1) Measure neuronal sensitivity to stimulus variations
2) Measure behavioral sensitivity to stimulus variations
3) Compare neuronal and behavioral sensitivity
4) Correlate response fluctuations with behavioral choices
5) Manipulate neural activity and test effect on behavior
"Correlation" = "Coherence"
<table>
<thead>
<tr>
<th>Coherence</th>
<th>Direction of Motion</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.75%</td>
<td>L</td>
</tr>
<tr>
<td>1.5%</td>
<td>R</td>
</tr>
<tr>
<td>3%</td>
<td>L</td>
</tr>
<tr>
<td>6%</td>
<td>R</td>
</tr>
<tr>
<td>12%</td>
<td>L</td>
</tr>
<tr>
<td>24%</td>
<td>R</td>
</tr>
<tr>
<td>48%</td>
<td>L</td>
</tr>
</tbody>
</table>

"TWO-ALTERNATIVE FORCED CHOICE"
"METHOD OF CONSTANT STIMULI"
Open Bars: Responses to motion in Preferred Direction
Filled Bars: Responses to motion in Null Direction

How to compare neuronal responses to behavior?

Ideal Observer Analysis
Signal Detection Theory
ROC (Receiver Operating Characteristic) Analysis:
- Choose a range of ‘criterion’ response values spanning the range of observed neuronal responses (e.g., 0->100 spikes/sec for example on previous page).
- Choose a set of response distributions for one particular value of motion coherence
- For each criterion response level, compute the proportion of trials in which the neuron’s response to the Null direction of motion exceeded the criterion value [call this P(null > crit)]. Also compute the proportion of trials in which the Preferred direction response exceeded this criterion value [P(pref > crit)].
- Plot P(pref>crit) vs. P(null>crit) to trace out the ‘ROC curve’ for this value of motion coherence. Compute the area under this curve (range: 0.0->1.0) to determine the ability of an ideal observer to discriminate between Null and Preferred direction motion using only the response of the neuron.
- Repeat for each different motion coherence.
Questions to Ponder

- If the average single neuron is as sensitive as the monkey, then why isn’t the monkey a whole lot better than it is?
  - Shouldn’t the monkey be able to do better by combining the responses of multiple neurons? Why or why not? What factors limit this?

- Is there deep meaning to the finding that the average ratio of neuronal/psychophysical thresholds is near one, or might it just have been an accidental finding? What aspects of the experimental design may play a role here?

- If the actual N:P threshold ratio can depend on other factors, then is this result telling us anything meaningful?

- How does correlated noise among neurons affect neuronal sensitivity? Does it help or hurt? Why?
For positive ‘signal correlations’ (correlation of mean response values), positive ‘noise correlations’ (correlation of residual responses around the mean) can hurt performance (top left)

For negative signal correlations, positive noise correlations could improve performance (bottom left)

Computing Neural Sensitivity Using $d'$

In many cases, neural sensitivity can be estimated effectively from tuning curves, even without access to all of the individual trial responses.

Can take advantage of the fact that cortical neurons typically have approximately Poisson statistics: variance = mean.

Example: how well can the V1 neuron (right) discriminate between orientations of 0 and 5 degrees?

$$d' = \frac{|\mu_2 - \mu_1|}{\sqrt{0.5(\sigma_1^2 + \sigma_2^2)}} = \frac{|\mu_2 - \mu_1|}{\sigma} \quad \text{when } \sigma_1 = \sigma_2$$

$|x|$ denotes absolute value of $x$.

$\mu_1 = 60$ spikes/sec $= \sigma_1^2$ \quad $\mu_2 = 30$ spikes/sec $= \sigma_2^2$

$$d' = \frac{|30-60|}{\sqrt{0.5(30 + 60)}} = \frac{30}{\sqrt{45}} \approx 30/7 \approx 4.5$$

$d' = 1.6$ corresponds to $\approx 80\%$ correct.
Assume you have $N$ neurons with identical tuning curves, with responses denoted $r_1$, $r_2$, ….. $r_N$. When you present a stimulus repeatedly, each neuron gives a mean response ($m_1$, $m_2$, …, $m_N$) and has a response variance ($v_1$, $v_2$, …. $v_N$) and a standard deviation ($sd_1$, $sd_2$, …, $sd_N$), where $sd = \sqrt{v}$.

If all neurons have independent variability (noise), then:

Summed response = $m_1 + m_2 + \ldots + m_N = N \cdot m$ (since identical tuning)

Variance of sum = $v_1 + v_2 + \ldots + v_N = N \cdot v$

Std Dev of sum = $\sqrt{N} \cdot sd$

Now, assume that you compare population responses to two stimuli by computing $d'$. Let $S_A$ and $S_B$ be the summed responses of the population to the two stimuli (A and B), and $sd_A$ and $sd_B$ are the standard deviations of summed responses (assumed to be equal)

$$d'_{\text{sum}} = \frac{|S_A - S_B|}{sd} = \frac{|N \cdot m_A - N \cdot m_B|}{(\sqrt{N} \cdot sd)}$$

$$= N \cdot \frac{|m_A - m_B|}{(\sqrt{N} \cdot sd)} = \sqrt{N} \cdot \frac{|m_A - m_B|}{sd} = \sqrt{N} \cdot d'$$

So summing responses of $N$ independent neurons increases $d'$ by $\sqrt{N}$

If neurons have correlated noise, then less is gained by pooling (summing) responses.