Is V1 actively sparsifying visual input?

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Introduction to sparse coding

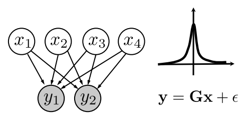
It is widely believed that one of the main principles underlying functional organization of the early visual system is the reduction of the redundancy of relayed input from the retina. Sparse coding refers to a possible implementation of this general principle, whereby each stimulus is encoded by a small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

Advantages of a sparse representation:
- low metabolic cost
- improved signal to noise ratio
- reduced dependencies and thus increased mutual information w. input
- easier detection of co-activation patterns
- improved storage capacity in associative memories

} lifetime sparseness

} population sparseness

Sparse coding model reproduce simple cell RFs



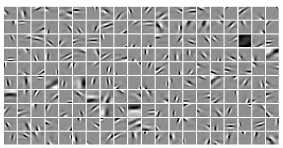
$\mathbf{y} = \mathbf{G}\mathbf{x} + \epsilon$

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



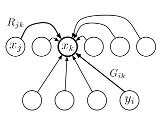
Sampling-based, sparse coding neural network

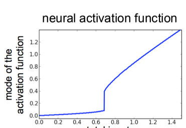
Assuming that neural activity represents Gibbs samples from posterior distribution:

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

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 (cf. Dayan and Abbott, 2001; Hoyer and Hyvarinen, 2003; Rozell *et al.*, 2008):





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/population sparseness: sum over time/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

Experimental evidence for sparseness in visual cortex

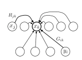
Animal	Reference	Awake	Lifetime	Population
	Tolhurst et al., J Neurosci, 2009	✗	✔	✗
	Yen et al., Neurophysiol, 2007	✗	✔	✔
	Lehky et al., Vision Res, 2005	✗	✔	✗
	Weliky et al., Neuron, 2003	✗	✔	✔
	Vinje and Gallant, J Neurosci, 2002	✔	✔	✗
	Vinje and Gallant, Science, 2000	✔	✔	✗
	Baddeley, Proc R Soc London B, 1997	✗ ✔	✔	✗
	this poster	✔ + 3 levels of anesthesia	✔	✔

Outstanding issues

1. Sparseness measurements under *anesthesia* are not representative of values in awake condition
2. Efficient coding ideas are related to *population sparseness*, yet this has not been measured in the awake condition.
3. Is high sparseness due to optimal sparse representation or just neural selectivity? (Lehky et al., 2005)
   We need a *relative* measurement of sparseness

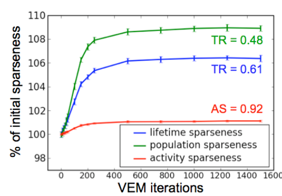
Sparseness decreases over development

Sparse coding model



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

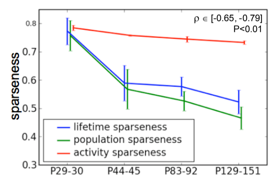
Test set of 1800 natural image patches. 50 samples collected using Gibbs sampling and an annealing scheme



Neural data

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

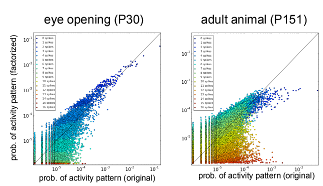
15 awake ferrets at various stages of development, from eye opening (P29) to adulthood. Multi-unit recordings from linear array of 16 electrodes, implanted in V1. Neural activity was collected in 10ms bins. Stimuli were movie scenes, 15 sessions of 100 seconds each (25 min total)

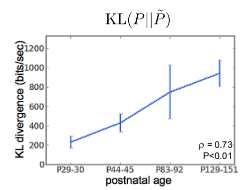


Sparseness decreases over development, in contrast to trend predicted by sparse coding models.

Control distribution:

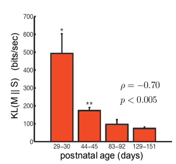
$$\tilde{P}(x_1, \ldots, x_N) = P(x_1) \cdot \ldots \cdot P(x_N)$$



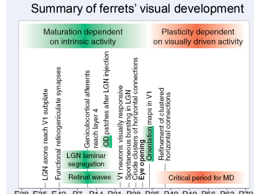


Decrease in sparseness seems to be due to increase in dependencies between neurons.

Could hyperparameters optimization explain a decrease in sparseness?
1. We can exclude a strategy like noise annealing, which would make the units sample from the prior
2. Setting the hyperparameters to a strong prior seems to be a counterproductive strategy, as it would distort the representation at the onset of learning
3. Would not explain the anesthesia results



Summary of ferrets' visual development



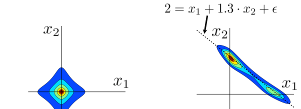
(Sengpiel and Kind, 2002)

Active sparsification requires competition between units

Sparse coding requires an *active sparsification process* mediated by recurrent connections.

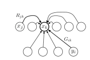
Smple example with one input component modeled by two sparse variables:

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

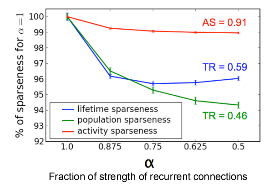


Sparseness increases with anesthesia

Sparse coding model



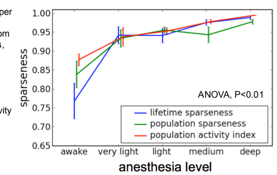
Sparseness **decreases** when lateral connections are weakened



Neural data

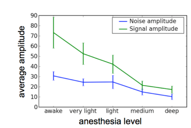
Lifetime and population sparseness **increase** with deeper anesthesia

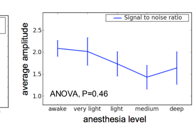
3 adult rats, 5-11 units per session (total 39 units). Multi-unit recordings from bundle of 16 electrodes, implanted in V1. Recorded in awake animals and under different levels of isoflurane anesthesia (0.6-2.0%). Neural activity collected in 25ms bins. stimulus was a 2 min movie from a camera mounted on a person walking in a forest.



Sparseness increases with development, in contrast to the trend predicted by sparse coding models.

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

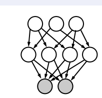




Conclusions

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 still consistent with a generalization of efficient coding as learning in a hierarchical, probabilistic model of visual input.



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