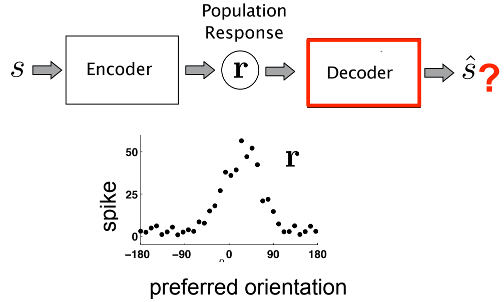
2. Decoding (continued)

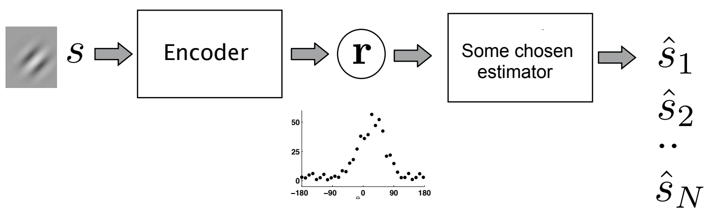
readings: Decoding D&A ch.3

Decoding: Summary of Last Lecture

- 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.

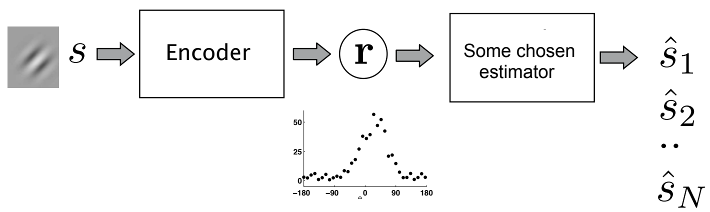


From Population Codes to Psychophysical Performances



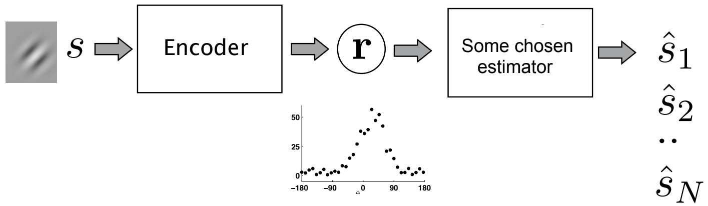
- E.g. stimulus = oriented Gabor patch;
- Encoder = set of noisy tuning curves, e.g. in V1;
- ***r*** =population response;
- Estimator/Decoder = model we choose for this (e.g optimal);
- $\hat{s}$ = perceived orientation of Gabor patch;
- **How can we relate this model of perception with measured psychophysical performance?**

From Population Codes to Psychophysical Performances



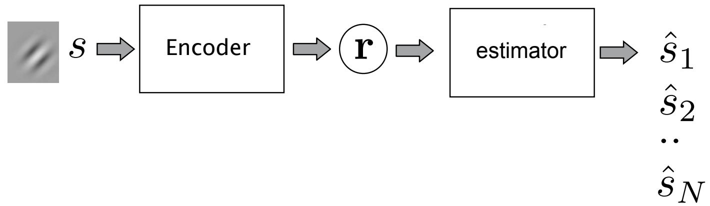
- **what is the influence of the shape of the tuning curves and noise in our visual cortex on our performances in perception?**

From Population Codes to Psychophysical Performances

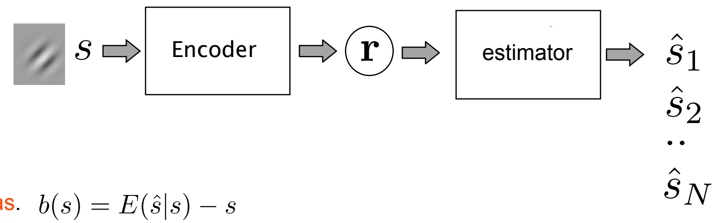


- performances change with learning, attention, aging etc.. can we figure out what is changing in the brain?

How can we describe the performances of our estimator ?



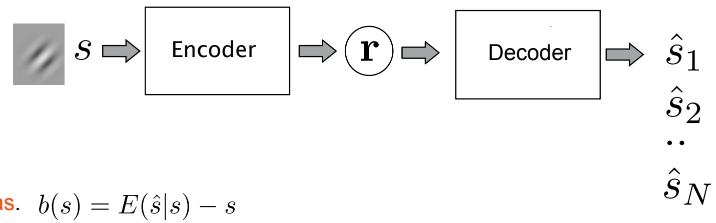
How can we describe the performances of our estimator ?



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

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

How can we describe the performances of our estimator ?



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

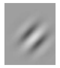
  If $E(\hat{s}|s) = s$ the estimator is said to be unbiased.

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

  Estimation theory tells us that, knowing the encoder model P[r|s], there is a lower bound on the variance that can be achieved by any decoder. This quantity is known as the Cramer-Rao Bound. The denominator is known as Fisher Information which is a function of P[r|s]

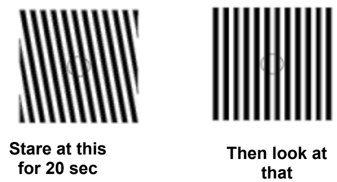
$$var(\hat{s}) \geq \frac{(1 + b'(s))^2}{I_F(s)}$$

what is being measured in psychophysics ?

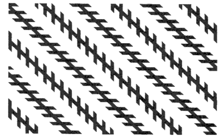


a) Estimation tasks

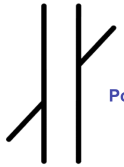
✳ The measured quantity is the difference between the perceived orientation and the real orientation: $< \hat{s} > - s$



Tilt after-effet

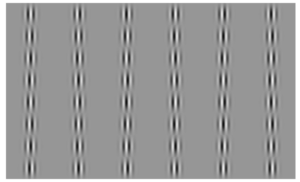


Zollner Illusion

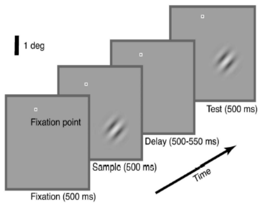


Poggendorf Illusion

Fraser Illusion



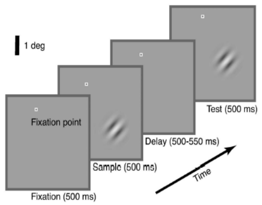
b) Discrimination Tasks



✳ **Is the second grating of the same orientation as the first grating, or a different orientation?**

✳ The measured quantity is the Discrimination Threshold a.k.a Just Noticeable difference (JND) - on average detected on 76% of the trials.

b) Discrimination Tasks

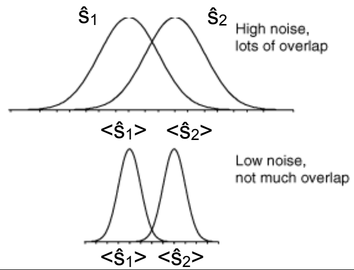


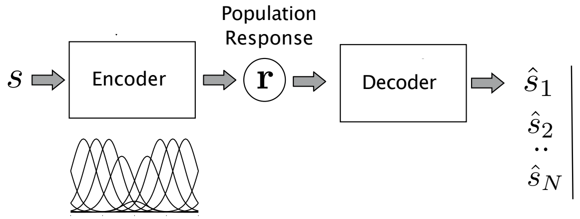
✳ **Is the second grating of the same orientation as the first grating, or a different orientation?**

✳ The measured quantity is the Discrimination Threshold a.k.a Just Noticeable difference (JND) - on average detected on 76% of the trials.

Discrimination threshold depends on the overlap between the internal 'representation' of the 2 stimuli: p[$\hat{s}_1$|**r**] and p[$\hat{s}_2$|**r**]:

- The bias of the internal representation (expansion/contraction of the 'distance' between the stimuli)
- How noisy the internal representation is (the variance of the estimates)





Linking the statistics of the model and psychophysics

$b(\hat{s}) = <\hat{s}> - s$ ⟷ perceptual bias

$\mathrm{var}(\hat{s})$

$\mathrm{threshold}(\hat{s}) = \frac{\mathrm{std}(\hat{s})}{1+b'(\hat{s})}$ ⟷ discrimination threshold (76% correct)
just noticeable difference

From the Cramer Rao Bound, knowing the encoder model and independently of the decoder, it is known that the threshold is bounded by the sqrt of Fisher information: $\mathrm{threshold}(\hat{s}) \geq \frac{1}{\sqrt{I_F(s)}}$

[Series et al, 2010]

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

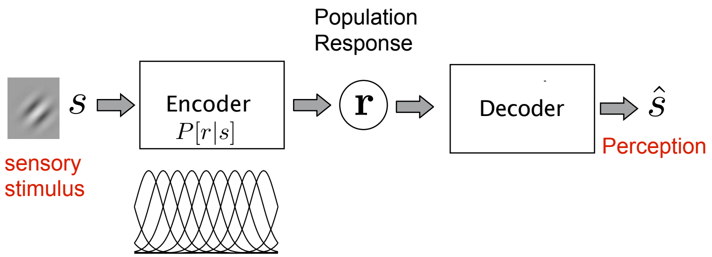
$$I_F(s) = -< \frac{\partial^2 \ln P[r|s]}{\partial s^2} >$$

- ∗ Interpreted as a measure of 'information' in the responses;
- ∗ a useful tool to relate directly the properties of the neural responses with discrimination performance.
- ∗ is related with Mutual information and Stimulus Specific Information (Brunel and Nadal 1998, Yarrow, Challis and Series 2012).

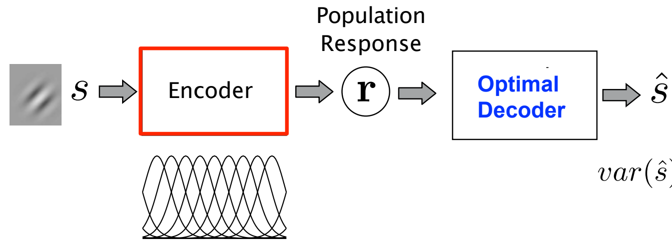
From Population Responses to Psychophysics

Two strategies:

- ∗ Assume the decoder is optimal: Compute Fisher information from P[r|s]. This gives us the minimal possible variance of any unbiased decoder, and the minimal threshold of any decoder (biased or unbiased).
- ∗ Construct explicitly the decoder (e.g. population vector). Compute explicitly bias, variance, and threshold of estimates.



From Population Responses to Psychophysics



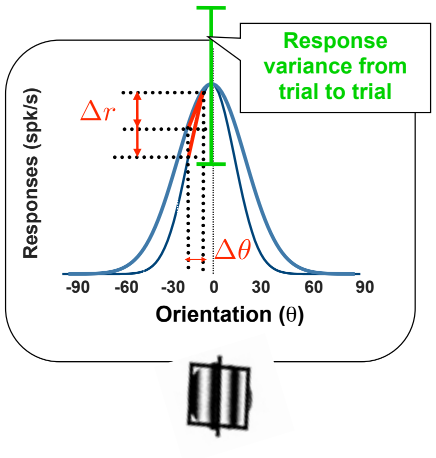
$$var(\hat{s}) \simeq \frac{1}{I_F(s)}$$

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

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?



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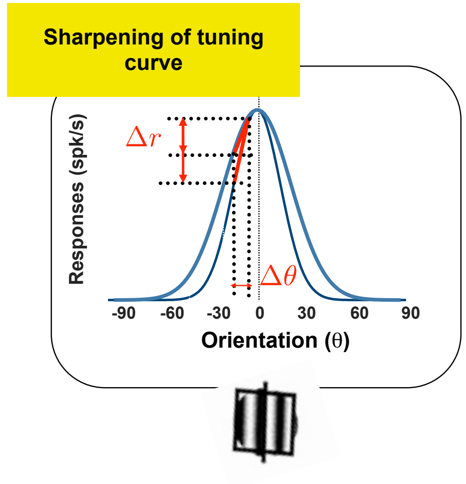

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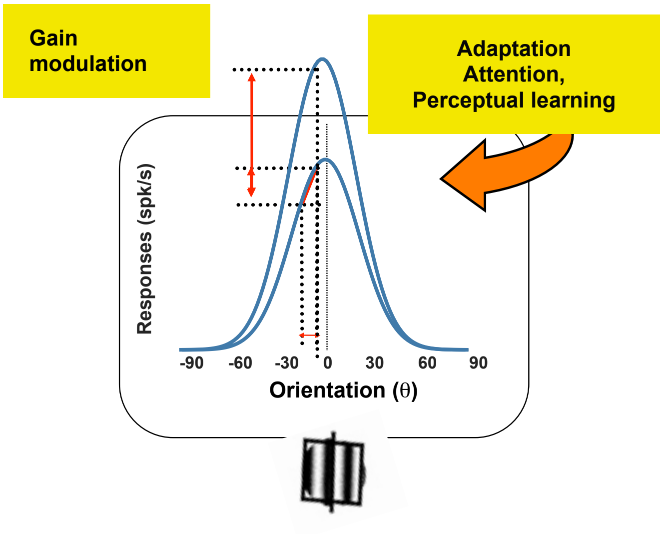

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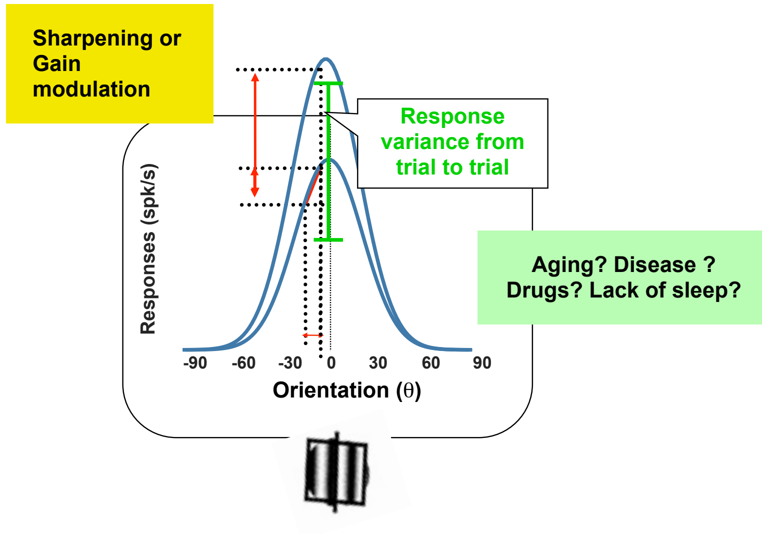


What are the factors that control performance?

* ✴ Fisher information formalises intuition and provides a tool to explore these questions precisely.
* ✴ For Poisson noise

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

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

Slope ²
variance

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

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

What are the factors that control performance?

For Gaussian correlated noise:

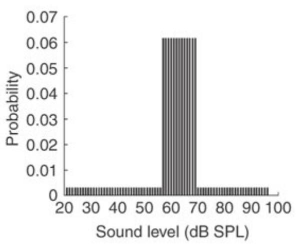
$$P[\mathbf{r}|s] = \frac{1}{\sqrt{(2\pi)^N |\mathbf{Q(s)}|}} e^{-\frac{1}{2}(\mathbf{r}-\mathbf{f(s)})^\mathbf{T}\mathbf{Q}^{-1}(\mathbf{s})(\mathbf{r}-\mathbf{f(s)}))}$$

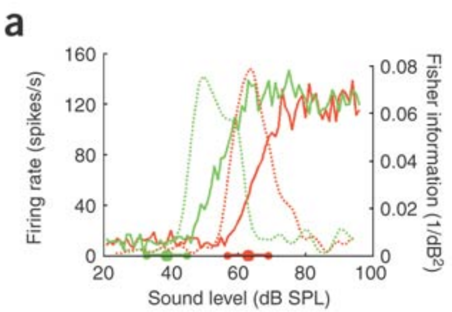
$$I_F(s) = \mathbf{f}'(\mathbf{s})\mathbf{Q}^{-1}(\mathbf{s})\mathbf{f}'(\mathbf{s}) + \frac{1}{2}\mathrm{Trace}[\mathbf{Q}^{-1}(\mathbf{s})\mathbf{Q}'(\mathbf{s})\mathbf{Q}^{-1}(\mathbf{s})\mathbf{Q}'(\mathbf{s})]$$

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 ?



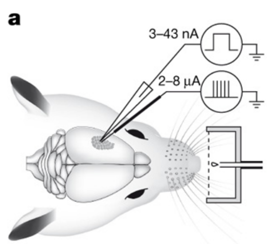


Neurons in auditory midbrain of the guinea pig adjust their response to improve the accuracy of the code close to the region of most commonly occurring sound levels.

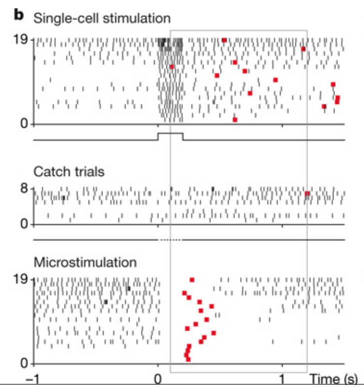
[Dean, Harper & McAlpine, Nature Neuro, 2005]

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). stimulating (MT: Salzman, Britten, Newsome 1990).



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



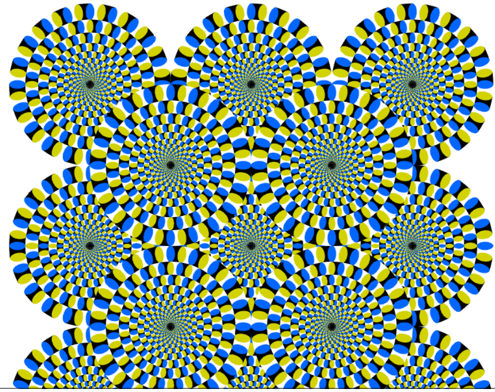
Research questions (3)

✴ 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 and attention act by changing correlations? [Cohen & Maunsell 2009; Gutnisky & Dragoi 2008]

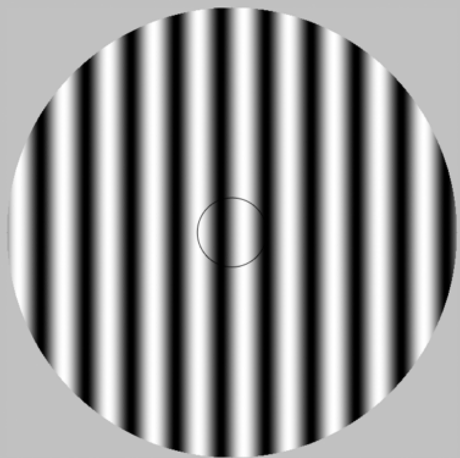
Research questions (4)

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



Sensory Adaptation

Verify that this grating is vertical

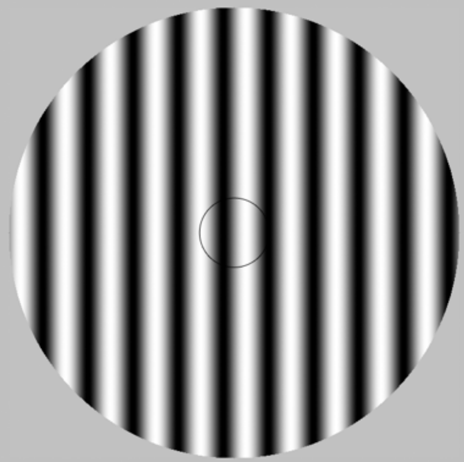


Sensory Adaptation

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:

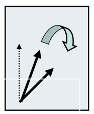
❖ estimation tasks: strong biases (mainly repulsion)

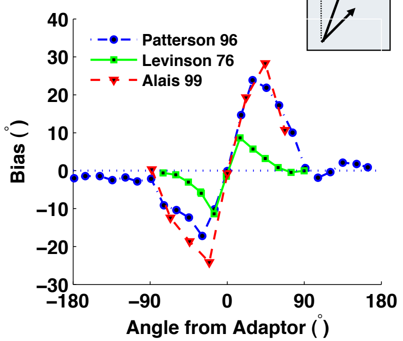
Visual Adaptation: Psychophysics

Visual adaptation leads to:

❖ estimation tasks: strong biases (mainly repulsion)

Repulsion



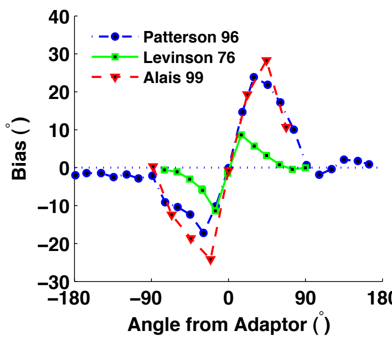


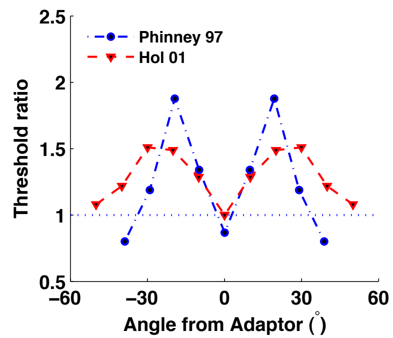
Visual Adaptation: Psychophysics

Visual adaptation leads to:

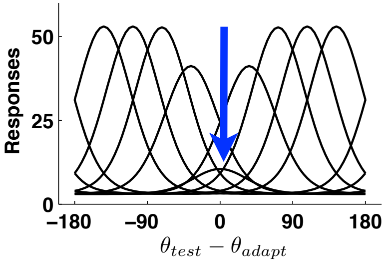
❖ estimation tasks: strong biases (mainly repulsion)

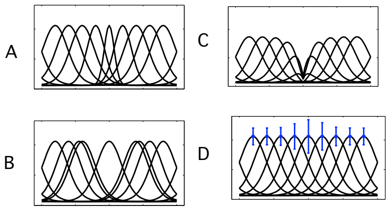
❖ discrimination tasks: changes in performance





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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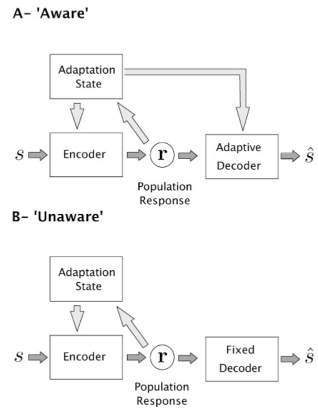
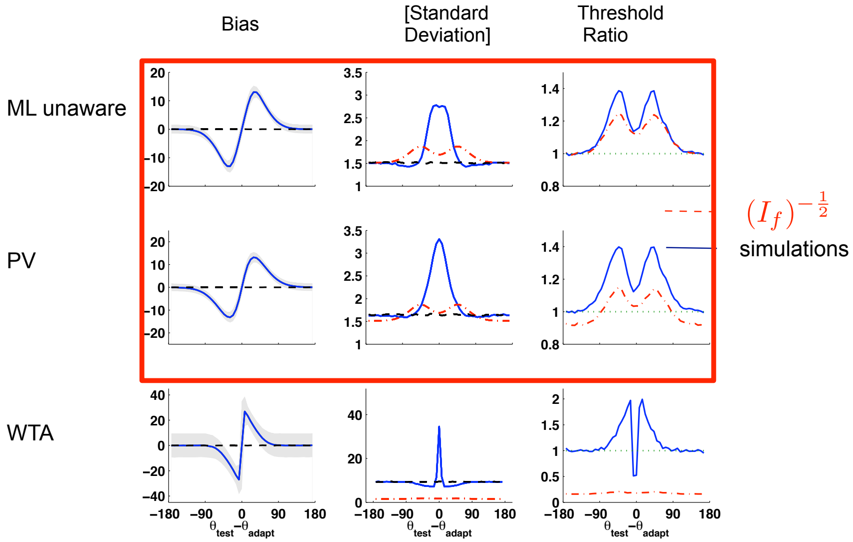
Neural activity and perception are both affected by sensory history. The work presented here explores the relationship between the physiological effects of adaptation and their perceptual consequences. Perception is modeled as arising from an encoder-decoder cascade, in which the encoder is defined by 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.