeed maximises the marginal entropy in the limit of infinite messages.

- We provide empirical evidence that a trained artificial neural networks exhibits properties of an optimally coding system, i.e., activation in deep layers optimally encodes the input. Thus, the similar representations in different layers of an artificial neural network and the ventral stream may be due to both networks optimally coding the inputs irrespective of the specific task they implement.
2 Optimal Coding

In this section, we introduce a notion of optimal coding for communication of messages between a sender and receiver node. While the channel capacity reflects a theoretical upper bound on the achievable information transmission rate in the limit of infinitely many bits, it does not characterise the information transfer of a concrete system. In contrast, the characterisation presented here assesses the quality of a given implemented (en-)-coding routine by investigating the minimum decoding error that can potentially be achieved with this representation.

For this consider communication over noisy memoryless channels

$M \xrightarrow{\text{encoder}} X^n \xrightarrow{\text{channel}} Y^n \xrightarrow{\text{decoder}} \hat{M}$

where the sender node $M$ is a random variable taking discrete values $m \in \mathcal{M}$ according to $p_M$; the values $x^n = [x_1, ..., x_n]$ of the sender bits $X^n$ are determined by the encoder function $f_{\text{enc}} : \mathcal{M} \rightarrow \mathcal{X}^n$ assigning codewords to messages; noise corruption of the received bits $Y^n$ is governed by the conditional distribution $p_{Y^n|X^n} (y^n|x^n) = \prod_{j=1}^{n} p_{Y_j|X_j} (y_j|x_j)$;\(^1\) and the decoder $f_{\text{dec}} : \mathcal{Y}^n \rightarrow \mathcal{M} \cup \{\epsilon\}$ reconstructs a message from the received bit values or declares an error. The message distribution $p_M$, the encoder $f_{\text{enc}}$, the channel $p_{Y|X}$, and the decoder $f_{\text{dec}}$ fully determine the distribution of the receiver node $\hat{M}$ and as such the probability of error $\mathbb{P} [M \neq \hat{M}]$.

Thence, for given message distribution $p_M$ and channel $p_{Y|X}$ the code, that is the choice of $f_{\text{enc}}$ (and corresponding $f_{\text{dec}}$), fully determines the behaviour of information transmission. The minimum probability of error is attained if choosing the maximum a posteriori (MAP) decoder $\arg \max_{m \in \mathcal{M}} p_M|Y^n (m|y^n)$. Thus, for any code $f_{\text{enc}}$, the expected minimal probability is the MAP error $\mathcal{E} (f_{\text{enc}}) := \mathbb{E}_{Y^n} \left[ 1 - \max_{m \in \mathcal{M}} p_M|Y^n (m|y^n) \right]$. We characterise optimality of a code $f_{\text{enc}}$ by the following Proposition.

Proposition 1. For communication of a message $M \sim p_M$ with finite range over a noisy memoryless channel $p_{Y|X}$ using $n$ bits the MAP error $\mathcal{E} (f_{\text{enc}})$ can be bounded in terms of the mutual information $I (Y^n; M) = H (Y^n) - H (Y^n|M)$ as

$$\gamma (-I (Y^n; M)) \leq \mathcal{E} (f_{\text{enc}}) \leq \Gamma (-I (Y^n; M))$$

where $\gamma$ and $\Gamma$ are strictly monotonically increasing functions.

Proof. [FM94, Theorem 1] establishes the following relation (notation adapted)

$$\Phi (\mathcal{E} (f_{\text{enc}})) \geq H (M|Y^n) \geq \phi^* (\mathcal{E} (f_{\text{enc}}))$$

where $\Phi$ and $\phi^*$ are continuous and strictly monotonically increasing, hence invertible, functions (cf. [FM94] for their definitions). Recall $H (M|Y^n) = H (M) + H (Y^n|M) -$

\(^1\)To ease notation we assume $p_{Y_j|X_j} = p_{Y_j|X_j}$ for all $j \in [n]$. The results presented in this manuscript only require a memoryless channel and still hold true if noise corruption is bit-specific, i.e., $p_{Y^n|X^n} = \prod_{j=1}^{n} p_{Y_j|X_j}$.
\(H(Y^n)\) and note that \(H(M)\) is fix for fixed \(p_M\). The inequality follows for \(\gamma(h) := \Phi^{-1}(H(M) + h)\) and \(\Gamma(h) := \phi^{-1}(H(M) + h)\) which are strictly monotonically increasing functions in \(h\).

That is, codes \(f_{\text{enc}}\) that result in high \(I(Y^n; M) = H(Y^n) - H(Y^n|M)\) result in a low upper bound on the MAP error. In particular, of all codes resulting in the same conditional entropy \(H(Y^n|M)\) a code with maximal entropy \(H(Y^n)\) has the lowest upper bound on the MAP error. The following Propositions simplify this result for equal entropy channels and independent additive noise channels: The lowest upper bound on the MAP error is achieved for codes \(f_{\text{enc}}\) that maximise the entropy of receiver bits \(H(Y^n)\) and the entropy of sender bits \(H(X^n)\), respectively.

**Definition 2.** A noisy memoryless channel \(p_{Y|X}\) with \(H(Y|X = x_1) = H(Y|X = x_2)\) for all \(x_1, x_2 \in X\) is an equal entropy channel.

**Proposition 3.** For equal entropy channels \(p_{Y|X}\) the conditional entropy \(H(Y^n|M)\) is independent of the choice of \(f_{\text{enc}}\).

**Proof.** The channel is memoryless such that \(H(Y^n|M) = \sum_{j=1}^{n} H(Y_j|M)\). For any \(x \in X\) and \(j \in \mathbb{N}_{1:n}\)

\[
H(Y_j|M) = \sum_{m \in M} p_M(m) H(Y_j|X_j = f_{\text{enc}}(m_i)_j) = \sum_{m \in M} p_M(m_i) H(Y_j|X_j = x)
\]

which shows that \(H(Y_j|M)\) and hence \(H(Y^n|M)\) is independent of the choice of \(f_{\text{enc}}\). \(\square\)

**Definition 4.** A noisy memoryless channel \(p_{Y|X}\) with \(Y^n|X^n = X^n + N^n\) for mutually independent noise variables \(N^n \sim p_{N^n} = \prod_{i=1}^{n} p_{N_i}\) that are independent of \(X^n\) is an independent additive noise channel. Independent additive noise channels are equal entropy channels.

**Proposition 5.** For independent additive noise channels with noise variables \(N^n\) the entropy of the receiver bits \(H(Y^n) = H(X^n) + H(N^n)\) only depends on the choice of \(f_{\text{enc}}\) via the entropy of the sender bits \(H(X^n)\).

In conclusion, optimality of a code \(f_{\text{enc}}\) for communication over a noisy memoryless channel with message distribution \(M \sim p_M\) can be characterised by the upper bound on the MAP error that results from this code. The respective bounds for different channels are summarised in Table 1. Importantly, without knowing specific details about how the representation may be communicated to other layers/areas of the brain, maximising entropy turns out to be a sensible heuristic for learning a robust representation of inputs (here messages). Intuitively, high entropy distributed codes are more robust against independent noise.
Table 1: Upper bounds on the MAP error $E(f_{\text{enc}})$ for communication of a message $M \sim p_M$ with finite range over different channels where $\Gamma, \Gamma', \Gamma''$ are strictly monotonically increasing functions.

| Channel Type                              | Bound                                                   |
|-------------------------------------------|---------------------------------------------------------|
| noisy memoryless channel                  | $E(f_{\text{enc}}) \leq \Gamma(-I(Y^n;M))$             |
| equientropic channel                      | $E(f_{\text{enc}}) \leq \Gamma'(\ -H(Y^n))$           |
| independent additive noise channel        | $E(f_{\text{enc}}) \leq \Gamma''(-H(X^n))$            |

### 2.1 AWGN random coding example

The AWGN channel is an ubiquitous and well-understood channel model. Here it serves as an instructive example for the optimality concept introduced in the previous section.

The AWGN channel is an independent additive noise channel and described by

$$Z \sim \mathcal{N}(0, NI_{n \times n})$$

$$Y_i = gX_i + Z_i \text{ for } i \in \mathbb{N}_1:n$$

where $g$ is the channel gain and $N$ the noise level. We employ the power constraint that each codeword $x^n = f_{\text{enc}}(m) \in X^n$ has to satisfy

$$\frac{1}{n} \sum_{i=1}^{n} (x_i)^2 \leq P$$

and without loss of generality assume $N = 1$ such that the received power is $S = g^2 P$.

The Shannon-Hartley theorem establishes the channel capacity

$$C = \max_{p_X; E[X^2] \leq P} I(X;Y) = \frac{1}{2} \log (1 + S)$$

Achievability of this upper bound on the rate is commonly proven by random coding, i.e., for any rate $R := \frac{\log_2 |\mathcal{M}|}{n} \leq C$ the error probability tends to zero as $n = \log_2 |\mathcal{M}| \to \infty$ if using random coding.

Here we show that random coding not only achieves the optimal rate but also is optimal in the sense of Proposition 1 that $H(Y^n) = \sum_{i=1}^{n} H(Y_i)$ (and the $Y_i$ are Gaussian maximising the individual entropies) in the limit $n \to \infty$.

In random coding the encoder function $f_{\text{enc}}$ is defined by a random codebook, i.e., an independent sample of $C_n \sim \mathcal{N}(0, PI_{n \times n})$ is assigned to each message $m_i$ as codeword $f_{\text{enc}}(m_i) = [c_{i1}, \ldots, c_{in}]$. Once a codebook is fixed and we observe samples of the system each receiver bit $Y_j$ is a mixture of Gaussians with probability density function (pdf) $p_{Y_j}(y_j) = \sum_{i=1}^{M} p_M(m_i) \varphi(y_j|c_{ij}, 1)$ where $\varphi(y|\mu, \sigma^2)$ denotes the pdf of the Gaussian distribution $\mathcal{N}(\mu, \sigma^2)$ evaluated at $y$. For this setup we prove the following

**Proposition 6.** Using random coding in the AWGN channel with $p_M \sim \text{Unif}(\mathcal{M})$ the joint entropy $H(Y_1, \ldots, Y_k) \xrightarrow{n \to \infty} \sum_{i=1}^{k} H(Y_i)$ for any number of $k$ pairwise different receiver bits $Y_{j1}, \ldots, Y_{jk}$. Furthermore, the distribution of each $Y_j$ approaches a Gaussian distribution $\mathcal{N}(0, P + 1)$ as $n \to \infty$. 

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Proof. In random coding the random codebook is generated by drawing each \( c_{ijl} \) from independent random variables \( C_{ijl} \sim \mathcal{N}(0, \mathbf{P}) \), which then defines the joint pdf

\[
p_{Y_{j_1}, \ldots, Y_{j_k}} (y_{j_1}, \ldots, y_{j_k}) = \sum_{i=1}^{|\mathcal{M}|} p_M (m_i) (2\pi)^{-k/2} e^{-\frac{1}{2} \sum_{l=1}^k (y_{jl} - c_{ijl})^2}
\]

and marginal pdfs

\[
p_{Y_{jl}} (y_{jl}) = \sum_{i=1}^{|\mathcal{M}|} p_M (m_i) (2\pi)^{-1/2} e^{-\frac{1}{2} (y_{jl} - c_{ijl})^2}
\]

for \( l \in \mathbb{N}_{1:k} \) and \( y_{j_1}, \ldots, y_{j_k} \in \mathcal{Y} \). In general \( p_{Y_{j_1}, \ldots, Y_{j_k}} \neq \prod_{l=1}^k p_{Y_{jl}} \).

For all \( l \in \mathbb{N}_{1:k} \) and \( y_{j_1}, \ldots, y_{j_k} \in \mathcal{Y} \) define the random variables

\[
\hat{p}_{Y_{j_1}, \ldots, Y_{j_k}} (y_{j_1}, \ldots, y_{j_k}) = \frac{1}{|\mathcal{M}|} \sum_{i=1}^{|\mathcal{M}|} (2\pi)^{-k/2} e^{-\frac{1}{2} \sum_{l=1}^k (y_{jl} - c_{ijl})^2}
\]

and

\[
\hat{p}_{Y_{jl}} (y_{jl}) = \frac{1}{|\mathcal{M}|} \sum_{i=1}^{|\mathcal{M}|} (2\pi)^{-1/2} e^{-\frac{1}{2} (y_{jl} - c_{ijl})^2}
\]

By the law of large numbers

\[
\hat{p}_{Y_{j_1}, \ldots, Y_{j_k}} (y_{j_1}, \ldots, y_{j_k}) \xrightarrow{n \to \infty} \mathbb{E}_{C_{1j_1}, \ldots, C_{1j_k}} \left[ (2\pi)^{-k/2} e^{-\frac{1}{2} \sum_{l=1}^k (y_{jl} - C_{1jl})^2} \right]
\]

\[
\hat{p}_{Y_{jl}} (y_{jl}) \xrightarrow{n \to \infty} \mathbb{E}_{C_{1jl}} \left[ (2\pi)^{-1/2} e^{-\frac{1}{2} (y_{jl} - C_{1jl})^2} \right]
\]

where the first expectation factorises since the \( C_{1j_1}, \ldots, C_{1j_k} \) are mutually independent. It follows that for all \( y_{j_1}, \ldots, y_{j_k} \in \mathcal{Y} \)

\[
\hat{p}_{Y_{j_1}, \ldots, Y_{j_k}} (y_{j_1}, \ldots, y_{j_k}) \xrightarrow{n \to \infty} \prod_{l=1}^k \hat{p}_{Y_{jl}} (y_{jl}) \xrightarrow{n \to \infty} 0
\]

such that in the limit the pdf indeed factorises. Evaluating the expectation above we find that for each \( Y_j \) and \( y_j \)

\[
\hat{p}_{Y_j} (y_j) \xrightarrow{n \to \infty} (2\pi (P+1))^{-1/2} e^{-\frac{1}{2\pi (P+1)} y_j^2} = \varphi (y_j | 0, P + 1)
\]

which concludes the proof. \( \square \)

It is instructive to consider the analogous statement for any \( k \) pairwise different sender bits \( X_{j_1}, \ldots, X_{j_k} \). The proof follows analogous arguments and is another illustration of the fact that in independent additive noise channels the bound on the MAP error is fully determined by the entropy of the sender bits \( H (X^n) = H (Y^n) - H (Z^n) \).
3 Experimental Results

In the preceding sections, we proved that for equientropic channels an upper bound on the MAP error is minimised by maximising the marginal entropy of the transmitted codewords. This implies that optimally coding systems should tune their codewords to maximise entropy for a given input distribution. Perturbing the input distribution will then result in a decrease in entropy. Here, we test whether this property of an optimally coding system is expressed in a convolutional neural network trained on an object recognition task.

To test our prediction we analysed the pre-trained and improved version of the 16-layer network used by the VGG team in the ILSVRC2014 competition [SZ14, RDS +15] (in the paper, the model is denoted as the configuration D trained with scale jittering). This artificial neural network was trained to predict object classes. The ILSVRC2012-2014 training set consists of 1,281,167 images each assigned to one of 1,000 object classes $c_1, \ldots, c_{1000}$ which occur in the training set with probabilities $p_{c_1}, \ldots, p_{c_{1000}}$ respectively.

For our analysis we use the ILSVRC2012-2014 validation dataset [RDS +15] consisting of 50,000 images, 50 per object class. Since high dimensional entropy estimation is difficult we rely on low/high correlations between activations of pairs of neurons in a layer as a proxy for high/low entropy of activation in this layer. In the following we describe the procedure that we employed to test whether the activation entropy in layers 14 and 15 indeed was high and fine-tuned to the image distribution in the training set.

1. Sample 5,000 images from the validation dataset with class probabilities $p_{c_1}, \ldots, p_{c_{1000}}$

2. Compute all pairwise correlations $\rho_{\text{orig}}(i, j)$ between the activations of neurons $i \neq j$

3. For $k \in \mathbb{N}_{1:1000}$
   a) Repeat step 1. and 2. for random probability vectors $p_{c_1}^{(k)}, \ldots, p_{c_{1000}}^{(k)}$ computing all pairwise correlations $\rho_k(i, j)$
   b) Count the number $I_k$ and $D_k$ of pairs that resulted in an increase/decrease in absolute correlation, i.e., $|\rho_{\text{orig}}(i, j)| \leq |\rho_k(i, j)|$ and $|\rho_{\text{orig}}(i, j)| > |\rho_k(i, j)|$ respectively

4. Output $\frac{1}{1000} \sum_{k=1}^{1000} 1_{\leq 0}(I_k - D_k)$

That is, we compute the fraction of the 1,000 random image distributions that resulted in more decreased than increased absolute correlations compared to the image distribution in the training set. This fraction will be small if entropy was particularly high for the image distribution in the training set, i.e., if most other image distributions result in lower layer activation entropy. Indeed, confirming our prediction this procedure yielded the values $33/1000$ and $7/1000$ for layer 14 and 15 respectively. This finding is consistent with the interpretation that preceding layers of the artificial neural network implement optimal coding.
4 Discussion

We provide an optimal coding perspective on the representations learned by biological and artificial neural networks. Our empirical results indicate that indeed entropy is maximised in deep layers of artificial neural networks for object recognition. The analogy of representations of visual input across different layers may indicate that both biological and artificial neural networks implement optimal coding of the inputs with increasing layer depths. The optimal coding perspective raises interesting questions and clarifies ideas in different fields such as unsupervised training of artificial neural networks, information theory, and the efficient coding hypothesis in computational neuroscience.

Our findings suggest that artificial neural networks may be pre-trained to maximise the activation entropy on unlabelled data. If unlabelled and labelled data follow the same image distribution the pre-trained artificial neural network may learn a robust representation on the basis of the unlabelled images. This representation may at the same time be suitable for an object recognition task. After adding a final classification layer training this pre-trained artificial neural network for an object recognition task may be accomplished with fewer labelled images than are required when directly training the network for object classification.

According to the efficient coding hypothesis the brain implements an efficient code for representing sensory input by neuronal spiking [Bar61]. The necessity of an optimal coding is stressed by the fact that the number of neurons and the metabolic energy are constrained and must be used as efficiently as possible [Sim03, Zha06]. Building upon this hypothesis, we try to explain the striking similarity between processing of visual information in biological and artificial neural networks by presupposing that artificial neural networks also perform optimal coding in order to achieve high performance in object classification tasks. Hence, the requirement for optimal coding in both networks may constitute a fundamental organising principle underlying the observed similarity between representations while the artificial neural networks have not explicitly been trained to model the ventral stream.

What is more, our account allows to explain experimental results that seemingly contradict the efficient coding hypothesis. For example, observed dependencies between neurons and hence redundancies are assumed to challenge the efficient coding hypothesis [Bar61, Sim03]. The results presented in Section 1 clarify that an optimal code should maximise the joint entropy \( H(Y^n) \) of receiver (or sender) bits. For fixed marginal entropies \( H(Y_j) \) the maximum is indeed achieved if all units are mutually independent. However, since the marginal entropies are not fixed there can in general be configurations that have higher joint entropy while the units are not mutually independent. This also clarifies the intuition expressed in Shannon’s early work that the transmitted signals should approximate white noise to approximate the maximum information rate [Sha48, Section 25.].

In line with the efficient coding hypothesis our account predicts that sensory processing is fine-tuned to the statistics of natural stimuli. In fact, it is the explicit connection to the input distribution that allowed us to test our predictions for the artificial neural network. Given the striking similarity between biological and artificial neural networks
in processing visual inputs we would expect to observe similar effects in the brain after intentional perturbation of the natural image statistics. Experiments like these may further clarify how and if the brain is adapted to natural stimuli during evolution and/or development [DAR96].

**Acknowledgments**

The authors thank Tobias Sterbak for practical advice.

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