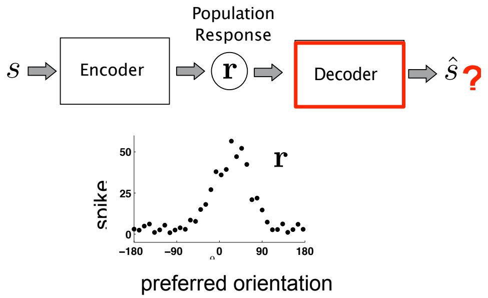
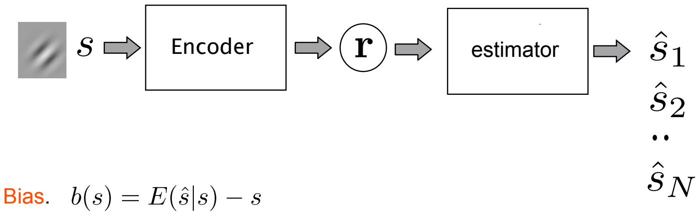
Decoding: Summary of previous slides

- Decoding: for neuro-prostheses and/or for understanding the relationship between the brain's activity and perception or action
- Different strategies are possible: optimal decoders (e.g. ML, MAP) vs simple decoders (e.g. winner take all, population vector), depending on what we know about the encoding model, and constraints.
- Promising applications, Brain Machine interfaces (BMI), fMRI analysis.



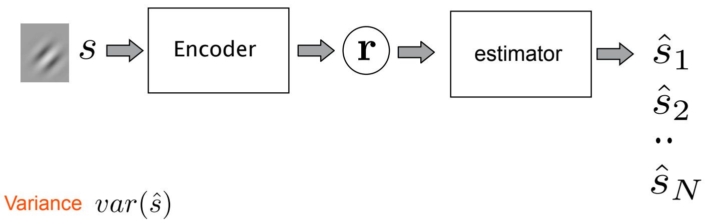
Measuring the performances of our model estimator (Estimation theory 101)



- 1) Bias. $b(s) = E(\hat{s}|s) - s$

  If $E(\hat{s}|s) = s$ the estimator is said to be unbiased.

Measuring the Performances of our model estimator (Estimation theory 101)



- 2) Variance $var(\hat{s})$

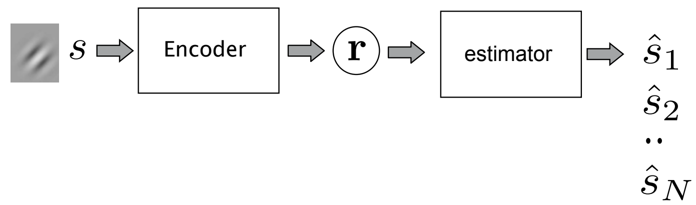
  If var = as small as possible, the (unbiased) estimator is said to be efficient

  The smallest possible variance is given by the Cramér-Rao Bound.
  The denominator is known as Fisher Information, a function of P[r|s].

$$var(\hat{s}) \geq \frac{(1+b'(s))^2}{I_F(s)}$$

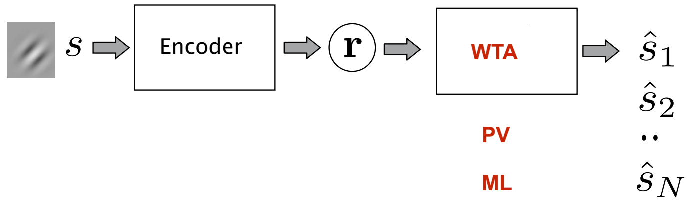
where $I_F(s) = - \left\langle \frac{\partial^2 \ln P[r|s]}{\partial s^2} \right\rangle$

Measuring the Performances of our model estimator (Estimation theory 101)



- As a consequence, the best possible estimator:
  - is unbiased,
  - has a variance defined by (the inverse of) Fisher Information.

Comparing different decoding schemes? (cf. assignment)



- We can use modelling to explore theoretically the different methods for decoding from populations of neurons:
  - Bias?
  - Variance?
  - are they optimal ? How does the variance compare to 1/ I_Fisher?

Fisher information: the best possible discrimination performance for a given encoder model

∗ Fisher information: gives the discrimination threshold that would be obtained (asymptotically) by an optimal decoder, for eg. ML (units of var ^-1)

∗Interpreted as a measure of 'information' in the neurons, in the responses for a given stimulus;

∗ is expressed in terms of the encoding model P[**r**|s], i.e. in terms of the tuning curves and the noise

$$I_F(s) = - < \frac{\partial^2 \ln P[r|s]}{\partial s^2} >$$

∗ is related with Mutual information and Stimulus Specific Information (Brunel and Nadal 1998, Yarrow, Challis and Series 2012).

Fisher Information in a population of neurons with Poisson noise

$$I_F(s) = - < \frac{\partial^2 \ln P[r|s]}{\partial s^2} >$$

with $P(\mathrm{r} = k|s) = \frac{e^{-f(s)} f(s)^k}{k!}$

∗ For Poisson noise, depends on:
- the slope of the tuning curve for that s
- and amplitude of the response

$$I_i(s) = \frac{f_i'(s)^2}{f_i(s)}$$

$\frac{\text{Slope}^2}{\text{variance= mean}}$

$$I(s) = \sum_i \frac{f_i'(s)^2}{f_i(s)}$$

For independent neurons, FI of the population is the sum of each neurons' FI

- it will thus also depend on the number of neurons active for that stimulus.

Fisher Information in a population of neurons with Gaussian noise

- For Gaussian uncorrelated noise, similarly:

$$I(s) = \sum_i \frac{f_i'(s)^2}{\sigma_i^2(s)}$$

$\frac{\text{Slope}^2}{\text{variance}}$

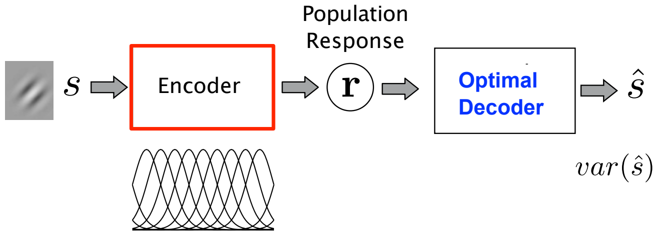
- For Gaussian correlated noise:

$$P[\mathbf{r}|s] = \frac{1}{\sqrt{(2\pi)^N |\mathbf{Q}(\mathbf{s})|}} e^{-\frac{1}{2}(\mathbf{r}-\mathbf{f}(\mathbf{s}))^{\mathbf{T}}\mathbf{Q}^{-1}(\mathbf{s})(\mathbf{r}-\mathbf{f}(\mathbf{s})))}$$

$$I_F(s) = \mathbf{f}'(\mathbf{s})\mathbf{Q}^{-1}(\mathbf{s})\mathbf{f}'(\mathbf{s}) + \frac{1}{2}\mathrm{Trace}[\mathbf{Q}^{-1}(\mathbf{s})\mathbf{Q}'(\mathbf{s})\mathbf{Q}^{-1}(\mathbf{s})\mathbf{Q}'(\mathbf{s})]$$

For correlated neurons, FI is modulated by correlations.

Understanding the influence of the population response properties: what limits performance?



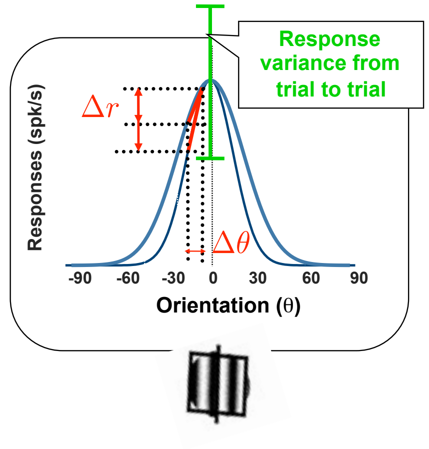
$$var(\hat{s}) \simeq \frac{1}{I_F(s)}$$

$$\mathrm{thres}(\hat{s}) \simeq \frac{1}{\sqrt{I_F(s)}}$$

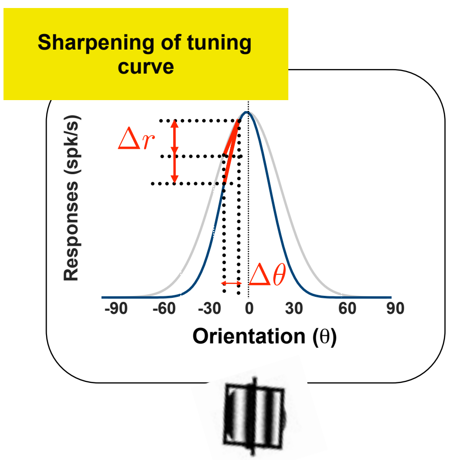
Questions that we can explore:
What changes in encoder would increase discrimination performances?

- Number of neurons?
- Tuning curves shape ?
- Noise correlations ?

What are the factors that control performance?



What are the factors that control performance?



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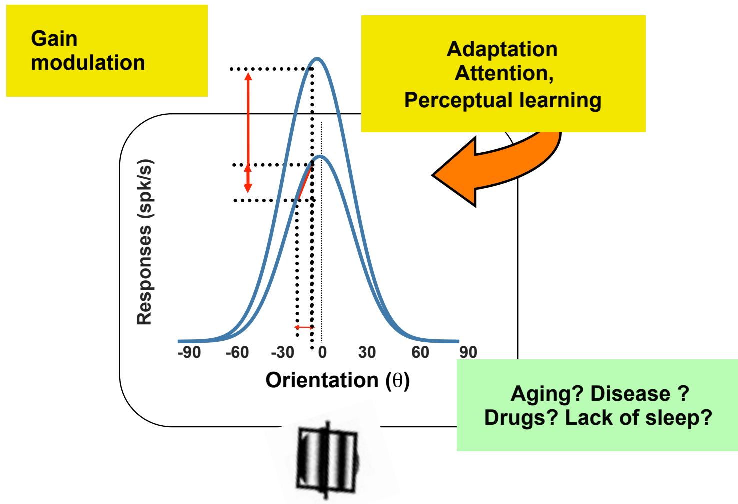


Fisher Information in a population of neurons

- **Fisher information formalises those intuitions, and leads to quantitative predictions.**

- For Gaussian uncorrelated noise:

$$I(s) = \sum_i \frac{f_i'(s)^2}{\sigma_i^2(s)}$$

$$\frac{\textbf{Slope}^{\,2}}{\textbf{variance}}$$

- For Gaussian correlated noise:

$$P[\mathbf{r}|s] = \frac{1}{\sqrt{(2\pi)^N |\mathbf{Q}(\mathbf{s})|}} e^{-\frac{1}{2}(\mathbf{r}-\mathbf{f}(\mathbf{s}))^{\mathbf{T}}\mathbf{Q}^{-1}(\mathbf{s})(\mathbf{r}-\mathbf{f}(\mathbf{s})))}$$

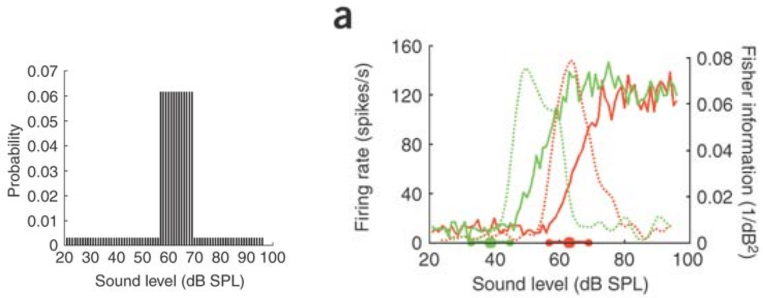
$$I_F(s) = \mathbf{f}'(\mathbf{s})\mathbf{Q}^{-1}(\mathbf{s})\mathbf{f}'(\mathbf{s}) + \frac{1}{2}\mathrm{Trace}[\mathbf{Q}^{-1}(\mathbf{s})\mathbf{Q}'(\mathbf{s})\mathbf{Q}^{-1}(\mathbf{s})\mathbf{Q}'(\mathbf{s})]$$

For correlated neurons, FI is modulated by correlations.

Research questions (1)

✴ What would be the 'optimal' shape for tuning curves?

✴ Are adaptation, attention and learning a step towards more 'optimal' tuning curves for the attended/trained stimulus ?



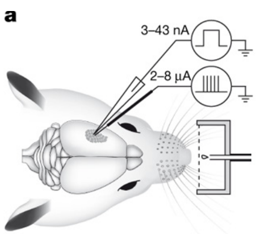
Neurons in auditory midbrain of the guinea pig adjust their response to improve the accuracy of the code close to the region of most commonly occurring sound levels.

[Dean, Harper & McAlpine, Nature Neuro, 2005]

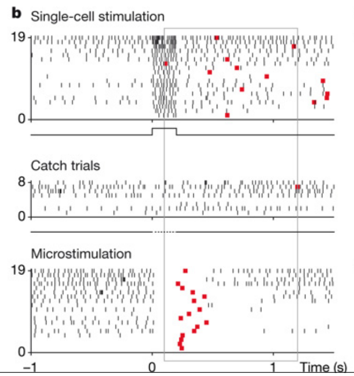
Research questions (2)

✴ How many neurons participate in a psychophysical task ? (see also, lab 1) 1, 10, 100, 10000? How can we find out ?

✴ comparing performance (e.g. MT: Britten et al 1992; Stuttgen & Schwartz 2008). stimulating (MT: Salzman, Britten, Newsome 1990).



Houweling & Brecht, Nature, 2008
Barrel cortex single cell stimulation.



Research questions (3)

✴ Pooling from large populations of neurons thought to be a way to average out the noise.

✴ Pairs of neurons show correlations in their variability: does pooling more and more neurons increases (linearly) the accuracy of the representation?

or Is information saturating over a certain number of neurons ? [Zohary et al 1994]

✴ Could that be that adaptation, attention and perceptual learning act by changing correlations? [Cohen & Maunsell 2009; Gutnisky & Dragoi 2008, Gu et al 2011, Bejjanki et al 2011]

ARTICLES

nature neuroscience

Attention improves performance primarily by reducing interneuronal correlations

Marlene R Cohen & John H R Maunsell

Visual attention can improve behavioral performance by allowing observers to focus on the important information in a complex scene. Attention also typically increases the firing rates of cortical sensory neurons. Rate increases improve the signal-to-noise ratio of individual neurons, and this improvement has been assumed to underlie attention-related improvements in behavior. We recorded dozens of neurons simultaneously in visual area V4 and found that changes in single neurons accounted for only a small fraction of the improvement in the sensitivity of the population. Instead, over 80% of the attentional improvement in the population signal was caused by decreases in the correlations between the trial-to-trial fluctuations in the responses of pairs of neurons. These results suggest that the representation of sensory information in populations of neurons and the way attention affects the sensitivity of the population may only be understood by considering the interactions between neurons.

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Perceptual learning reduces interneuronal correlations in macaque visual cortex

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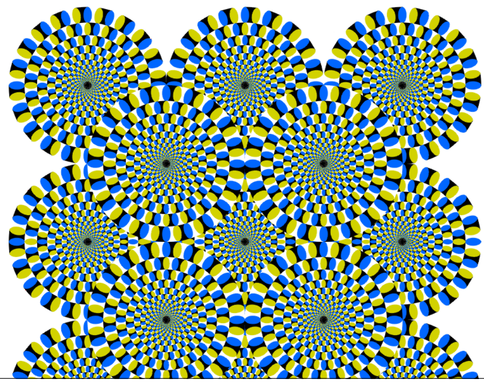
SUMMARY

Responses of neurons in early visual cortex change little with training, and appear insufficient to account for perceptual learning. Behavioral performance, however, relies on population activity, and the accuracy of a population code is constrained by correlated noise among neurons. We tested whether training changes interneuronal correlations in the dorsal medial superior temporal area, which is involved in multisensory heading perception. Pairs of single units were recorded simultaneously in two groups of subjects: animals trained extensively in a heading discrimination task, and "naïve" animals that performed a passive fixation task. Correlated noise was significantly weaker in trained versus naïve animals, which might be expected to improve coding efficiency. However, we show that the observed uniform reduction in noise correlations leads to little change in population coding efficiency when all neurons are decoded. Thus, global changes in correlated noise among sensory neurons may be insufficient to account for perceptual learning.

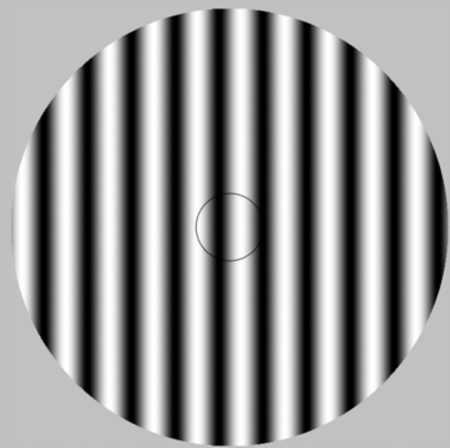
Research questions (4)

✶ Can the study of illusions inform us on the type of 'decoder' that is used in the brain? [Seriès, Stocker and Simoncelli 2009]



Sensory Adaptation

Verify that this grating is vertical

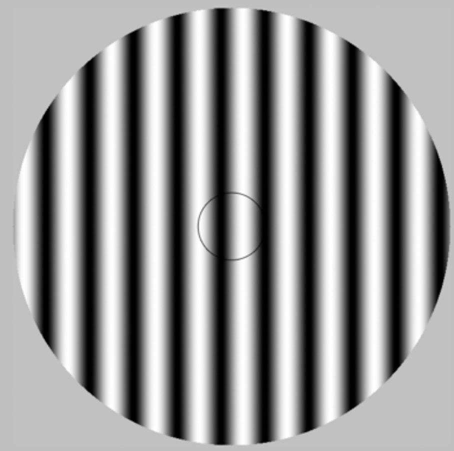


Sensory Adaptation

Fixate on the central circle for 30 sec

Sensory Adaptation

Now observe the grating again



The Tilt After-Effect

Visual Adaptation: Psychophysics

Visual adaptation leads to:

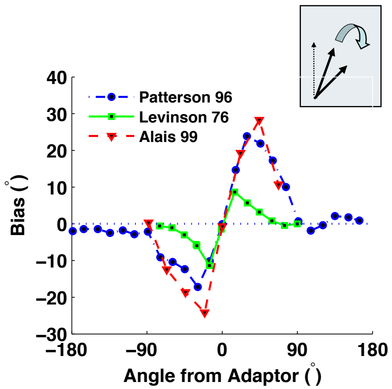
- estimation tasks: strong biases (mainly repulsion)

Visual Adaptation: Psychophysics

Visual adaptation leads to:

- estimation tasks: strong biases (mainly repulsion)

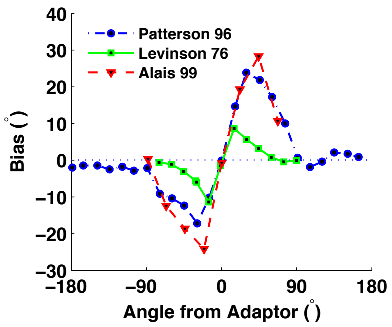
Repulsion

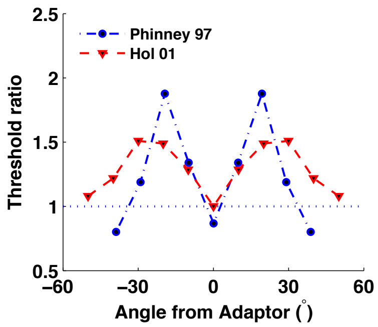


Visual Adaptation: Psychophysics

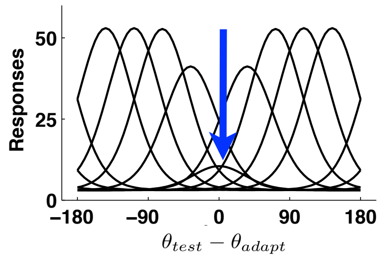
Visual adaptation leads to:

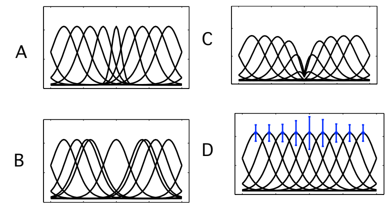
- estimation tasks: strong biases (mainly repulsion)
- discrimination tasks: changes in performance





Visual Adaptation: Physiology





Mainly a Gain change

[Van Wezel & Britten 2002, Krekelberg et al. 2006]

Other effects are controversial, dependent on time scale and area: shifts in preferred orientation, changes in width, changes in variability.

[Kohn & Movshon 2004, Dragoi et al, 2000]

ARTICLE — Communicated by Peter Dayan

Is the Homunculus "Aware" of Sensory Adaptation?

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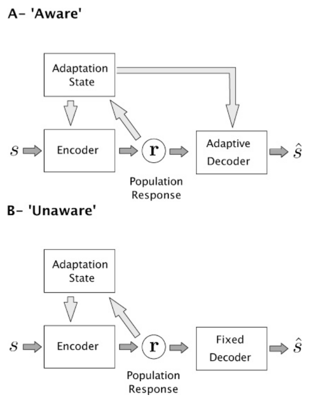
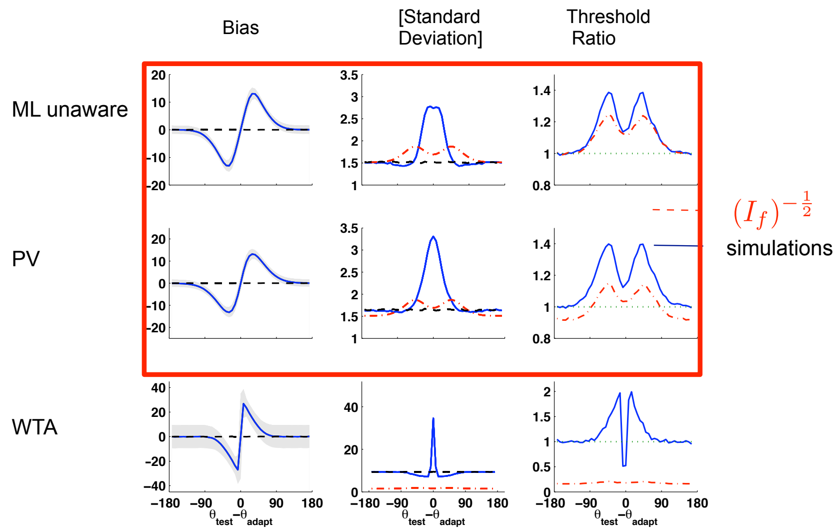
Neural activity and perception are both affected by sensory history. The work presented here explores the relationship between the physiological effects of adaptation and their perceptual consequences. Perception is modeled as arising from an encoder-decoder cascade, in which the encoder is defined by the probabilistic response of a population of neurons, and the decoder transforms this population activity into a perceptual estimate. Adaptation is assumed to produce changes in the encoder, and we examine the conditions under which the decoder behavior is consistent with observed perceptual effects in terms of both bias and discriminability. We show that for all decoders, discriminability is bounded from below by the inverse Fisher information. Estimation bias, on the other hand, can arise for a variety of different reasons and can range from zero to substantial. We specifically examine biases that arise when the decoder is fixed, "unaware" of the changes in the encoding population (as opposed to "aware" of the adaptation and changing accordingly). We simulate the effects of adaptation on two well-studied sensory attributes, motion direction and contrast, assuming a gain change description of encoder adaptation. Although we cannot uniquely constrain the source of decoder bias, we find for both motion and contrast that an "unaware" decoder that maximizes the likelihood of the percept given by the preadaptation encoder leads to predictions that are consistent with behavioral data. This model implies that adaptation-induced biases arise as a result of temporary suboptimality of the decoder.



Results (2) -- 'unaware' read-out



[Series, Stocker and Simoncelli, 2009]

Summary

- ✤ The efficiency of Estimators / Decoders can be characterized by the bias and the variance.
- ✤ The bias and variance of estimators used to read-out neural responses can be easily compared with psychophysical performance (estimation biases, and discrimination threshold).

- ✤ Fisher Information is related to the minimal variance of a unbiased estimator.
- ✤ In a model of a population of neurons, Fisher Information can be expressed in terms of the tuning curves and the noise.
- ✤ Fisher information can be used to relate population responses and discrimination performances. It gives a bound on the discrimination threshold
- ✤ Fisher Information can be used to explore the factors that impact on the precision of the code / behavioral performances.