Adaptive Response to Noise in the Inferior Colliculus

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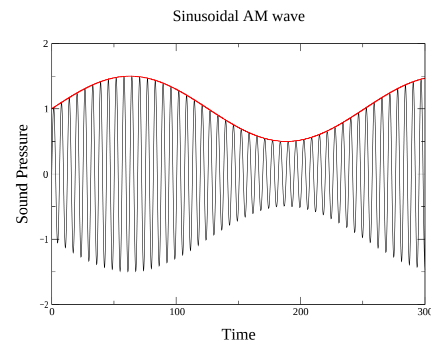
Adaptation

Experimental context:

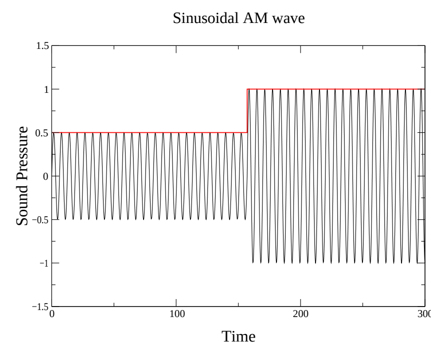
- We looked at the central nucleus of the inferior colliculus (ICC) of the cat
- ICC neuronal response is inherently nonlinear; units respond to the **modulation envelope** of an amplitude-modulated carrier



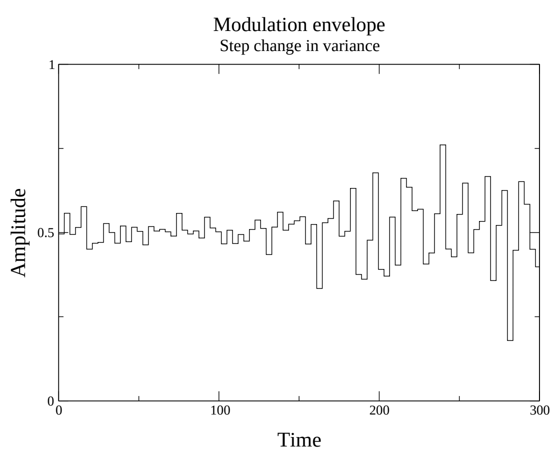
- Units typically respond to positive slope modulation envelope.

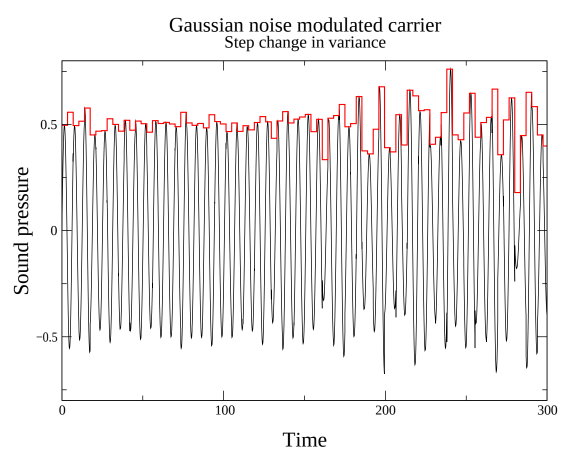
We investigate adaptation by looking at the response of neurons to sudden changes in modulation envelope properties.

- adaptation to the mean: sudden change in acoustic intensity



- adaptation to variance: sudden change in acoustic contrast

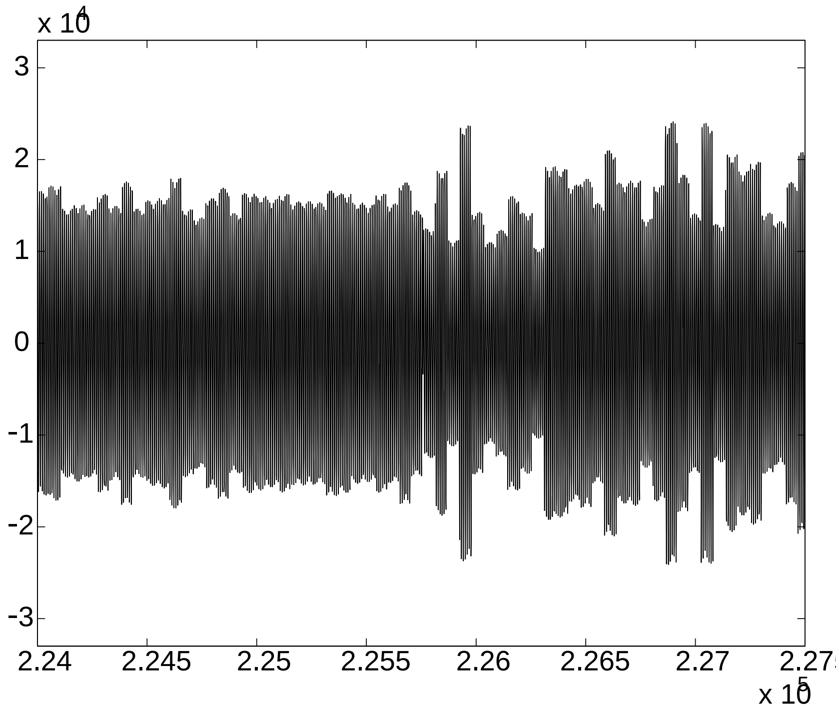




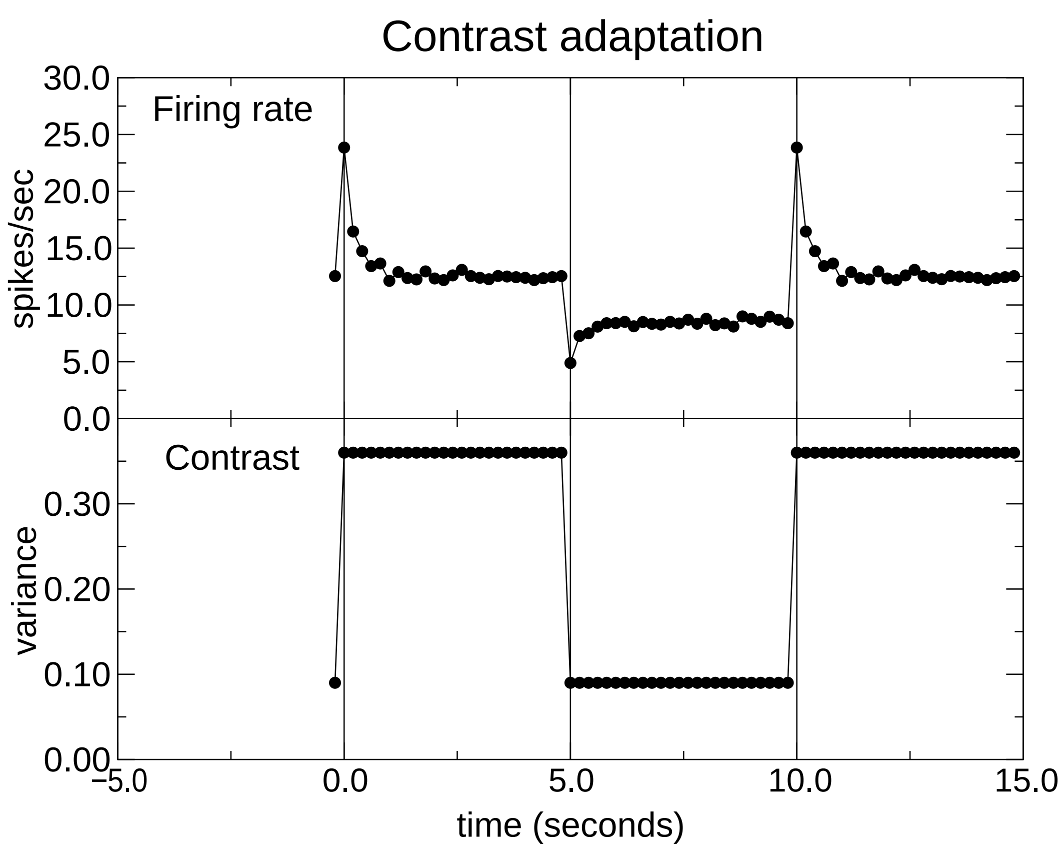
Auditory adaptation to variance

The stimulus is an 8 kHz carrier modulated by Gaussian white noise sampled at 800 Hz.

$$s(t) = [1 + bg(t)] \sin(\omega_c t) \qquad g(t) \in N(\mu, \sigma(t)) \tag{1}$$



Stimulus at the transition from low to high modulation depth.

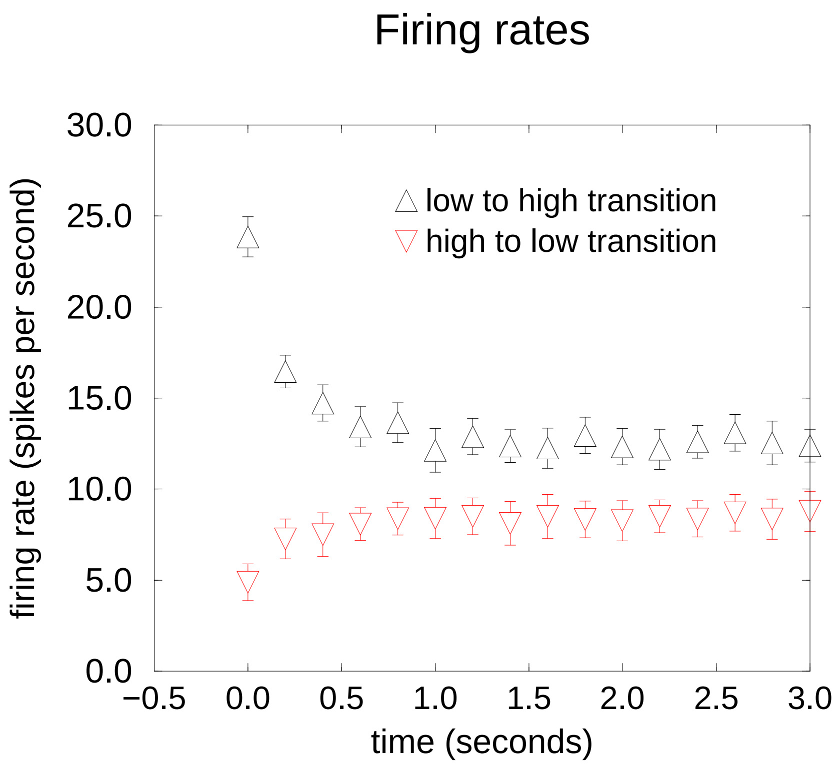


Firing rates for contrast stimuli.

Auditory adaptation: experimental results

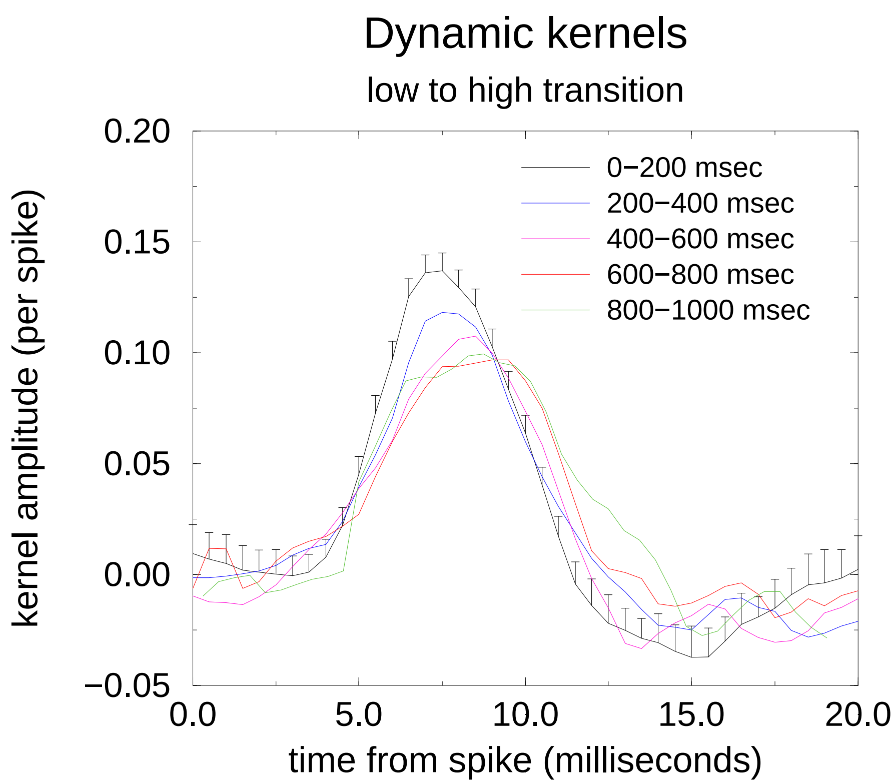
- 70-140 A-B trials, 20-30 dB above threshold
- ratio of variances: 4.0
- high to low: $\tau_{12} = 0.30 \pm 0.08$ sec
- low to high: $\tau_{21} = 0.14 \pm 0.05$ sec
- adaptation time asymmetry: $\tau_{12}/\tau_{21} = 2.1$ theory: 1.94

Firing rates as a function of time, immediately after a stimulus variance transition.



Dynamic kernels:

- partition high modulation interval into 200 msec time slices.
- average over many trials to compute linear kernel for each slice.



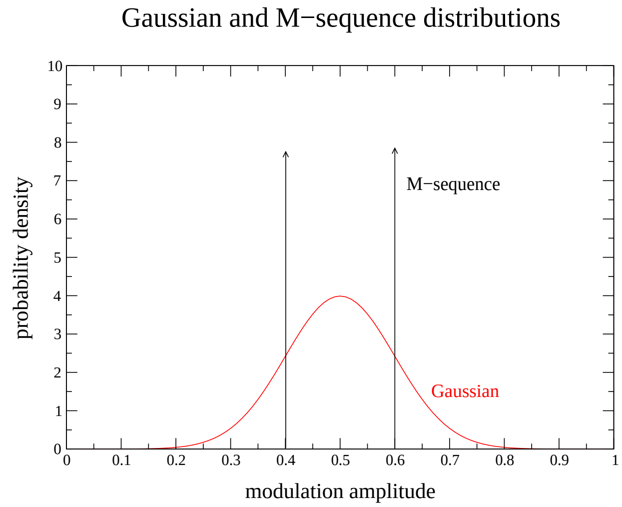
Dynamic kernels at 200 msec intervals.

Auditory adaptation: higher order effects

Does the system adapt to higher order information?

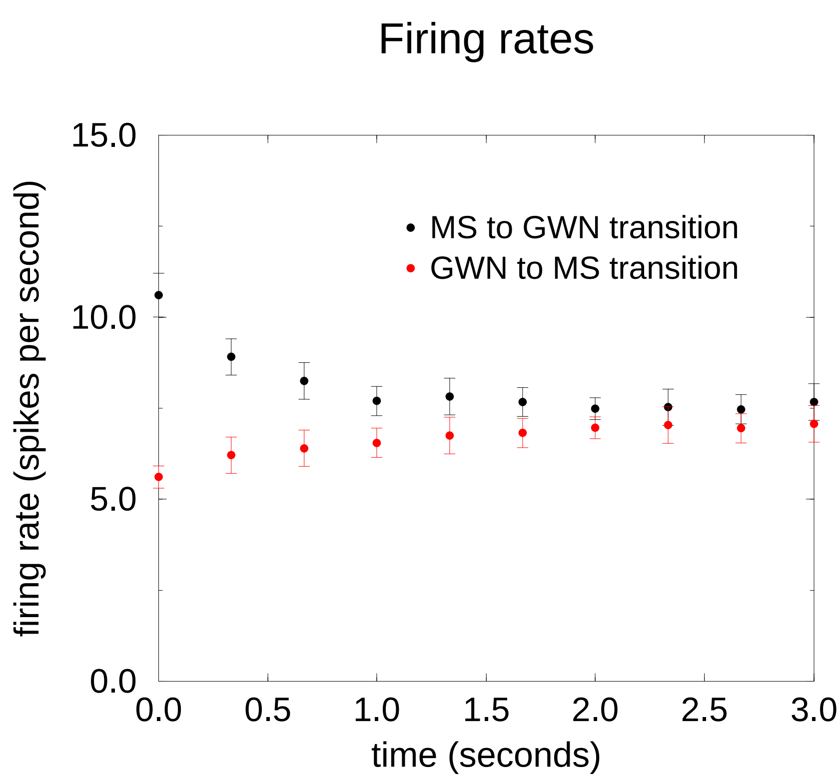
- Stimulus: alternating Gaussian white noise and m-sequence modulations

- Same mean and variance, different higher moments: Kurtosis of Gaussian: 0 Kurtosis of m-sequence: $2\sigma^4$



- GWN to MS: $\tau_{12} = 0.57 \pm 0.11$ sec
- MS to GWN: $\tau_{21} = 0.26 \pm 0.09$ sec
- adaptation time asymmetry: $\tau_{12}/\tau_{21} = 2.2$

Firing rates for alternation of GWN and m-sequence modulations.



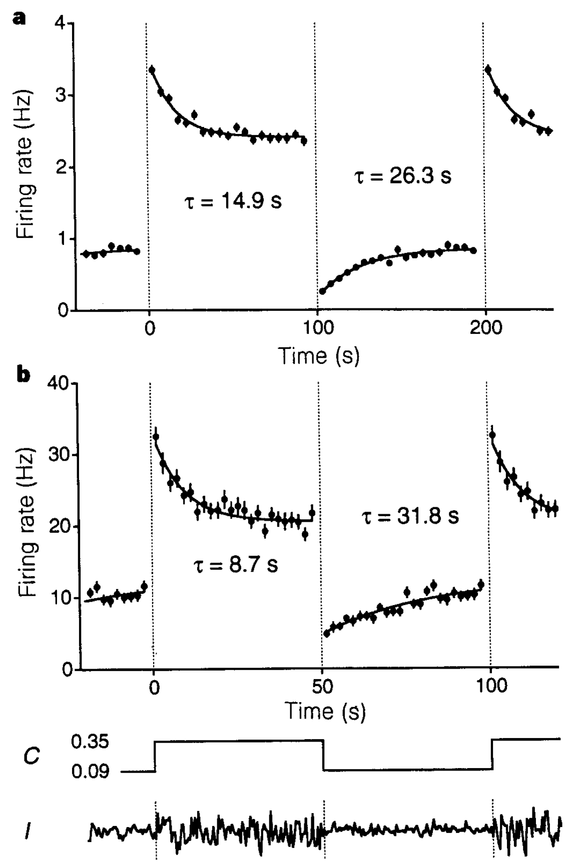
Adaptation in the visual system:

Light is a set of 600 teraHertz carrier waves modulated to produce changes in light intensity. Retinal cells are not responsive to the phase of the light, but are responsive to the modulation envelope.

- Adaptation to the mean: average light level
- Adaptation to the variance: contrast

Smirnakis, Berry, Warland, Bialek, and Meister:

Figure 1 Firing rate of a salamander (**a**) and a rabbit (**b**) ganglion cell under spatially uniform flicker stimulation, alternating every 100 (**a**) or 50 (**b**) seconds between contrast values of 0.09 and 0.35. Average firing rate values were computed in 5-s (**a**) or 2-s (**b**) time bins over 100 (**a**) or 25 trials (**b**). Continuous lines are exponential fits with decay time τ. The first and last segments are periodic repeats of the data. Trace below (**b**) shows the time course of the contrast, C. Bottom trace illustrates the time course of the flickering intensity, I; note that the random flicker sequence was different in each stimulus trial. Similar gradual changes in the firing rate were unambiguous in 75% of salamander and 51% of rabbit cells. Another 18% in salamander and 31% in rabbit showed the gradual firing rate decline after a contrast increase but no detectable recovery following a contrast decrease.



- Both rabbit and salamander retinas show adaptation to the variance of the light while the mean stays constant
- The adaptation times are asymmetric; the retina adapts faster to transitions from low to high variance.

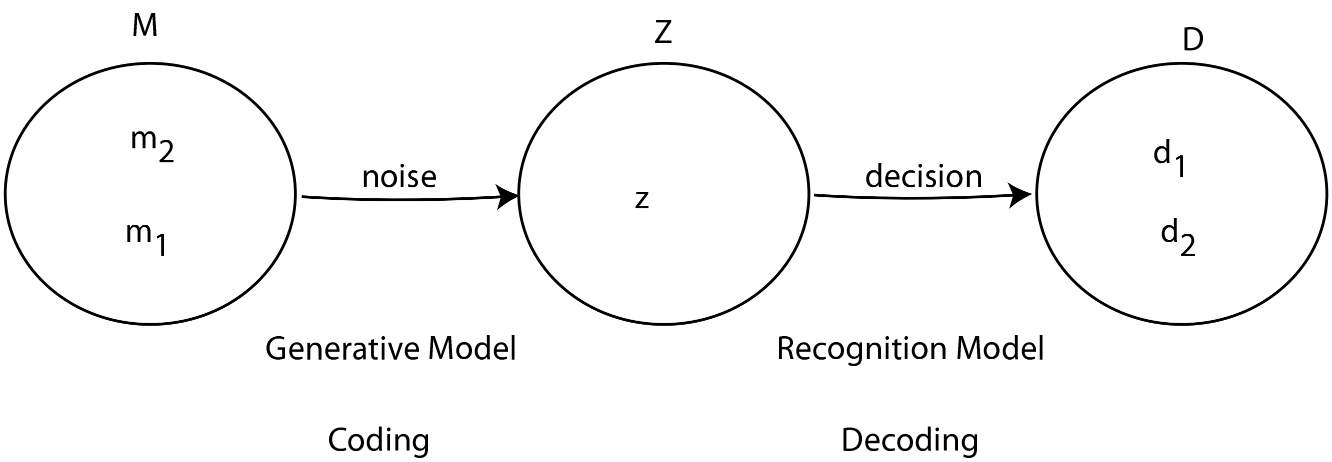
Statisitcal decision theory

Using observed data and any priors available, make a decision about the data in an optimal fashion.

Binary decisions

- 2 possible messages $m_1, m_2 \in M$
- 2 possible decisions $d_1, d_2 \in D$; if m_1 is sent, d_1 is correct
- observation $z \in Z$ generated by message plus corruption and/or transformation

Goal: select a decision rule $d(z) : Z \mapsto D$ that maps observations to decisions in an optimal manner.



The decision rule induces a partition of Z into Z_1 and Z_2 corresponding to d_1 and d_2.

Max likelihood crtierion

Given an observation z,

$$d(z) = \begin{cases} d_1 & \text{if } p(z|m_1) > p(z|m_2) \\ d_2 & \text{if } p(z|m_2) > p(z|m_1) \end{cases} \tag{2}$$

This can be restated as a likelihood ratio test

$$\Lambda(z) = \frac{p(z|m_2)}{p(z|m_1)}$$

with Z partitioned as

$$Z_1 = \{z : \Lambda(z) < 1\} \qquad \text{and} \qquad Z_2 = \{z : \Lambda(z) > 1\}$$

Neyman-Pearson criterion

There are four possible outcomes, two errors

$$\text{Type I: decide } d_2 \text{ when } m_1 \text{ is true} \quad p(d_2|m_1) = P\{z \in Z_2|m_1\} \tag{3}$$

$$\text{Type II: decide } d_1 \text{ when } m_2 \text{ is true} \quad p(d_1|m_2) = P\{z \in Z_1|m_2\} \tag{4}$$

and two correct decions $p(d_1|m_1)$ and $p(d_2|m_2)$.

Suppose m_1 represents a null hypothesis (no change)and m_2 a positive outcome (change). Then

$$p(d_2|m_1) : \quad \text{level of significance} \tag{5}$$

$$p(d_2|m_2) : \quad \text{power of the test} \tag{6}$$

Criterion: fix $p(d_2|m_1)$ at a preselected α_0 and maximize $p(d_2|m_2)$.

Radar lingo:

$$p(d_2|m_1) = \quad \text{false alarm rate} \tag{7}$$

$$p(d_2|m_2) = \quad \text{detection power} \tag{8}$$

$$\frac{p(d_2|m_2)}{p(d_2|m_1)} = \quad \text{ROC: receiver operating characteristic} \tag{9}$$

Decision theory for adaptation:

Hypothesis: The auditory system tracks changes in the amplitude distribution as quickly as possible.

Suppose the stimulus has two states characterized by probability distributions : $P_1(\theta_1), \qquad P_2(\theta_2)$.

The likelihoods of a stimulus set $(s_1, \ldots, s_k)$ are

$L_1(\{s_i\}) = Prob\,(s_1, \ldots, s_k|P_1) = \prod_{j=1}^{k} P_1(s_j)$

$L_2(\{s_i\}) = Prob\,(s_1, \ldots, s_k|P_2) = \prod_{j=1}^{k} P_2(s_j)$.

Average likelihoods:

$\bar{L}_{11} = \int L_1(\{s_i\}) \prod_{j=1}^{k} P_1(s_j) ds_j = \left[\int \left(P_1(s)\right)^2 ds\right]^k$

$\bar{L}_{12} = \bar{L}_{21} = \left[\int P_1(s) P_2(s) ds\right]^k$

$\bar{L}_{22} = \left[\int \left(P_2(s)\right)^2 ds\right]^k$

To determine the state, form average likelihood ratios:

$$\frac{\bar{L}_{12}}{\bar{L}_{11}} = T \quad \Longrightarrow \quad \tau_{12} = \frac{\ln T}{\ln\left(\frac{\int P_1(s) P_2(s) ds}{\int (P_1(s))^2 ds}\right)}$$

$$\frac{\bar{L}_{21}}{\bar{L}_{22}} = T \quad \Longrightarrow \quad \tau_{21} = \frac{\ln T}{\ln\left(\frac{\int P_1(s) P_2(s) ds}{\int (P_2(s))^2 ds}\right)}.$$

Then the asymmetry factor is

$$\alpha = \frac{\tau_{12}}{\tau_{21}} = \frac{\ln\left(\int P_1(s)P_2(s)ds\right) - \ln\left(\int (P_2(s))^2\, ds\right)}{\ln\left(\int P_1(s)P_2(s)ds\right) - \ln\left(\int (P_1(s))^2\, ds\right)}$$

Case 1 - adaptation to the mean: $N(\mu_1, \sigma^2)$, $N(\mu_2, \sigma^2)$

Result: $\alpha = 1$, or no asymmetry

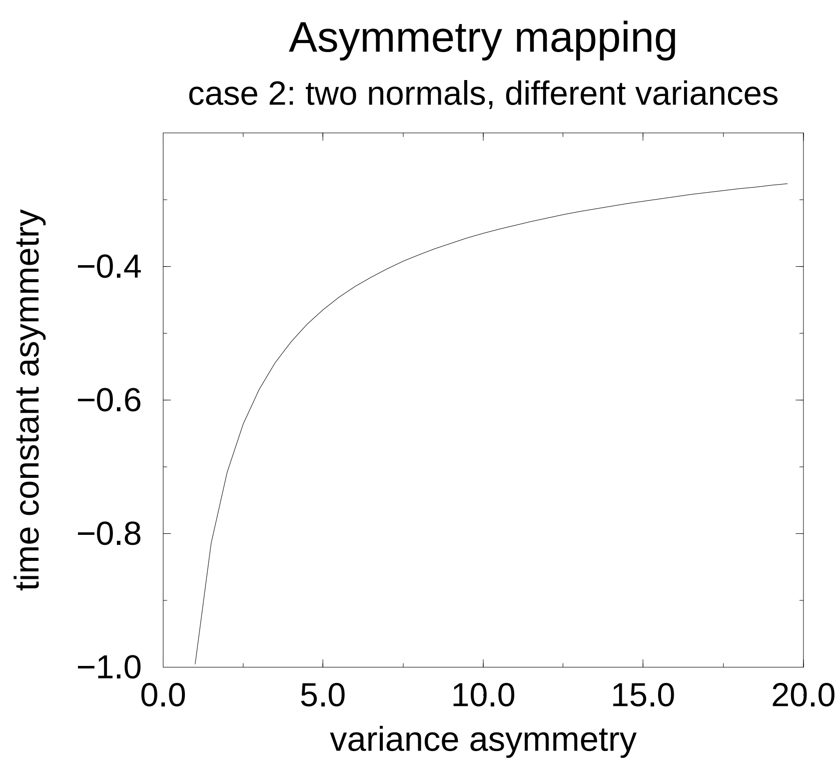
Case 2 - adaptation to the variance: $N(\mu, \sigma_1^2)$, $N(\mu, \sigma_2^2)$

Result: if $\sigma_2^2 = \gamma\sigma_1^2$ then

$$\alpha = \frac{\ln\left(\frac{1+\gamma}{2\gamma}\right)}{\ln\left(\frac{1+\gamma}{2}\right)}$$

As $\gamma \gg 1$ the asymmetry becomes $\alpha = -0.693/\ln(\gamma)$.

Adaptation time asymmetry as a function of the variance ratio.



Conclusions:

1. Adaptation to variance on a 100-200msec time scale is seen in the IC
2. Units also adapt to higher order information
3. Natural stimuli have time-varying contrasts:
   – short-term adaptation is good for detecting changes in contrast
   – Animal vocalizations have modulation spectral energy at 5-10 Hz.
4. Does adaptation to variance occur in the somatosensory domain?
5. psychophysical correlates?
6. future work:
   – adaptive response to spectro-temporal stimuli
   – adaptive response in MGN, AI
   – comparison to adaptive response to natural stimuli