THEORETICAL NEUROSCIENCE I

Lecture 13: Comparison of psychometric and neurometric functions

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2. Discrimination of visual motion: psychometric function

3. Discrimination of visual motion: neurometric function

4. Comparing neurometric and psychometric functions

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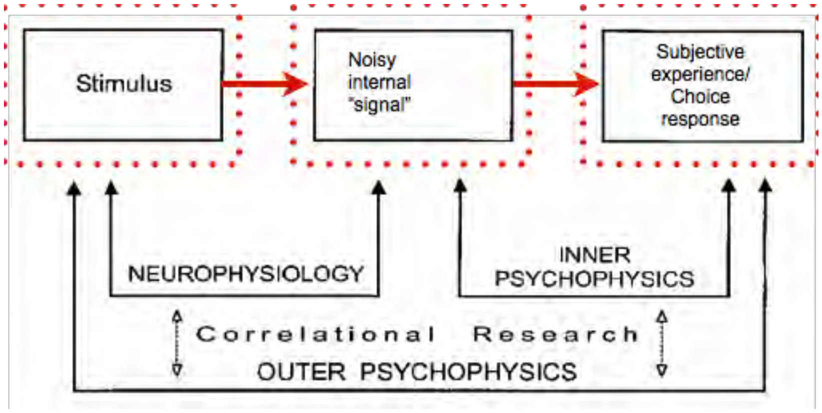
1 Recap from previous lecture



Signal-detection theory (recap)

- Consider choice task with two alternatives (signal and noise). Establish hit and false alarm fractions, possibly as a function of signal strength.

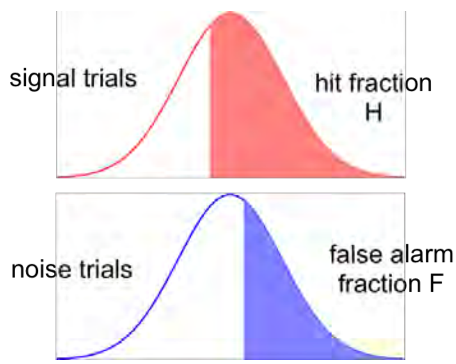


Figure 1: Signal-detection theory: Hit and false alarm fraction 1.

Signal-detection theory

- Assuming Gaussian distributions, infer relative placement of decision criterion and distribution peaks.

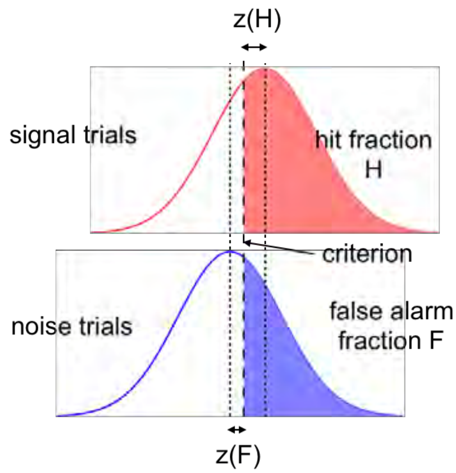


Figure 2: Signal-detection theory: Hit and false alarm fraction 2.

Signal-detection theory (recap)

- Interpret $z(H)$ and $z(F)$ in terms of discriminability d' and decision bias c.

$$d' = z(H) - z(F), \qquad c = -\frac{z(H) + z(F)}{2}$$

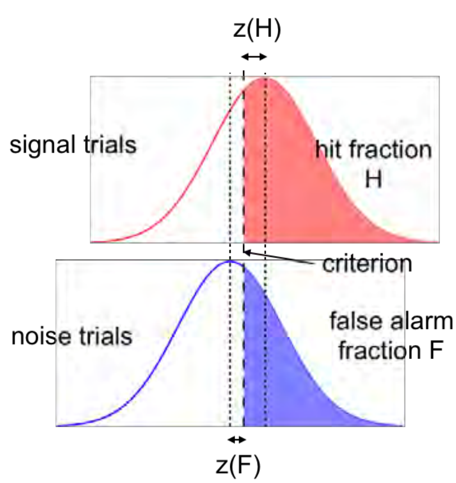


Figure 3: Signal-detection theory: Hit and false alarm fraction 3.

Identify neural correlates of sensory experience and choice response!

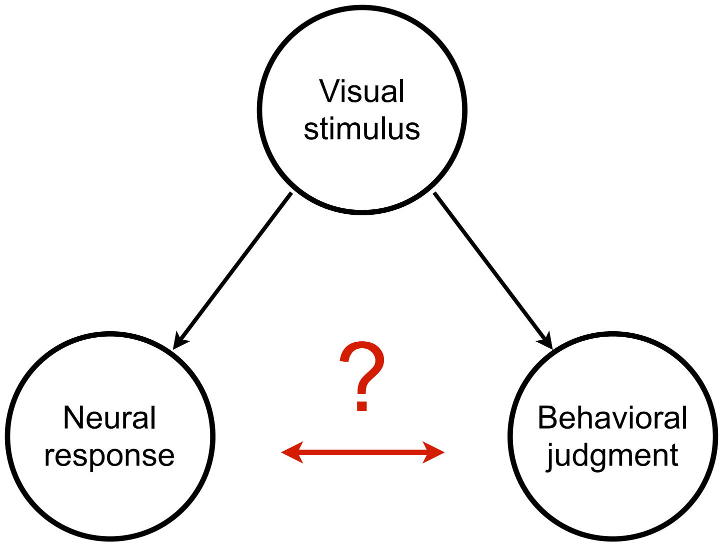


Figure 4: Neural correlates of sensory experience and choice response.

2 Discrimination of visual motion: psychometric function

Macaque monkeys viewed an array of moving dots and reported the prevailing direction of motion. Task difficulty varied with the fraction of dots moving coherently (**% coherence** or **% correlation**).

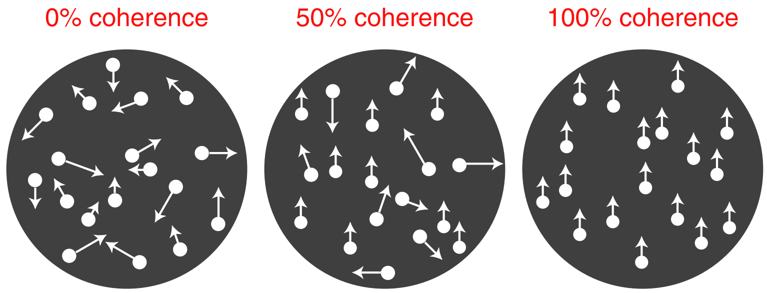


Figure 5: Percentage of coherence. [1]

Behavioral task

Animal views stimulus while holding fixation, uses subsequent eye movement to report perceived direction.

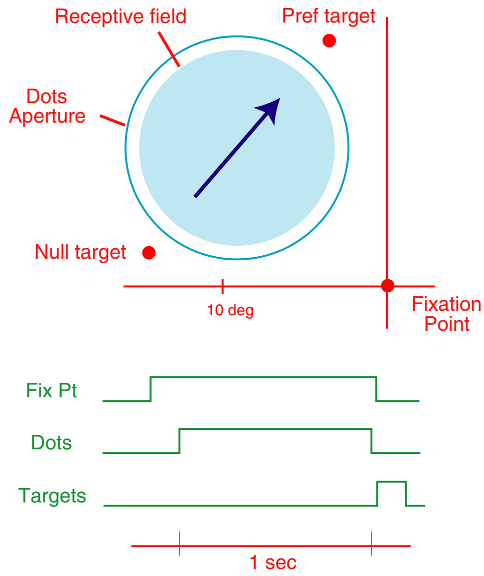


Figure 6: Behavioral task. [2]

Psychometric function

Behavioral performance **(% correct)** improves with stimulus strength **(% correlation)**.

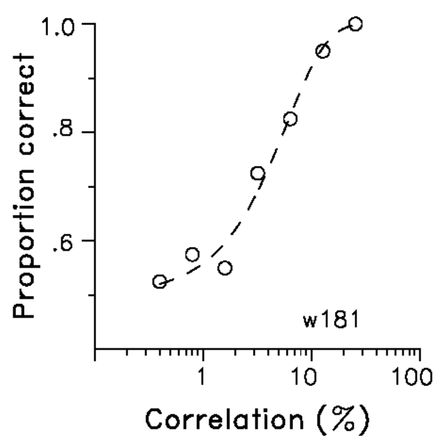


Figure 7: Psychometric function.

SDT assumptions

Assume neural response r with distinct normal distributions $p(r|+)$ or $p(r|-)$, depending on motion direction $+$ or $-$.

Assume means $k\,c$ and $-k\,c$ proportional to dot coherence c and a decision threshold θ.

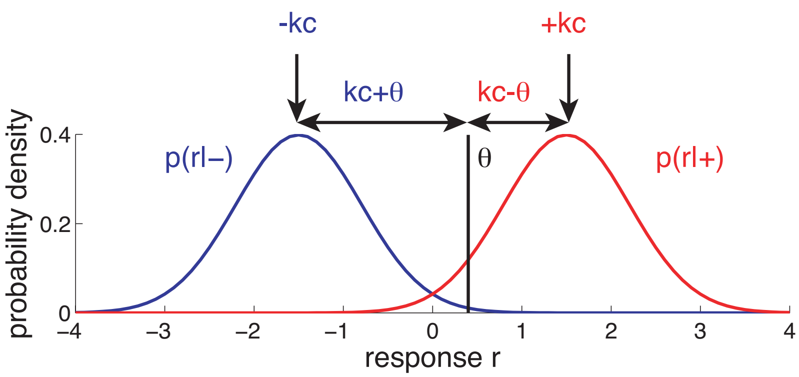


Figure 8: SDT assumptions.

The *hit* and *false alarm* rates are

$$H = \int_{-kc+\theta}^{\infty} p(r|+)\,dr \qquad\qquad z(H) = kc - \theta$$

$$F = \int_{kc+\theta}^{\infty} p(r|-)\,dr \qquad\qquad z(F) = -kc - \theta$$

Sensitivity or discriminability d' is

$$d' = z(H) - z(F) = 2\,k\,c$$

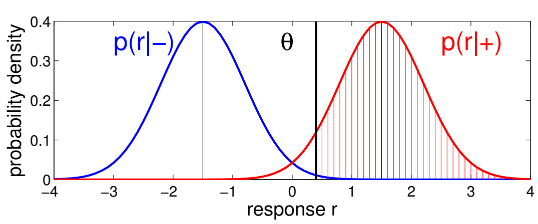


Figure 9: STD assumptions.

Different signal strengths (criterion $\theta = 0.2$)

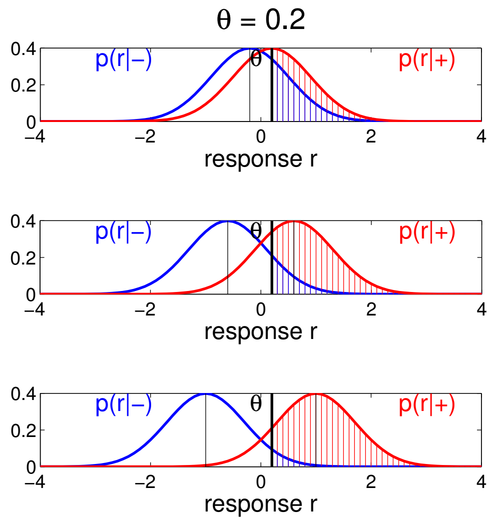


Figure 10: Different signal strength (criterion $\theta = 0.2$). Top: $kc = 0.2$. Middle: $kc = 0.6$. Bottom: $kc = 1.0$

Different signal strengths (criterion $\theta = -0.2$)

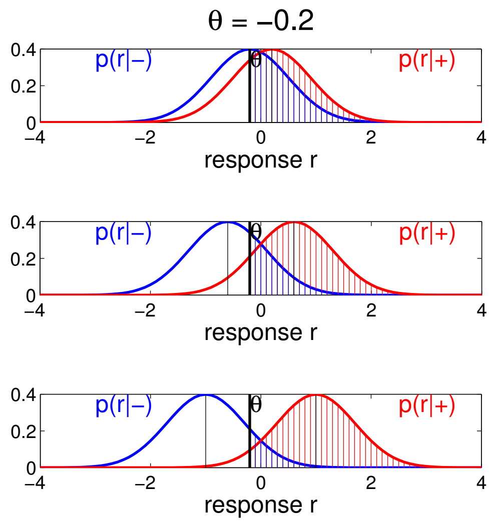


Figure 11: Different signal strengths (criterion $\theta = -0.2$).Top: $kc = 0.2$. Middle: $kc = 0.6$. Bottom: $kc = 1.0$

Theoretical psychometric function

Assuming that + and − motions occur equally often, the proportion correct is

$$P_{correct} = \frac{H}{2} + \frac{1-F}{2}$$

with

$$H(c) = \int_{-kc+\theta}^{\infty} N(r)\,dr = \frac{1}{2} + \frac{1}{2}\,erf\left(\frac{kc-\theta}{\sqrt{2}}\right)$$

$$F(c) = \int_{kc+\theta}^{\infty} N(r)\,dr = \frac{1}{2} + \frac{1}{2}\,erf\left(\frac{-kc-\theta}{\sqrt{2}}\right)$$

the dependence on c can be computed (see next page).

Theoretical psychometric function

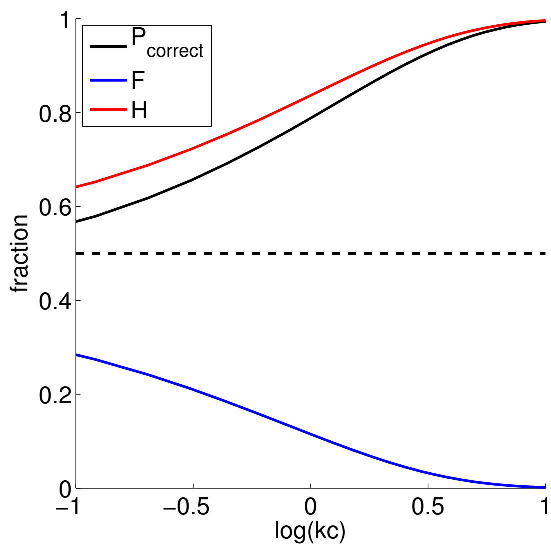


Figure 12: Theoretical psychometric function.

Experimental and theoretical psychometric function

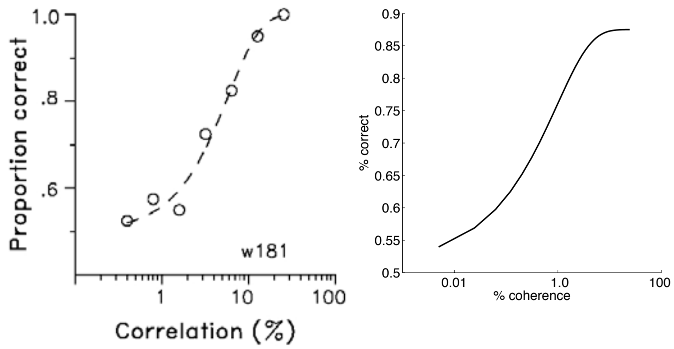


Figure 13: Experimental and theoretical psychometric function.

Summary psychometric function

- Quantitative relation between stimulus strength and sensory experience/choice response.
- Identical stimuli produce variable experience/response.
- Response probability consistent with comparison to fixed criterion
- Psychometric function is consistent with SDT assumptions.

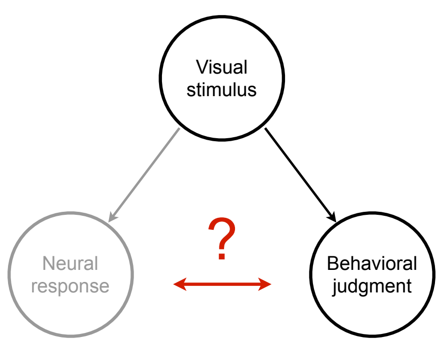


Figure 14: Relationship between neural responses and behavioral judgement.

3 Discrimination of visual motion: neurometric function

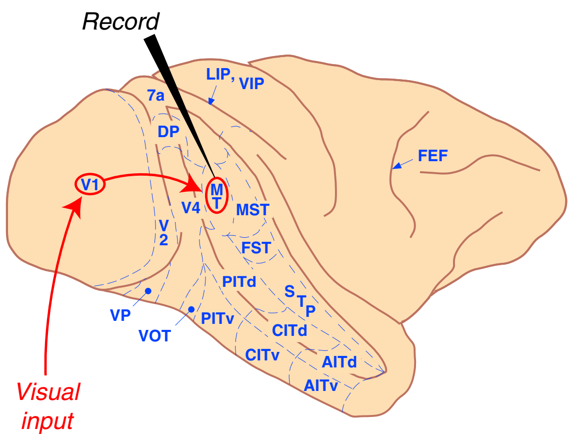


Figure 15: Discrimination of visual motion. [3]

Direction-selective neurons

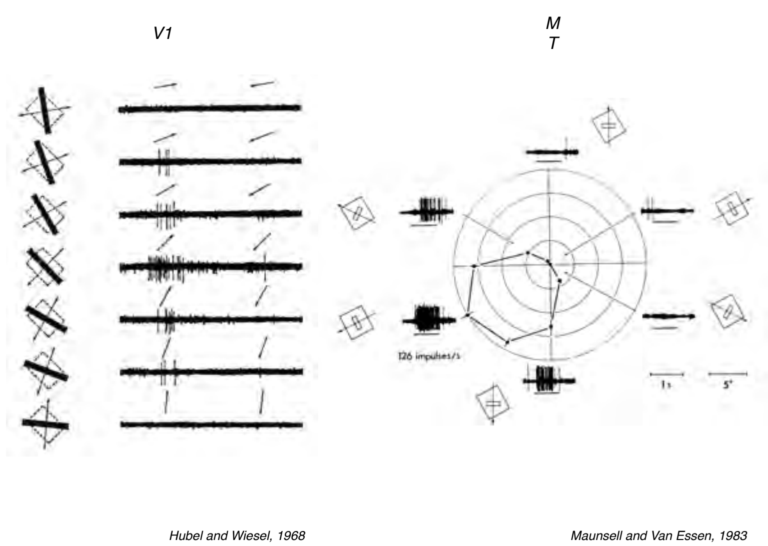


Figure 16: Direction-selective neurons. [4]

Tuning curve and response variability

Mean response varies with direction and coherence of motion.

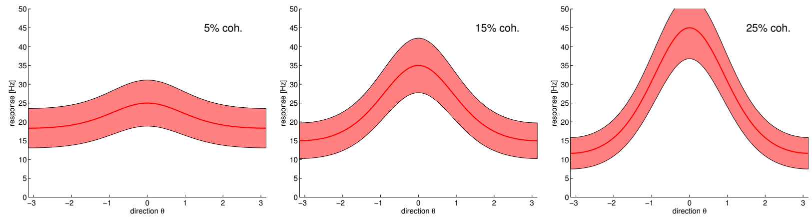


Figure 17: Tuning curve and response variability.

Preferred and anti-preferred direction

Present either ‘preferred’ or ‘null’ direction.

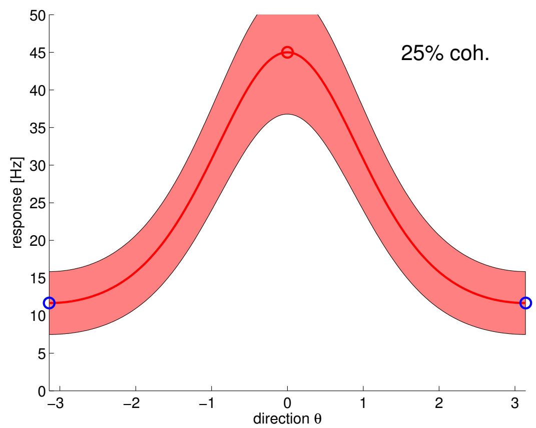


Figure 18: Preferred and anti-preferred direction.

Behavioral task

Animal views stimulus while holding fixation, uses subsequent eye movement to report perceived direction.

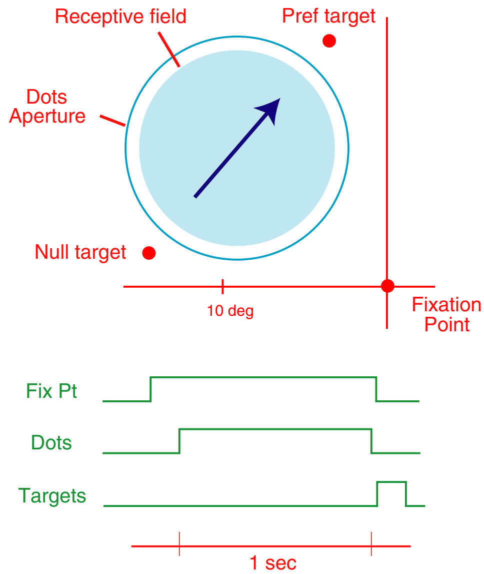


Figure 19: Behavioral task. [2]

Response in area MT

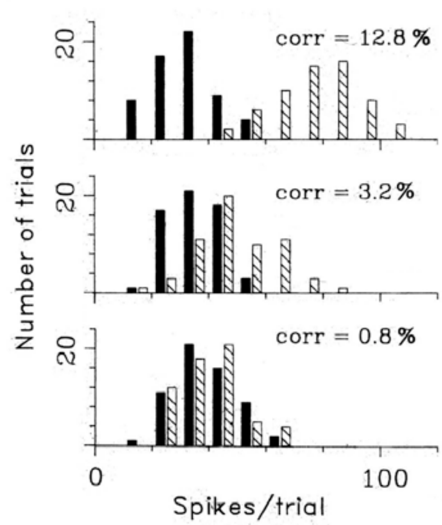


Figure 20: Response in area MT. Filled columns: antipreferred motion. Hatched columns: preferred motion. Different signal strengths (% corr). dentical stimuli result in variable responses!

How reliable would choice be, if based on this neural response?

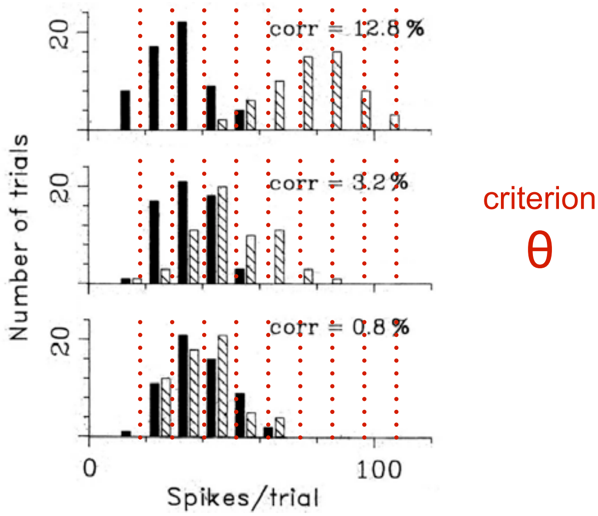


Figure 21: Neural response.

For each value of θ, obtain fraction of hits H and false alarms F
Receiver-operating characteristics

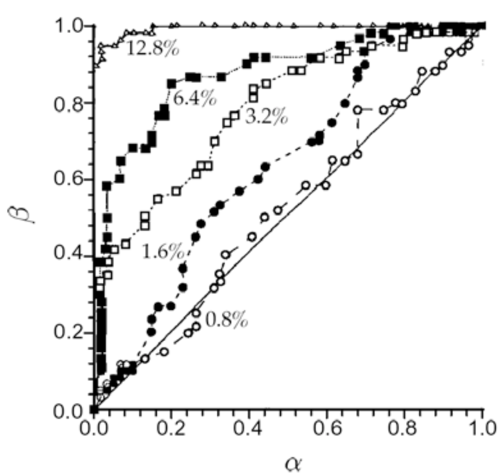


Figure 22: Receiver-operating characteristics.

Obtain ROC curves for different signal strengths (% coherence)

Neurometric function

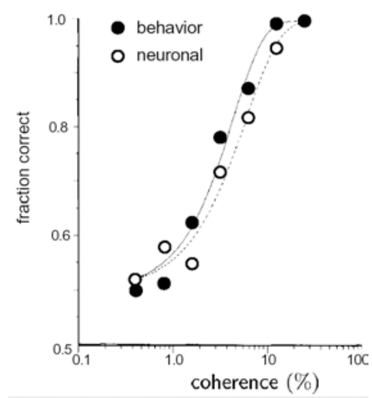


Figure 23: Neurometric function.

Use ROC to obtain optimal performance (% correct) curves for different signal strengths (% coherence)

Summary neurometric function

- Quantitative relation between stimulus strength and reliability of hypothetical choice response.
- Reliability of hypothetical choice quantifies the information encoded by neural activity.
- Natural unit for comparing 'psychometrics' and 'neurometrics'.

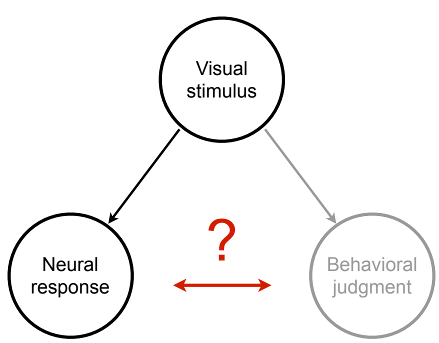


Figure 24: Relationship between behavioral judgement and neural response

4 Comparing neurometric and psychometric functions

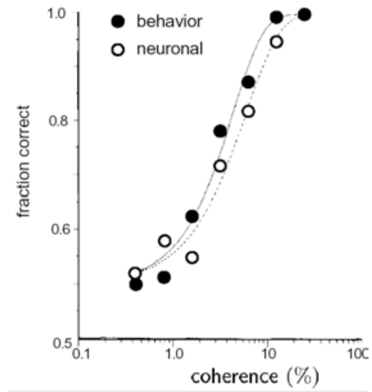


Figure 25: Comparing neurometric and psychometric functions.

Compare behavioral performance of animal with optimal (predicted) performance on the basis of a single neuron response.

Several neurons

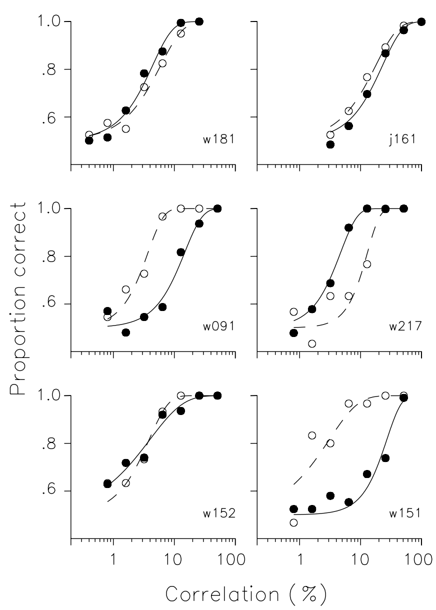


Figure 26: Functions of several neurons. Animal knows more than some neurons. Some neurons know more than (distracted?) animal. Some neurons know as much as animal.

Comparison neurometric and psychometric thresholds

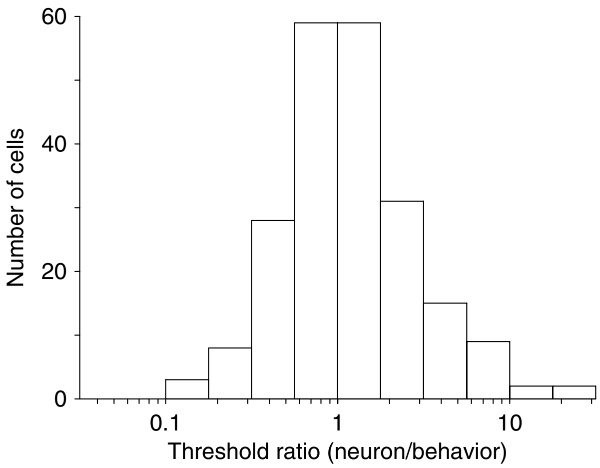


Figure 27: Comparison neurometric and psychometric thresholds.

On average, individual neurons know as much as entire animal.

Comparison of correct and error trials

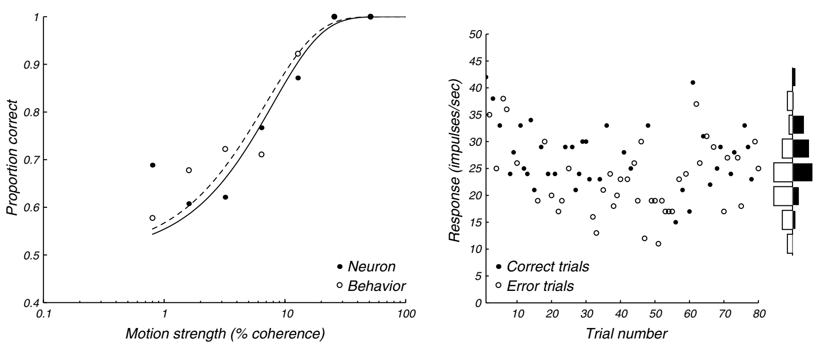


Figure 28: Comparison of correct and error trials.

Subjective experience/choice response and neural activity in area MT are correlated in comparison of 'correct' and 'error trials'.

Summary comparison

- Subjective experience and neuronal response were compared in units of behavioral performance.
- Excellent agreement at level of average performance and of trial-by-trial variability.
- Neural response is plausible contribution to subjective experience.

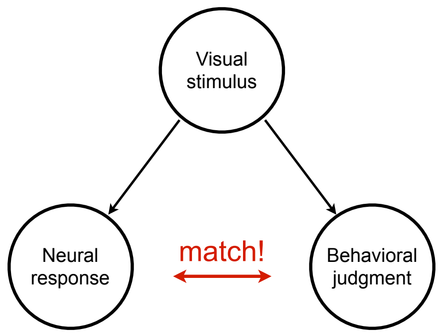


Figure 29: Match between neural response and behavioral judgement.

5 Too good to be true?

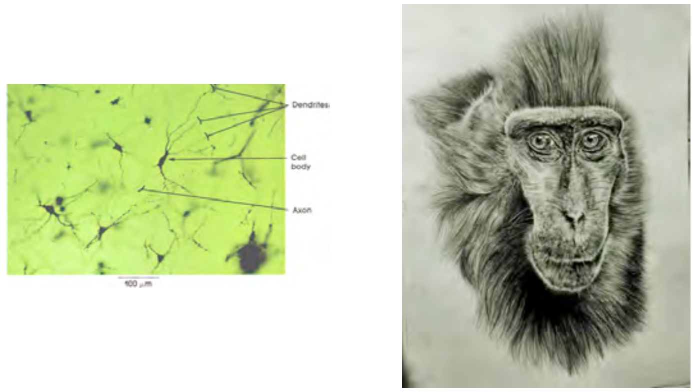


Figure 30: Neurons inside animal's brain [5], [6]

Why does an animal, with many thousands of neurons in its brain, not know more about a stimulus than an individual neuron does?

Sets of neurons with different direction-selectivity

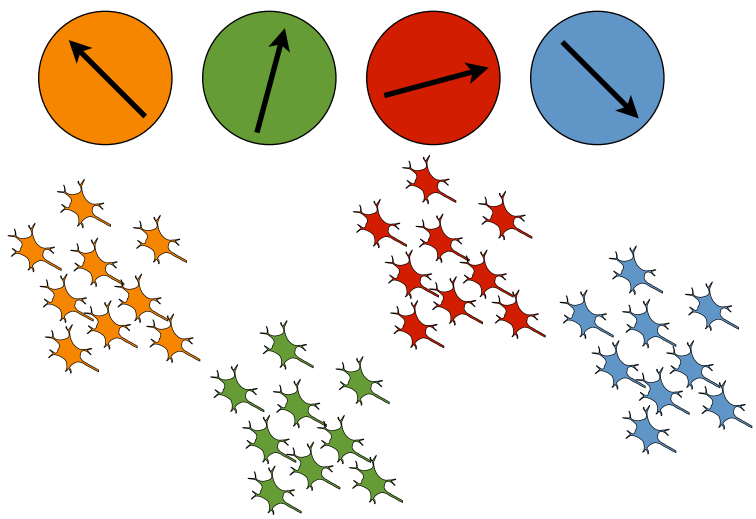


Figure 31: Sets of neurons with different direction-selectivity. [7]

$O(10^4)$ neurons respond to two alternative directions of visual motions and can be assumed to inform behavioral choice.

Decisions based on 'pooled' responses

When we 'pool' the responses of several neurons, we take the decision on the basis of an average, rather than an individual, response. How does this improve the decision?

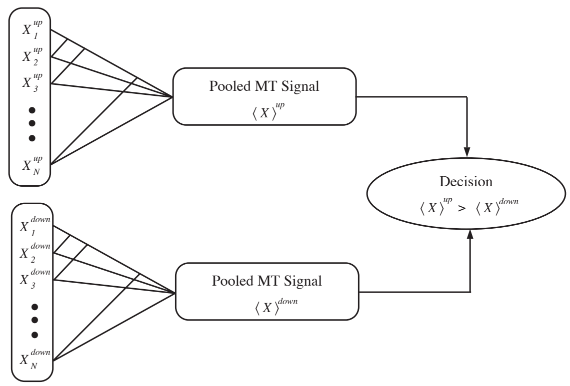


Figure 32: Decisions based on 'pooled' responses.

Individual activities

Consider *individual* activities as n *independent* random variables r_1, r_2, with means $\mu_1, \ldots, \mu_n$ and variances $\sigma_1^2, \ldots, \sigma_n^2$.

Discriminability d'_i based on *individual* activities will reflect the individual mean μ_{ind} and standard deviation σ_{ind}:

$$d'_{ind} \propto \frac{\mu_{ind}}{\sigma_{ind}}$$

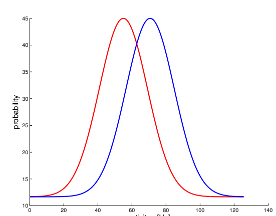


Figure 33: Discriminability.

Summed responses

The sum $r_{sum} = \Sigma\, r_i$ of all responses is another random variable. Its mean and variance are

$$\mu_{sum} = \sum_{i=1}^{n} \mu_i = n\,\mu_1$$

$$\sigma^2_{sum} = \sum_{i=1}^{n} \sigma^2_i = n\,\sigma^2_1$$

Discriminability d'_{sum} based on *summed* responses will be

$$d'_{sum} \;=\; \frac{\mu_{sum}}{\sigma_{sum}} = \frac{n\,\mu_{ind}}{\sqrt{n\,\sigma^2_{ind}}} = \sqrt{n}\,d'_{ind}$$

Summing *independent* responses of n neurons should improve discriminability by a factor of $\sqrt{n}$!

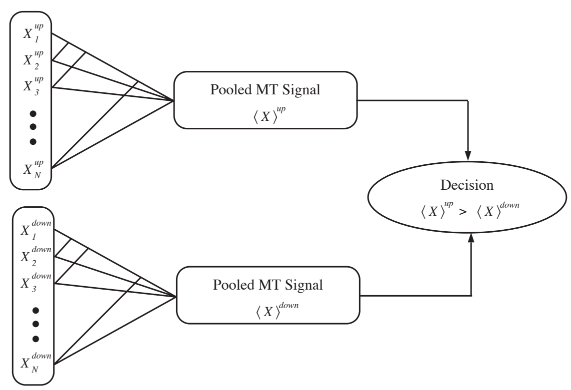


Figure 34: Summed responses.

Given 10^4 independently variable neurons, psychometric performance should be 100 times better than neurometric performance.

Summary Too good to be true?

- Averaging n *independently* variable responses is expected to increase sensitivity d' by a factor of $\sqrt{n}$.

- As psychometric and neurometric performance is comparable, neuronal response variability cannot be independent!

- Degree of dependence is measured by Pearson correlation coefficient c.

- For $c \in [0, 1]$, sensitivity improves by a factor of

$$\sqrt{\frac{n}{1 + (n - 1)c}}$$

6 SDT Tutorial: strength of correlations

Discrimination between moving dot patterns of different degrees of coherence can be modelled as follows. Assume **mean response** proportional to coherence:

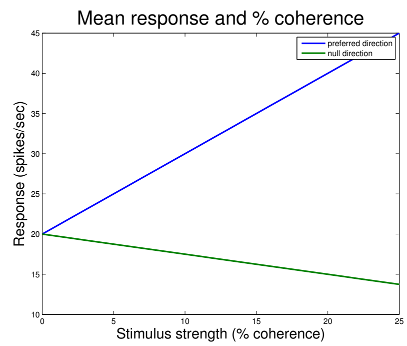


Figure 35: Mean response proportional to coherence.

Response variance

Assume **response variance** approximately equal to 1.5 times the mean response (Fano factor = 1.5).

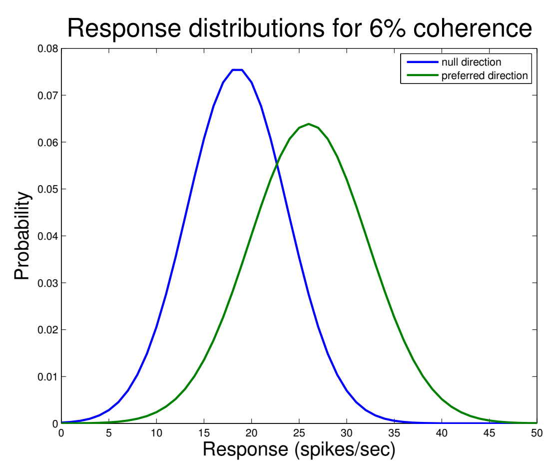


Figure 36: Response distribution.

Response variance

For each signal strength, convert response histograms into ROC curves and determine optimal performance (% correct)

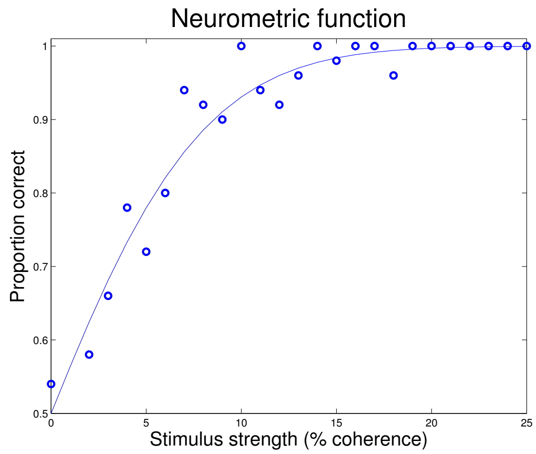


Figure 37: Neurometric function.

Summing responses of two neurons

Summing responses of two neurons increases the available information and improves performance:

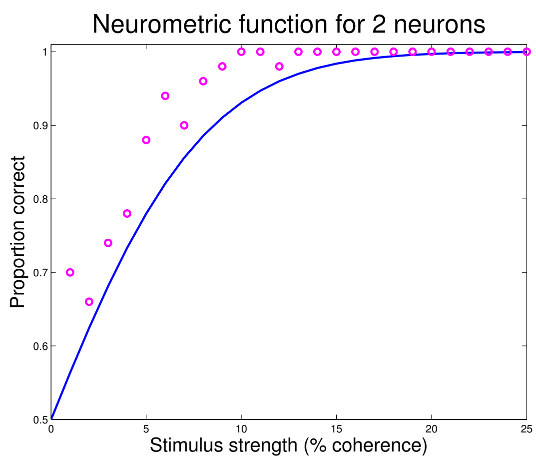


Figure 38: Neurometric function for 2 neurons.

Summing responses of *uncorrelated* neurone

Summing responses of 2, 10, and 100 neurons with uncorrelated responses would improve performance enormously. This is not observed!

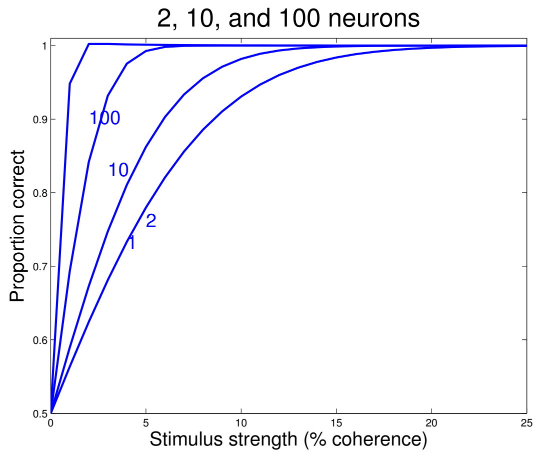


Figure 39: Responses for 2, 10 and 100 uncorrelated neurons.

Summing responses of *correlated* neurons

Summing correlated responses is much less beneficial. Even a small correlation ($c = 0.1$), limits effective pool size to O(100).

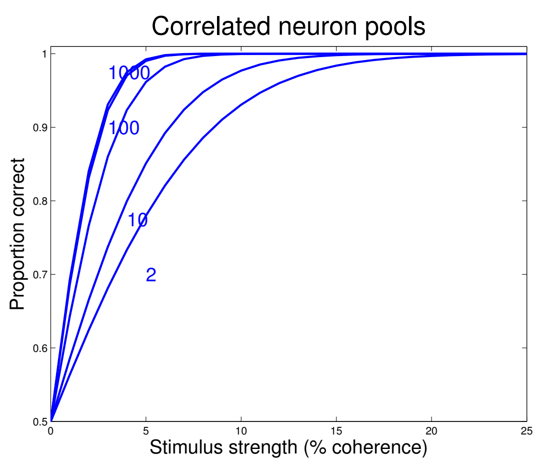


Figure 40: Responses for 2, 10 and 100 correlated neurons.

Summary SDT tutorial

- Realistic model of selectivity and variability of direction-selective responses.
- Predict behavioral performance (**% correct**) as a function of stimulus strength (**% correlation**).
- For independent responses, behavioral performance increases rapidly with neuron number.
- For correlated responses, behavioral performance saturates with neuron number.
- The similarity of psychometric and neurometric functions is a typical result and suggests that individual neuronal responses are correlated.

Overall summary

Choice performance (d' or % correct) quantifies information available to organism, or encoded in neural activity.

Signal-detection theory relates choice performance to underlying neural activity (actual or hypothetical).

Comparison of psychometric and neurometric functions identifies candidate neural populations on which choice response may be based.

When psychometric and neurometric functions are similar, neuronal activities are correlated and do not vary entirely independently.

7 Bibliography

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