No evidence for active sparsification in the visual cortex

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Sparse coding

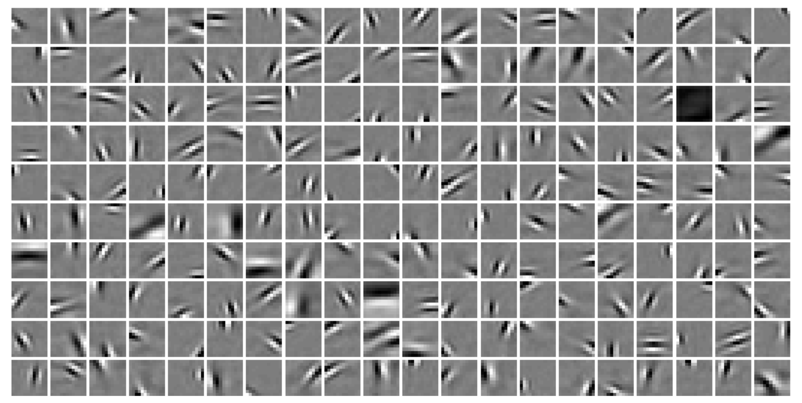
It is widely believed that one of the main principles underlying functional organization of the early visual system is the reduction of the redundancy of relayed input from the retina. Sparse coding refers to a possible implementation of this general principle, whereby each stimulus is encoded by a small subset of neurons.

Advantages of sparse representations

Low metabolic cost	Lifetime sparseness
Improved signal to noise ratio	Lifetime/population sparseness
Reduce dependencies	Population sparseness
Easier detection of co-activation patterns	Population sparseness
Improved storage capacity in associative memories	Population sparseness

Sparseness and simple cell RFs

Sparse coding models reproduce main characteristics of simple cells RFs (Olshausen & Field, 1996, 1997 ; Bell & Sejnowski, 1997; van Hateren and van der Schaaf, 1998) Reproduce changes due to manipulation of visual environment (Hsu & Dayan, 2007)



Experimental evidence

Several experimental studies report high sparseness in V1:

Weliky et al., 2003
Tolhurst et al., 2009

Baddeley et al., 1997
Yen et al, 2007

Baddeley et al., 1997
Vinje and Gallant, 2000, 2002
Lehky et al., 2005

1. Is high sparseness due to optimal sparse representation or just neural selectivity? (Lehky et al., 2005) Need *relative* measurement of sparseness.
2. Most of these studies are on *anesthetized* animals

Sparseness measures

Population sparseness measures are normalized to discard the effect of global firing rate changes. Alternative sparseness measures are highly correlated.

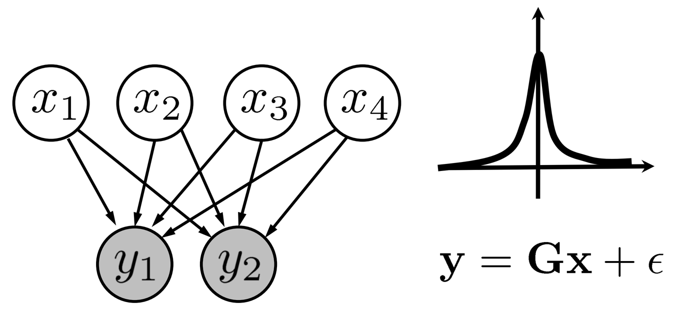
$$\mathrm{TR} = \left[1 - \frac{\left(\sum_{i=1}^{N} |r_i|/N\right)^2}{\sum_{i=1}^{N} r_i^2/N}\right] \Big/ (1 - 1/N)$$

- Lifetime sparseness: sum over time
- Population sparseness: sum over neurons
- Invariant to additive changes in firing rate
- Neural responses normalized by standard deviation for population sparseness

$$\mathrm{AS} = 1 - n_t/N$$

- Population sparseness: n_t is the number of neurons above threshold (1 standard deviation)
- Invariant to additive and multiplicative changes

The sparse coding model



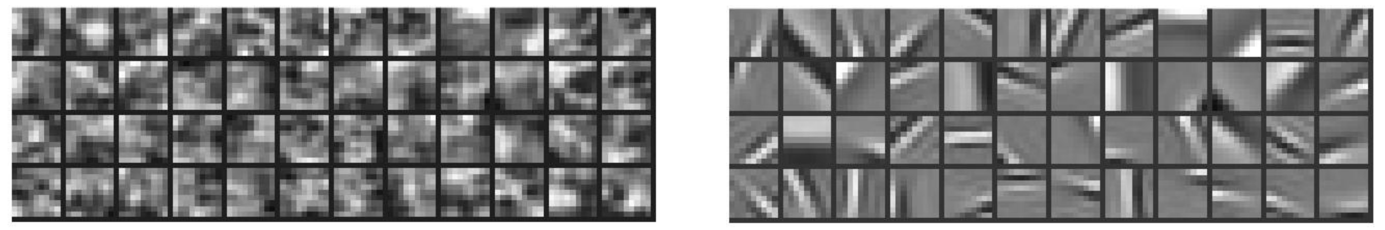
$$\mathbf{y} = \mathbf{G}\mathbf{x} + \epsilon$$

Prior: iid, sparse distribution (Student-t)

$$p(x_k) = \frac{1}{Z}\left(1 + \frac{1}{\alpha}\left(\frac{x_k}{\lambda}\right)^2\right)^{-\frac{\alpha+1}{2}}$$

(Olshausen & Field, 1996)

Sparse coding model was applied to 9x9 pixel natural image patches, reduced to 36 dimensions by PCA. Generative weights learned by VBEM for 1500 iterations, 3600 new patches at each iteration. Model parameters: K=48 (slightly overcomplete), alpha=2.5 (very sparse).



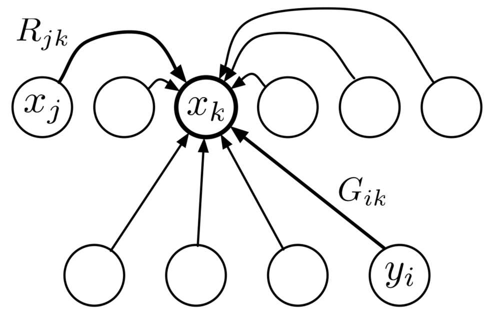
Sampling, sparse coding neural network

Assuming that neural activity represents Gibbs samples from posterior distribution:

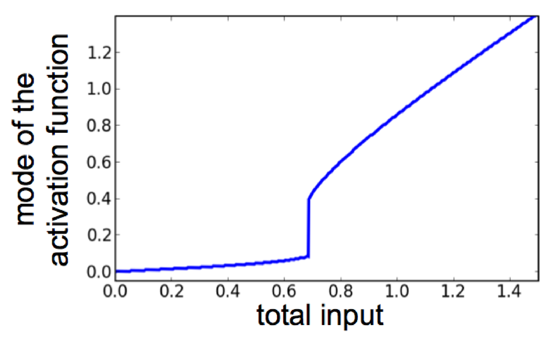
$$p(x_k | x_{i \neq k}, \mathbf{y}) \propto \exp\left(\frac{1}{\sigma_y^2}\left(\sum_i G_{ik} y_i\right) x_k + \frac{1}{\sigma_y^2}\left(\sum_{j \neq k} R_{jk} x_j\right) x_k - \frac{1}{2\sigma_y^2} x_k^2 + f(x_k)\right)$$

with $\mathbf{R} = -\mathbf{G}^T\mathbf{G}$

This expression can be translated in a simple, one-layer neural network with feed-forward and recurrent connections:



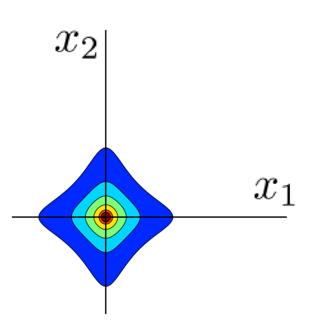
Neural activation function



Sparse coding requires active sparsification process

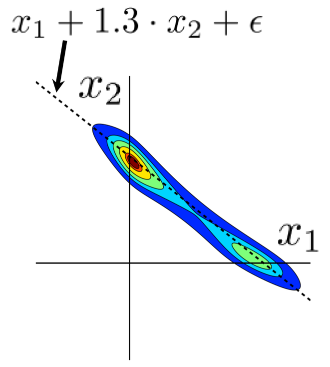
Simple example with one input component modeled by two sparse variables: $y = x_1 + 1.3 \cdot x_2 + \epsilon$

Prior



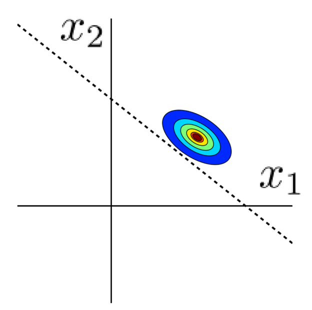
Posterior for y=2

$2 = x_1 + 1.3 \cdot x_2 + \epsilon$



Posterior for y=2

with recurrent connections reduced by half



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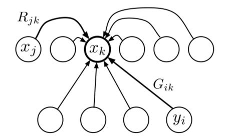
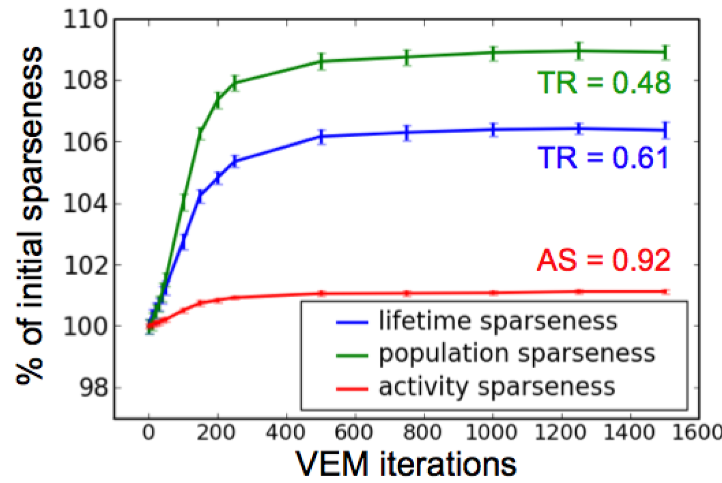
Sparseness over learning

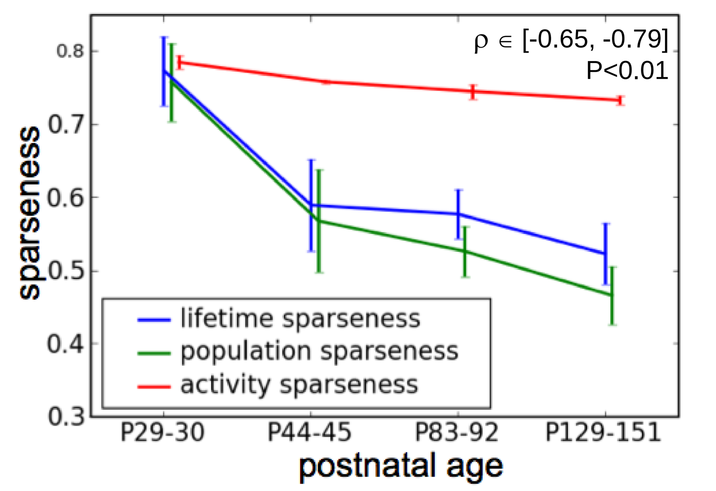


Lifetime and population sparseness **increase** monotonically with learning



Test set of 1800 natural image patches. 50 samples collected using Gibbs sampling and an annealing scheme.

Lifetime and population sparseness **decrease** with visual experience



15 awake ferrets at various stages of development, from eye opening (P29) to adulthood

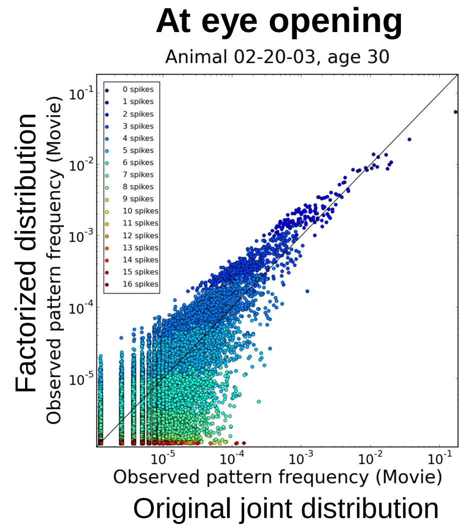
Multi-unit recordings from linear array of 16 electrodes, implanted in V1. Neural activity was collected in 10ms bins.

Stimuli were movie scenes, 15 sessions of 100 seconds each (25 min total).

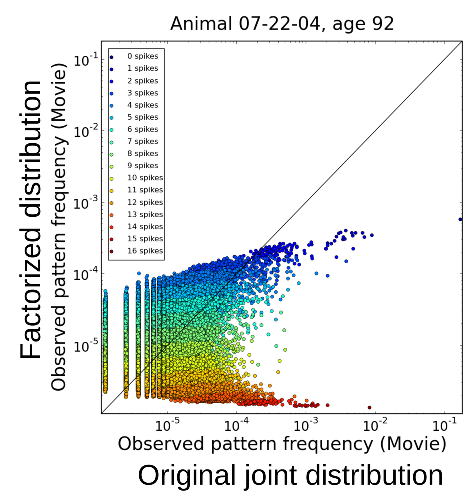
Decrease in sparseness seems to be due to increase in dependencies between neurons: compare joint distribution of neural activity in 2ms bins with factorized distribution

$$\tilde{P}(x_1, \ldots, x_N) = P(x_1) \cdot \ldots \cdot P(x_N)$$

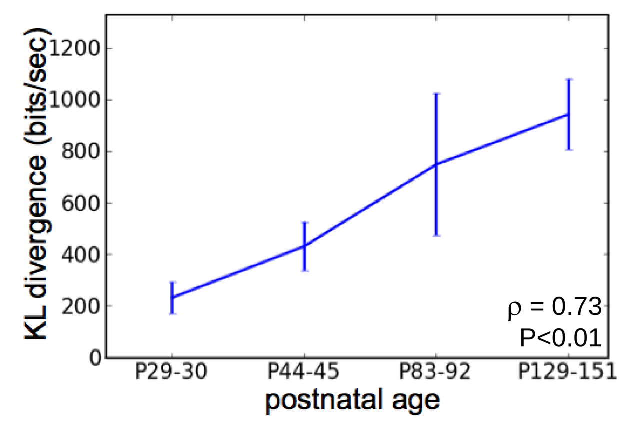
At eye opening



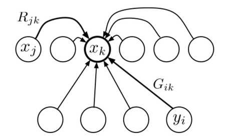
Adult animal



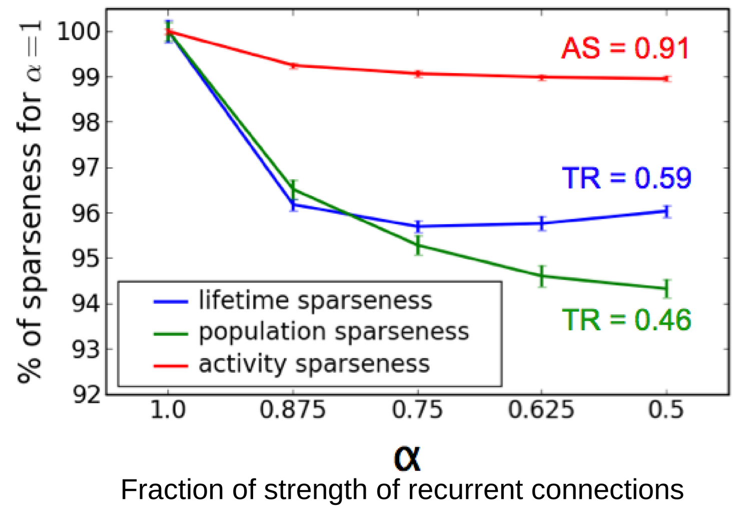
$\mathrm{KL}(\tilde{P}||P)$



Active sparsification and anesthesia

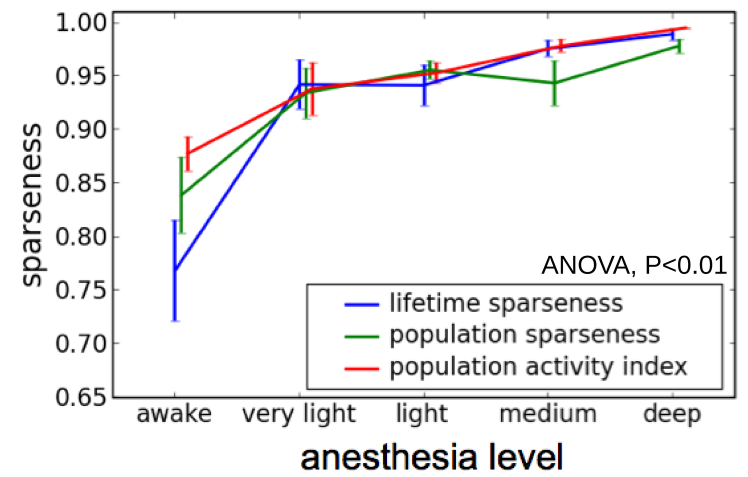


Lifetime and population sparseness **decrease** when lateral connections are weakened



Optimal sparseness requires a process of active sparsification mediated by recurrent connections

Lifetime and population sparseness **increase** with deeper anesthesia



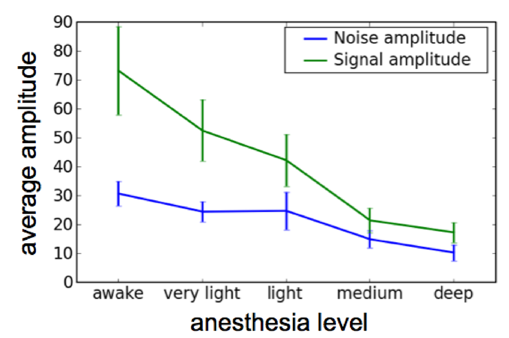
3 adult Long-Evans rats, 5-11 units per session (total 39 units)

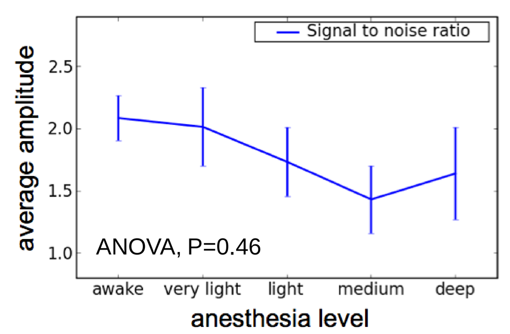
Multi-unit recordings from bundle of 16 electrodes, implanted in V1. Recorded in awake animals and under different levels of isoflurane anesthesia (0.6-2.0%). Neural activity collected in 25ms bins.

Stimulus was a 2 min movie from a camera mounted on a person walking in a forest.

Increase in sparseness is unlikely to be due to loss of feed-forward information:

- Feed-forward RF properties of neuron in V1 do not change significantly with anesthesia (Schiller et al., 1976; Snodderly & Gur, 1995; Lamme et al., 1998)
- Light levels of isoflurane affect mainly cortico-cortical connections (Detsch et al., 1999; Hentschke et al., 2005)
- Signal-to-noise ratio of responses to periodic flashing stimulus does not change significantly with anesthesia:





Conclusions

Neural data shows trends of lifetime and population sparseness over development and under anesthesia that are opposite to those predicted by the sparse coding hypothesis, suggesting that the sparse responses of visual neurons are not due to an active sparsification process.

However, the results are consistent with a generalization of efficient coding as learning in a hierarchical, probabilistic model of visual input.