
Adaptive compressed sensing – a new class of self-organizing coding models for neuroscience

William K. Coulter

University of California, Berkeley
156 Stanley Hall, MC# 3220
Berkeley, CA 94720-3220
wcoulter@berkeley.edu

Christopher J. Hillar*

Mathematical Sciences Research Institute
17 Gauss Way
Berkeley, CA 94120
chillar@msri.org

Guy Isely

University of California, Berkeley
156 Stanley Hall, MC# 3220
Berkeley, CA 94720-3220
gisely@gmail.com

Friedrich T. Sommer

University of California, Berkeley
156 Stanley Hall, MC# 3220
Berkeley, CA 94720-3220
fsommer@berkeley.edu

Abstract

Sparse coding networks, which utilize unsupervised learning to maximize coding efficiency, have successfully reproduced response properties found in primary visual cortex [1]. However, conventional sparse coding models require that the coding circuit can fully sample the sensory data in a one-to-one fashion, a requirement not supported by experimental data from the thalamo-cortical projection. To relieve these strict wiring requirements, we propose a sparse coding network constructed by introducing synaptic learning in the framework of compressed sensing. We demonstrate that the new model evolves biologically realistic spatially smooth receptive fields despite the fact that the feedforward connectivity subsamples the input and thus the learning has to rely on an impoverished and distorted account of the original visual data. Further, we demonstrate that the model could form a general scheme of cortical communication: it can form meaningful representations in a secondary sensory area, which receives input from the primary sensory area through a “compressing” cortico-cortical projection. Finally, we prove that our model belongs to a new class of sparse coding algorithms in which recurrent connections are essential in forming the spatial receptive fields.

keywords: adaptive coding, biological system modeling, random codes, image coding, nonlinear circuits

1 Introduction

Guided by the early ideas on efficient sensory coding [2, 3], self-organizing network models for sparse coding have been critical in understanding how essential response properties, such as orientation selectivity, are formed in sensory areas through development and experience [1, 4]. There is now a wealth of such models, all based on a set of similar connectivity patterns: a neuron receives feedforward drive from the afferent input and competes with other neurons in the network through mainly inhibitory lateral connections, see [5, 1, 6, 7, 8]. Some of these models are capable of reproducing the response properties in primary visual cortex quantitatively, for instance, the network

*Hillar is supported under an NSA Young Investigators Grant and an MSRI postdoctoral fellowship

model proposed in [6] that implements an algorithm called optimized orthogonal matching pursuit [9].

While these models match physiological data quite impressively, their correspondence to the anatomical connectivity in cortex is problematic. According to the models, the neurons must have access to the full data, for instance, to all pixels of an image patch. Many models even suggest that each neuron has the feedforward wiring in place so that the synaptic structure in the feedforward path can match the receptive field exactly. It is unclear if the development of the thalamic projections into V1 can reach such connection density and microscopic precision – even though thalamic receptive fields do match the receptive fields of monosynaptically connected V1 cells with some precision [10, 11]. Here we explore learning schemes for neural representations that relieve these requirements on the feedforward wiring. In addition, we assess the ability of these learning schemes to account for learning in cortico-cortical projections, for which it has been established that only a fraction of local cells in the origin area send fibers to a target area [12] and therefore conventional sparse coding on the receiver end could not work.

To construct sparse coding networks with less restrictive wiring conditions we build on *compressed sensing* or *compressed sampling*, a method originally developed for data compression by subsampling. The decompression step in these algorithms has a close similarity to sparse coding models and thus these methods can form a framework for developing a new class of neural networks for self-organizing neural representations in cortical areas. Specifically, we explore the hypothesis of a generic scheme of cortical communication in which each cortical area unwraps subsampled input data into a sparse code to perform local computations and then sends a subsampled version of its local representation to other cortical areas.

2 Adaptive compressed sensing

Conventional sparse coding is governed by the following objective function:

$$E(\mathbf{x}, \mathbf{a}, \Psi) = \frac{1}{2} \|\mathbf{x} - \Psi \mathbf{a}\|^2 + S(\mathbf{a}). \quad (1)$$

Here $\mathbf{x} \in \mathbb{R}^m$ is the input data, Ψ is a real $m \times n$ matrix whose columns form a dictionary for constructing the input, and \mathbf{a} is a coefficient vector for this reconstruction: $\tilde{\mathbf{x}} = \Psi \mathbf{a}$. The function $S(\mathbf{a})$ is a sparseness constraint that penalizes neural activity and forces the coefficient vector to be sparse.

For a given input \mathbf{x} , the sparse coding operation is given by an energy minimization

$$\mathbf{a}(\mathbf{x}) := \arg \min_{\mathbf{a}} E(\mathbf{x}, \mathbf{a}, \Psi) \in \mathbb{R}^n. \quad (2)$$

The adaptation of the dictionary to the data is performed by minimizing $E(\mathbf{x}, \mathbf{a}(\mathbf{x}), \Psi)$ from Eq. 1 and Eq. 2 with respect Ψ . Using gradient descent for the adaptation yields a Hebbian synaptic learning rule for the Ψ components [1, 6].

Compressed sensing has been proposed as a technique for data compression using a random projection matrix Φ to compress the data $\mathbf{x} \in \mathbb{R}^m$ to $\Phi \mathbf{x} \in \mathbb{R}^k$ with $k < m$. The decompression uses energy minimization (2) of an error-bases energy function very similar to Eq. 1:

$$E(\mathbf{x}, \mathbf{a}, \Phi) = \frac{1}{2} \|\Phi \mathbf{x} - \Phi \Psi \mathbf{a}\|^2 + S(\mathbf{a}). \quad (3)$$

The original data is reconstructed as $\tilde{\mathbf{x}} = \Psi \mathbf{a}(\Phi \mathbf{x})$. In conventional compressed sensing a fixed dictionary Ψ is chosen. The decompression can be shown to work if (i) a dictionary Ψ is chosen in which the data can be sparsely represented, (ii) the two matrices Φ and Ψ are incoherent and (iii) the dimension of the data compression k is larger than the sparsity of the data [13, 14].

Building on a previous model by Rehn and Sommer [6], we introduce *adaptive compressed sensing (ACS)*, an adaptive version of compressed sensing governed by:

$$\begin{aligned} E(\mathbf{x}, \mathbf{a}, \Phi, \Theta) &= \frac{1}{2} \|\Phi \mathbf{x} - \Theta \mathbf{a}\|^2 + \lambda \|\mathbf{a}\|_{L_0} \\ &= -\mathbf{x}^\top \Phi^\top \Theta \mathbf{a} + \frac{1}{2} \mathbf{a}^\top \Theta^\top \Theta \mathbf{a} + \lambda \|\mathbf{a}\|_{L_0} + \text{const.} \end{aligned} \quad (4)$$

Learning is executed by gradient descent in Θ in exactly the same fashion as in conventional sparse coding, e.g. [1, 6]. Note, however, the difference between ACS and conventional sparse coding. The new algorithm (4) forms a dictionary of the compressed data, the $k \times n$ matrix Θ , whereas conventional sparse coding forms a dictionary of the original data, an $m \times n$ matrix. Although we use here the L_0 -sparseness constraint to penalize the number of active units, $S(\mathbf{a}) = \lambda \|\mathbf{a}\|_{L_0}$, similar schemes of adaptive compressed sensing can be realized with other types of sparseness constraints.

Network implementation of ACS: Analogous to earlier models of sparse coding, the coding in ACS can be implemented in a network in which each neuron i computes the gradient of the two differentiable terms in Eq. 4 as

$$\frac{\partial E'}{\partial a_i} = -(\mathbf{x}^\top \Phi^\top \Theta)_i + (\Theta^\top \Theta \mathbf{a})_i, \quad (5)$$

see [6] for further detail. In the neural network for the ACS method the *feedforward weights* are $FF := \Phi^\top \Theta$ and the competitive *feedback weights* are $FB := -\Theta^\top \Theta$. Note that if Φ is the identity matrix, ACS coincides with conventional sparse coding for which the corresponding neural network would be defined by $FF = \Psi$ and $FB = -FF^\top FF$ [1, 6]. The important difference between the two wiring schemes is that the feedforward weights of ACS subsample and mix the original data. Thus, coding and weight adaptation in ACS are lacking the full access to the original data that is available to conventional sparse coding. Remarkably, the simulation experiments described in the next section demonstrate that the neurons in the ACS network still develop biologically realistic receptive fields, despite the limited exposure to the original data.

3 Simulation experiments with adaptive compressed sensing

The coding networks described in section 2 were compared in their ability to code patches of natural scene images and form receptive fields. The images were preprocessed by “whitening,” as described in [1]. The coding circuits encoded patches of 12×12 pixels, making the dimension of the data $m = 144$. For ACS we used a sampling matrix Φ that downsampled the original data to $k = 60$ dimensions. All our coding circuits contained $n = 432$ neurons, thereby producing representations of the original data $a \in \mathbb{R}^n$ that were three times overcomplete. In addition to image coding in a primary sensory area we also tested whether the ACS model could be used by a secondary sensory area (2nd stage). Our model of the 2nd stage receives a subsampled version of the sparse code generated in the primary visual area $\Phi_2 \mathbf{a}(\mathbf{x}) \in \mathbb{R}^k$ and produces a sparse codes $\mathbf{a}_2 \in \mathbb{R}^n$, again with $k = 60$ and $n = 432$. All models used a coefficient $\lambda = 0.1$ in the sparseness constraint of Eq. 4.

Since the ACS model learns a dictionary of the compressed data rather than the original data, the original image cannot be reconstructed from the adapted Θ matrix. Note that computing the data dictionary from Θ would require an ill-posed step of matrix factorization: $\Theta = \Phi \Psi$. Therefore, to assess the quality of the emerging codes in the ACS model we measured receptive fields in the trained circuit (as physiologists do from the responses of real neurons). We compute the *receptive fields* for a set I of visual stimuli $\mathbf{x} \in \mathbb{R}^m$ as

$$RF := \frac{1}{|I|} \sum_{\mathbf{x} \in I} \mathbf{x} \cdot \mathbf{a}(\mathbf{x})^\top. \quad (6)$$

Notice that RF is an $m \times n$ real matrix, the i -th column representing the receptive field of the i -th neuron.

The following two figures show the feedforward weights and the receptive fields of the different coding circuits. While the feedforward weights and receptive fields in Fig 1 are very similar for sparse coding, they are markedly different for ACS in Fig 2. Interestingly, while subsampling makes the feedforward weights somewhat amorphous and noisy, the resulting receptive fields of ACS are smooth and resemble the receptive fields of sparse coding. When used in a secondary sensory area (2nd stage), ACS forms response properties that are similar to those in the primary sensory area, though the response properties differ on a neuron-by-neuron basis.

To assess the degree to which the sparse codes describe the original input, we computed image reconstructions. For sparse coding we used the basis functions Ψ , for ACS the measured receptive fields RF . Fig 3 demonstrates that the ACS forms representations in the primary and secondary

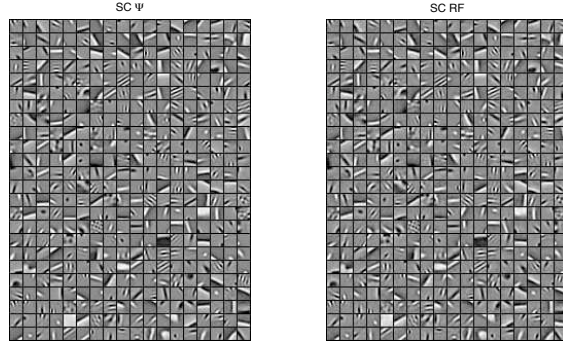


Figure 1: Feedforward weights and receptive fields of sparse coding circuit [6]. The patterns look indistinguishable to the eye and can actually be proven to be the same, see Theorem 1.

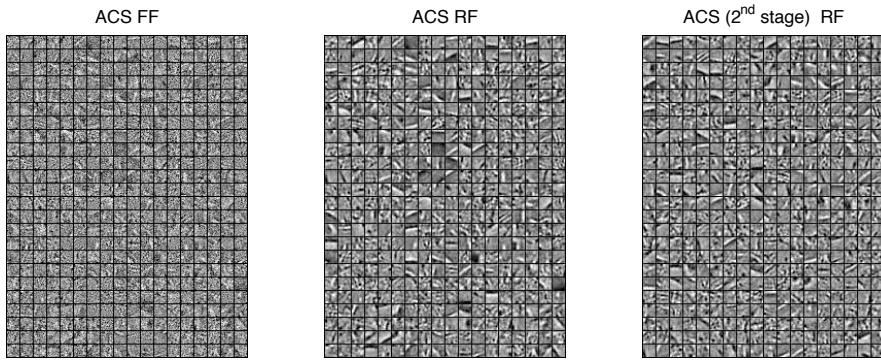


Figure 2: Feedforward weights (ACS FF) and receptive fields (ACS RF) of adaptive compressed sensing circuit. The plot “ACS (2nd stage) RF” depicts receptive fields learned in a cascaded secondary sensory area receiving $\Phi_2 \mathbf{a}(\mathbf{x})$ as the input.

area that can be used for reconstruction, although the quality of the reconstructions obtained from conventional sparse coding is not achieved.

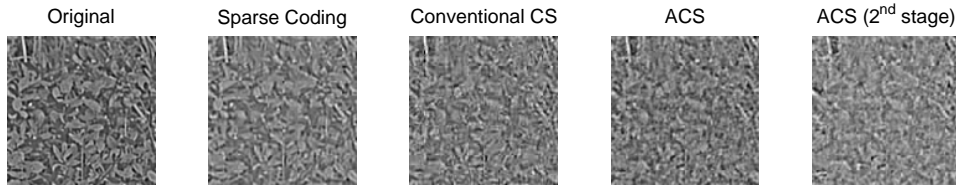


Figure 3: Original image and reconstruction using the different methods on 12 by 12 image patches. For reconstructing the images from the representations formed by ACS (in the first and 2nd stage), we used the receptive fields.

Fig 4 compares the reconstruction quality of conventional compressed sensing (using the basis functions that were adapted to the original data) and adaptive compressed sensing. The mean reconstruction qualities do not differ, though ACS performs with lower variance over the set of input patches we tested.

These simulation results suggest that ACS is able to form representations of sensory data that convey its essential structure although the coding network receives only a subsampled version of the data. In the following section we try to understand the mathematical differences between conventional sparse coding and adaptive compressed sensing.

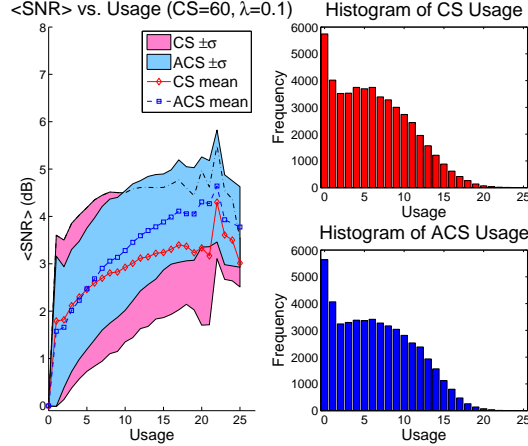


Figure 4: Left: Signal-to-noise ratio (mean and range of standard deviation) in reconstructions with conventional compressed sensing (red) and with ACS (blue). The means do not differ significantly, but the performance of ACS has smaller variance. Right: The histograms of the number of used neurons per reconstruction are very similar for both methods.

4 Differences between ACS and conventional sparse coding models

In this section we derive two theorems to establish that ACS defines a class of sparse coding algorithms whose properties differ qualitatively from those of conventional sparse coding models.

4.1 Receptive fields and feedforward weights coincide in conventional sparse coding networks

Assuming that \mathbf{x} is a column vector of random variables on a measure space Ω with probability measure μ , the matrix RF will be an approximation to the correlation of \mathbf{x} and $\mathbf{a}(\mathbf{x})$:¹

$$\text{Cor}(\mathbf{x}, \mathbf{a}) = \int \mathbf{x}\mathbf{a}(\mathbf{x})^\top d\mu.$$

The strong law of large numbers guarantees that given enough samples, the matrix RF will be close to the integral above. Moreover, inequalities such as Hoeffding's give analytic estimates making more precise this relationship. For these reasons (and expositional clarity), we shall make the assumption that $RF = \text{Cor}(\mathbf{x}, \mathbf{a})$. We are interested in calculating the necessary relationships between the quantities RF , FF , FB , Φ , and Θ . (Recall that $FF = \Phi^\top \Theta$ and $FB = -\Theta^\top \Theta$.)

In our setup, the data \mathbf{x} are assumed to come from a sparse number k of independent causes (nonzero values in \mathbf{a}). Moreover, the method of recovering $\mathbf{a}(\mathbf{x})$ from a particular \mathbf{x} is assumed to be exact (or near exact) in solving Eq. 2 and *independently distributed*; that is, $\Phi\mathbf{x} = \Theta\mathbf{a}(\mathbf{x})$ and we have:

$$D = \int \mathbf{a}(\mathbf{x})\mathbf{a}(\mathbf{x})^\top d\mu,$$

in which D is an $n \times n$ diagonal matrix. With these assumptions, one calculates:

$$\Phi RF = \int \Phi\mathbf{x}\mathbf{a}(\mathbf{x})^\top d\mu = \Theta \int \mathbf{a}(\mathbf{x})\mathbf{a}(\mathbf{x})^\top d\mu = \Theta D. \quad (7)$$

In particular, this implies the following.

Theorem 1 *If Φ is the identity, then the receptive fields are scalar multiples of the feedforward weights.*

¹For our purposes, we shall assume that $\mathbf{a}(\mathbf{x})$ in fact forms a vector of random variables; that is, it is a vector of *measurable functions* on Ω . Moreover, we shall assume that $\mathbf{a}(\mathbf{x})$ has zero mean.

We remark that one can easily check the scalar multiple condition by way of a quadratic optimization problem in n real variables. For expositional simplicity, however, we shall assume that $D = cI$ is a scalar multiple of the identity matrix I so that this optimization is over one variable. Given two matrices \mathbf{A} and \mathbf{B} of the same size (with $\mathbf{B} \neq \mathbf{0}$), we have

$$\arg \min_t \|\mathbf{A} - t\mathbf{B}\| = \frac{\text{tr}(\mathbf{A}^\top \mathbf{B})}{\|\mathbf{B}\|^2}, \quad \min_t \|\mathbf{A} - t\mathbf{B}\| = \left\| \mathbf{A} - \frac{\text{tr}(\mathbf{A}^\top \mathbf{B})}{\|\mathbf{B}\|^2} \mathbf{B} \right\|. \quad (8)$$

Thus, a measure of whether \mathbf{A} is a scalar multiple of \mathbf{B} is given by the right-most quantity in (8).

4.2 In the ACS model receptive fields are co-shaped by feedback

In the compressive sensing regime, the matrix Φ is no longer the identity but instead a compressive sampling matrix. In this case, the receptive fields are almost never scalar multiples of the feedforward weights. A precise analytic relationship is given by the following theorem. As an important consequence, we shall obtain the qualitative interpretation found in Theorem 4 below. One may skip the technical argument without sacrificing much intuition.

Theorem 2 *Suppose that FF , Φ , and Θ are all nonzero and that $\Theta\Theta^\top$ is invertible. Then the following inequality holds:*

$$\min_t \|RF - tFF\| \geq \frac{|\text{tr}(RF^\top FF)|}{\|FF\|^2 \cdot \|\Phi\| \cdot \|\Theta^\top(\Theta\Theta^\top)^{-1}\|} \cdot \min_t \|tI - \Phi\Phi^\top\|.$$

Proof: Set $l = \arg \min_t \|RF - tFF\| = \frac{\text{tr}(RF^\top FF)}{\|FF\|^2}$ and let $\mathbf{M} = RF - lFF$. Then, we have that

$$\begin{aligned} \min_t \|tI - \Phi\Phi^\top\| &\leq \|cI/l - \Phi\Phi^\top\| \\ &= \|\Phi\mathbf{M}\Theta^\top(\Theta\Theta^\top)^{-1}\|/|l| \\ &\leq \|\Phi\| \cdot \|\Theta^\top(\Theta\Theta^\top)^{-1}\| \cdot \min_t \|RF - tFF\|/|l|. \end{aligned} \quad (9)$$

Here, the second line follows from (7) with $D = cI$ and the following matrix identity:

$$cI - l\Phi\Phi^\top = \Phi\mathbf{M}\Theta^\top(\Theta\Theta^\top)^{-1}.$$

Rearranging (9) gives us the inequality stated in the theorem. \square

What is important here is not the technical statement of Theorem 2, but rather the following qualitative version of the result.

Corollary 1 *If $\Phi\Phi^\top$ is not (close to) a scalar multiple of the identity, then RF is not (close to) a scalar multiple of FF .*

In fact, we can do somewhat better than this.

Theorem 3 *If the feedback weights are not a scalar multiple of $FF^\top FF$, then the receptive fields are not a scalar multiple of the feedforward weights.*

Proof: We shall verify the contrapositive. Suppose that RF is a scalar multiple of FF ; then we must show that FB is a scalar multiple of $FF^\top FF$. By Theorem 2, the assumption implies that $\Phi\Phi^\top$ is a scalar multiple of the identity. In particular, we have

$$FF^\top FF = \Theta^\top \Phi\Phi^\top \Theta = t\Theta^\top \Theta,$$

for some scalar t , which proves the claim. \square

Finally, we remark that in the compressive sensing regime $k \ll n$ and Φ is a random matrix; thus, the hypothesis of the previous corollary will be satisfied generically:

Theorem 4 *In the adaptive compressed sensing regime, the receptive fields are almost surely not scalar multiples of the feedforward weights.*

5 Discussion and Conclusions

Here we have proposed *adaptive compressed sensing (ACS)*, a new scheme of learning under compressed sensing that forms a dictionary adapted to represent the compressed data optimally. The coding and learning scheme of ACS can be formulated as a neural network, building on an earlier model of sparse coding [6]. Our model employs learning in the weights of the coding circuit and keeps the random projection fixed, as opposed to a previous suggestion using learning in the random projection to optimize the compression performance [16].

Our study focuses on the application of the proposed learning scheme to understand how cortical regions in ascending sensory pathways can analyze and represent signals they receive through thalamo-cortical or cortico-cortical connections. Conventional sparse coding theories were successful in reproducing physiological responses in primary sensory regions but they require exact matches between feedforward connections and receptive field patterns of cortical neurons (see Theorem 1 and Fig 1 for an example). Although it has been shown that thalamocortical wiring is to some extent specific [10, 11], exact matches between feedforward circuitry and receptive fields are not supported by experimental data. In addition, a recent quantitative study of cortico-cortical projections suggests that the number of fibers reaching a target area can only be a fraction of the local neurons in the area of origin [12].

We have tested whether or not the ACS network could serve as a computational model for how cortical areas can form a representation of data received through afferent projections that sample the activity pattern in the previous stage only incompletely and not in a one-to-one fashion. Our simulation experiments demonstrate that ACS can form representation of visual data, though, unlike in conventional sparse coding models, the coding circuit receives only a subsampled version of the original data. Further, we have demonstrated that the algorithm is stackable in a hierarchy. The sparse code formed by ACS in a primary sensory area, when sent through another compressing projection can be decoded in a secondary sensory area into another meaningful visual representation. The shown simulation experiment is not a realistic model for the V1-V2 cascade in the visual stream since it omits the internal nonlinear operations in the primary region, such as the transformation from simple cell to complex cells, or operations based on pattern similarity [17, 18]. The simulation results are rather a proof of concept showing how the ACS model can serve as a generic building block explaining what information is computed and sent between cortical areas. The scheme consists of repeated cycles of compression and expansion into high-dimensional sparse codes. That is, a sparse local representations is compressed, sent through cortico-cortical projections and expanded to sparse local representations again. A communication scheme using compression expansion cycles is reminiscent of Braitenberg's picture of the pump of thought [19] and it can potentially reconcile the debate over whether representations in the brain are sparse [20, 21] or dense [22, 23] since the type of code could be lamina-specific.

In addition, we mathematically characterized the differences between the ACS model and conventional sparse coding models. Theorem 1 proves that, in conventional sparse coding models, the feedforward weights resemble the receptive fields of the neurons very closely. Theorem 4 proves that ACS belongs to a class of sparse coding networks in which the receptive fields are dissimilar from the feedforward weights. Thus, we conclude that ACS belongs to a new class of competitive circuits derived from efficient sparse coding in which the recurrent weights are important for shaping the spatial receptive fields when learning on subsampled data. Regarding the still debated role of recurrent circuitry in producing orientation selectivity (e.g., [24, 25, 26]), the ACS model suggests that if the input subsamples the data then feedback in shaping the receptive fields becomes essential for coding efficiency.

References

- [1] B. A. Olshausen and D. J. Field. Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, 381:607–608, 1996.
- [2] F. Attneave. Some informational aspects of visual perception. *Psychological Review*, 61:183 – 193, 1954.
- [3] H. B. Barlow. *Understanding natural vision*. Springer-Verlag, Berlin, 1983.
- [4] Anthony J. Bell and Terrence J. Sejnowski. The independent components of natural images are edge filters. *Vision Research*, 37:3327–3338, 1997.

- [5] P. Földiák. Forming sparse representations by local anti-Hebbian learning. *Biological Cybernetics*, 64:165–170, 1990.
- [6] M. Rehn and F. T. Sommer. A network that uses few active neurones to code visual input predicts the diverse shapes of cortical receptive fields. *Journal of Computational Neuroscience*, 22:135–146, 2007.
- [7] C. J. Rozell, D. H. Johnson, R. G. Baraniuk, and B. A. Olshausen. Sparse coding via thresholding and local competition in neural circuits. *Neural Computation*, 20:2526–2563, 2008.
- [8] W. Yin, S. Osher, D. Goldfarb, and J. Darbon. Bregman iterative algorithms for l_1 -minimization with applications to compressed sensing. *SIAM J. Imaging Sciences*, 1(1):143 – 168, 2008.
- [9] L. Rebollo-Neira and D. Lowe. Optimised orthogonal matching pursuit approach. *IEEE Signal Processing Letters*, 9:137–140, 2002.
- [10] B. Chapman, K. R. Zahs, and M. P. Stryker. Relation of cortical cell orientation selectivity to alignment of receptive fields of the geniculocortical afferents that arborize within a single orientation column in ferret visual cortex. *J. of Neuroscience*, 11(5):1347–1358, 1991.
- [11] C. R. Reid and J.-M. Alonso. Specificity of monosynaptic connections from thalamus to visual cortex. *Nature*, 378:281–284, 1995.
- [12] A. Schüz, D. Chaimow, D. Liewald, and M. Dortemann. Quantitative aspects of corticocortical connections: a tracer study in the mouse. *Cerebral Cortex*, 16:1474–1486, 2006.
- [13] E. Candes, J. Romberg, and T. Tao. Stable signal recovery from incomplete and inaccurate measurements. *Communications on Pure and Applied Mathematics*, 58(8):1207–1223, 2006.
- [14] E. Candes and M. Wakin. An introduction to compressed sampling. *IEEE Signal Processing Magazine*, 25(2):21–30, 2008.
- [15] R. Horn and C.R. Johnson. *Topics in matrix analysis*. Cambridge University Press, Cambridge, UK, 1994.
- [16] Y. Weiss, H. S. Chan, and W. T. Freeman. Learning compressed sensing. *Allerton Conference Proceedings*, <http://www.cs.huji.ac.il/~weiss:1> – 9, 2007.
- [17] G. Palm. *Neural Assemblies*. Springer, Berlin, 1982.
- [18] A. Lansner. Associative memory models: from the cell-assembly theory to biophysically detailed cortex simulations. *Trends in Neurosciences*, 32(3):178–186, 2009.
- [19] V. Braitenberg. Cell assemblies in the cerebral cortex. In R. Heim and G. Palm, editors, *Theoretical Approaches to Complex Systems*. Springer, 1977.
- [20] M. R. DeWeese and A. M. Zador. Non-gaussian membrane potential dynamics imply sparse, synchronous activity in auditory cortex. *J. Neuroscience*, 26(47):12206 – 12218, 2006.
- [21] T. Hromadka, M. R. Deweese, and A. M. Zador. Sparse representation of sounds in the unanesthetized auditory cortex. *PLoS Biol.*, 6(1):16–24, 2008.
- [22] M.N. Shadlen and W.T. Newsome. Noise, neural codes and cortical organization. *Current Opinion in Neurobiology*, 4:569–579, 1994.
- [23] M.N. Shadlen and W.T. Newsome. Is there a signal in the noise? [comment]. *Current Opinion in Neurobiology*, 5:248–250, 1995.
- [24] D. H. Hubel and T. N. Wiesel. Receptive fields, binocular interaction and functional architecture in the cat’s visual cortex. *J. Physiol.*, 160:106–154, 1962.
- [25] J. A. Hirsch, J.-M. Alonso, R. C. Reid, and L. M. Martinez. Synaptic integration in striate cortical simple cells. *Journal of Neuroscience*, 18:9517 – 9528, 1998.
- [26] D. Ferster and K. D. Miller. Neural mechanisms of orientation selectivity in the visual cortex. *Annual Review of Neuroscience*, 23:441–471, 2000.