

THEORETICAL NEUROSCIENCE I

Lecture 12: Psychophysics and signal-detection theory

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1. Psychophysics
2. Signal-detection theory (forwards)
3. Signal-detection theory (backwards)
4. Big picture

1 Psychophysics

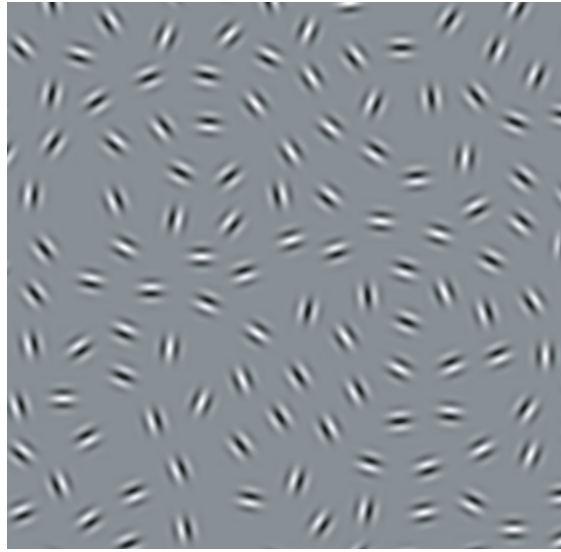


Figure 1: Psychophysics image. [1]

Do you see the peanut?

Stimulus and choice response

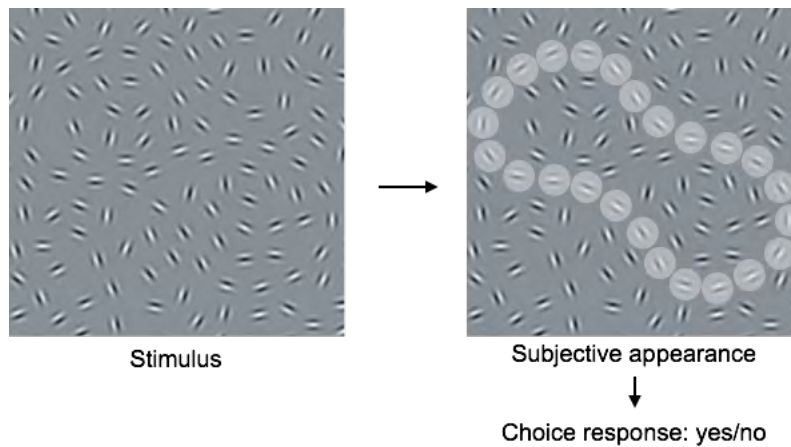


Figure 2: Stimulus and subjective appearance. [2]

Psychophysics is the science of objectively measuring subjective experience. It uses carefully controlled physical stimuli to systematically

manipulate subjective experience.

Thresholds

- *Detection (absolute threshold)*: Can you still hear this tone?
- *Discrimination (difference threshold)*: Is it a high or low tone?
- *Identification*: Which word is it?

Methods

- *Method of constant stimuli*: fixed range of stimulus intensities.
- *Method of limits*: stimulus intensity adjusted according to correct or incorrect responses.
- *Method of adjustment*: subjects adjust intensity of comparison stimulus to match a given probe stimulus.

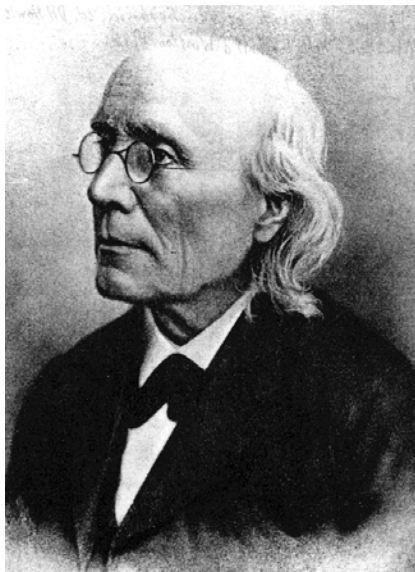


Figure 3: Left: Gustav-Theodor Fechner (1801-1877). Right: Ernst-Heinrich Weber (1795-1878). [3] [4]

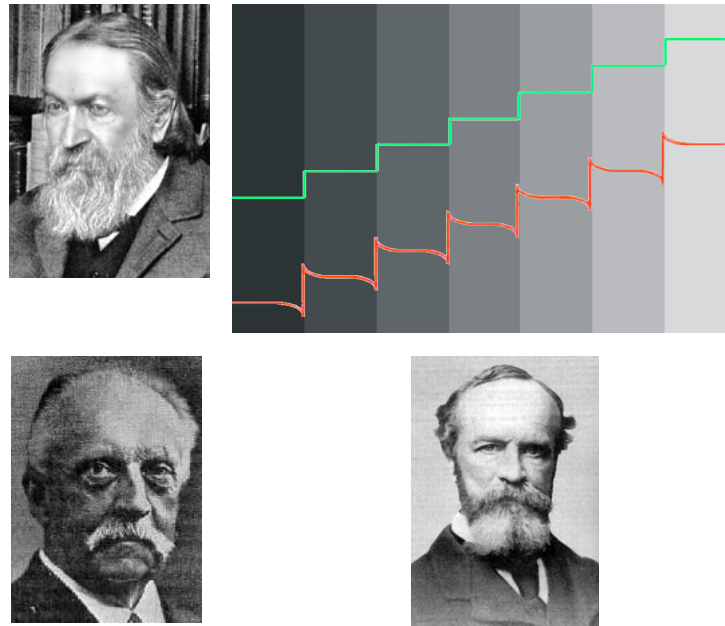


Figure 4: Top: Ernst Mach (1838-1916). Left: Hermann von Helmholtz (1821-1894). Right: William James (1842-1910) [5] [6] [7]

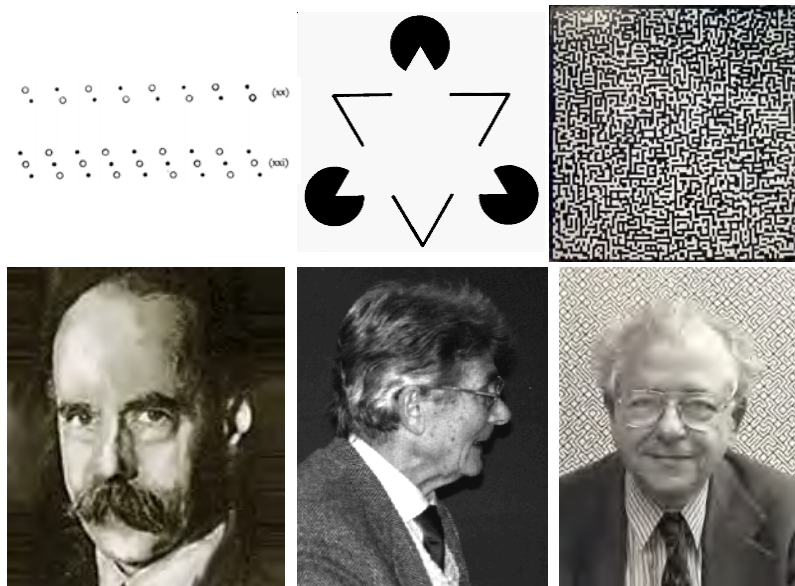
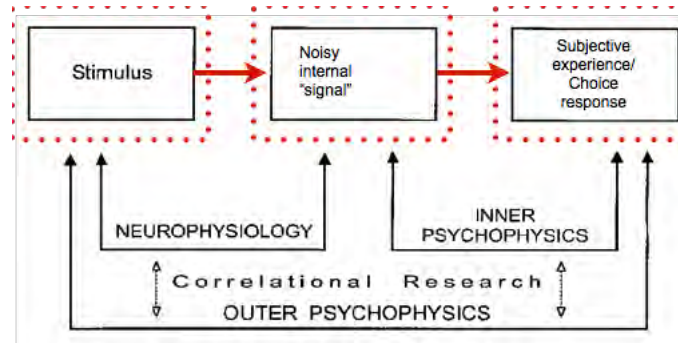


Figure 5: Left: Max Wertheimer (1880 - 1943). Middle: Gaetano Kanizsa (1913 - 1993). Right: Bela Julesz (1928 - 2003) [8] [9] [10] [11] [12]

Physical stimulus \rightarrow neural response \rightarrow subjective

experience



SDT quantifies reportable information about discrete stimulus classes at the level of subjective experience. It sets a *lower bound* on such information at the level of neural responses.

Neural versus behavioral ‘response’

- Neural ‘response’: neuronal activity, spike rate, ...
- Behavioural ‘response’: categorical action or perception (e.g., in a choice-response task or a detection/discrimination task)

2 Signal-detection theory (forwards)

Nearly all reasoning and decision making takes place in the presence of some uncertainty. Signal detection theory provides a precise language and graphical notation for analyzing decision making in the presence of uncertainty. Signal detection theory applies directly to sensory experiments (psychophysics). It also applies to decision problems in many other areas that face uncertainty:

- Telecommunication
- Economics
- Medical diagnostics
- Medical therapeutics

SDT was developed in the context of radar research and adapted to psychophysics by Green & Swets (1966). It allows the separate quantification of *sensitivity* and *decision criterion*.

We will develop SDT in four steps, reasoning from neural activity *forwards* to behavioral performance:

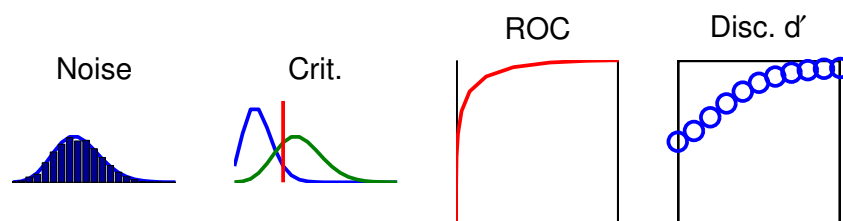


Figure 6: Four steps of SDT.

Flash detection

An observer is asked to detect very dim flashes of light in a dark room. At regular intervals, a sound signal prompts the observer to respond ‘‘*yes*’’ if he just saw a flash and ‘‘*no*’’ if he didn’t. However, flashes are present only in half the trials (chosen randomly).

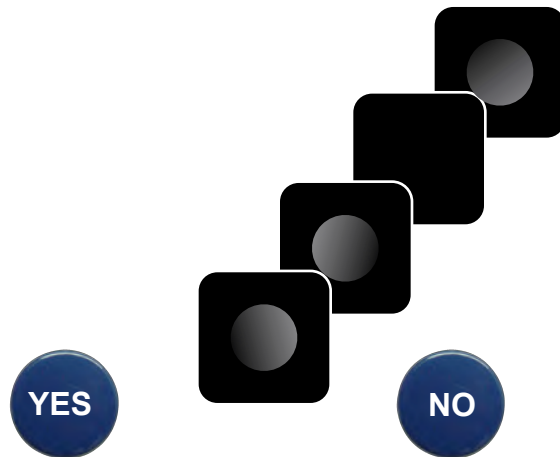


Figure 7: Flash detection test.

Variable sensory signal

For the sake of concreteness, we consider a sensory signal with known variability: isomerization of photopigments in the retina. Isomerizations are independent and their number varies from trial to trial. Number of isomerizations k is Poisson distributed around an average of $\langle k \rangle = \lambda$

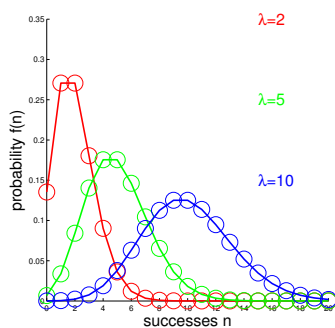


Figure 8: Variable sensory signal at 3 levels of Poisson distribution.

$$P_k = \frac{\lambda^k e^{-\lambda}}{k!} \quad \sum_{k=0}^{\infty} P_k = 1 \quad \langle k \rangle = \sum_{k=0}^{\infty} k P_k = \lambda$$

Noise trial

In the absence of a flash, we assume that, on average, $\lambda_N = 3$ photopigment molecules in the observer's retinal isomerize spontaneously, due to thermal noise.

$$P_k^{Noise} = \frac{3^k e^{-3}}{k!} \quad \langle k \rangle_{Noise} = 3$$

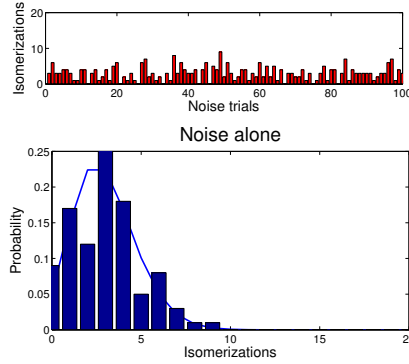


Figure 9: Trial in absence of flash.

Signal trial

In the presence of a flash, we assume that 8 photopigment molecules isomerize, on average:

$$P_k^{Signal} = \frac{8^k e^{-8}}{k!} \quad \langle k \rangle_{Signal} = 8$$

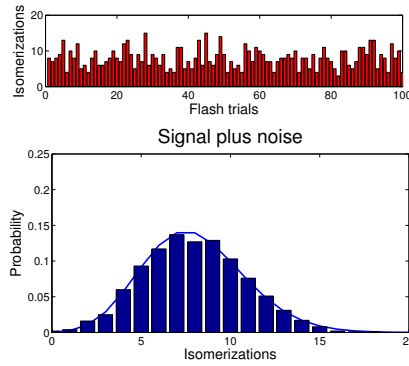


Figure 10: Trial in presence of flash.

Summary first step: noise

- Identical sensory events result in variable neural responses (isomerizations).
- Neural response (isomerization) is a random variable with some probability distribution (here: Poisson distribution).
- In our example, variability is due to exclusively to external noise (photon absorption).

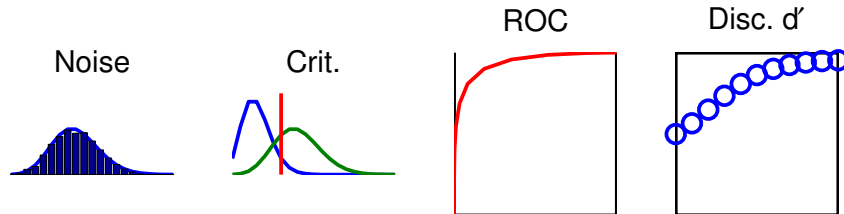


Figure 11: Four steps of SDT.

Observer report

Assume that an observer has introspective (phenomenal) access to the number of isomerizations in terms of the perceived flash intensity and

that she is able to describe her visual experience. For example, an observer could (if so instructed) report the perceived flash intensity on a scale of 1 to N.

Alternatively, an observer can classify (if so instructed) the perceived flash intensity in terms of “present/yes” or “absent/no” categories. Given only two response choices, the observer is thus obliged to adopt a **decision criterion**.

Criterion for binary decision

Suppose that a particular observer adopts a *criterion* $c = 6$ isomerizations, reporting “*yes*” when the perceived intensity exceeds this value and “*no*” when it falls short.

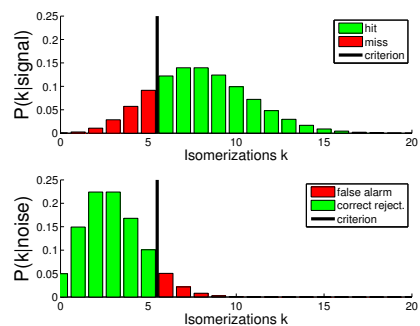


Figure 12: Overlap distributions of signal and noise.

Note that signal and noise distributions **overlap!** Thus, the observer is bound to make mistakes (report incorrectly). In the presence of uncertainty, decisions cannot always be accurate!

Hits

Four possible outcomes: **hits**, false alarms, misses, rejections.

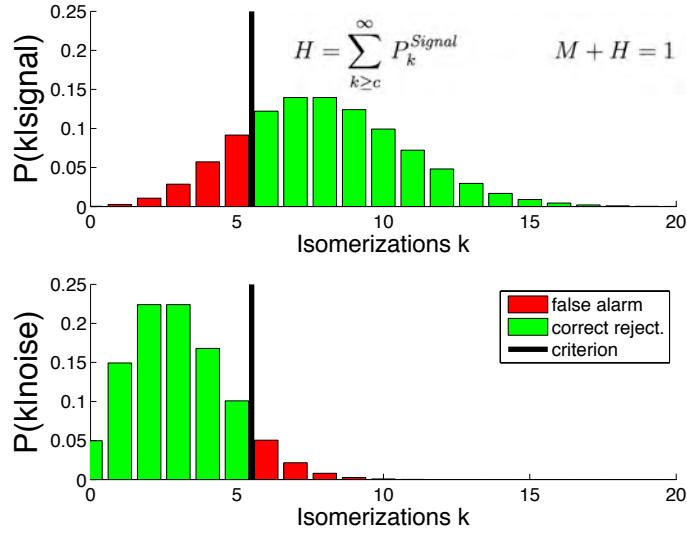


Figure 13: Hits.

False alarms

Four possible outcomes: hits, **false alarms**, misses, rejections.

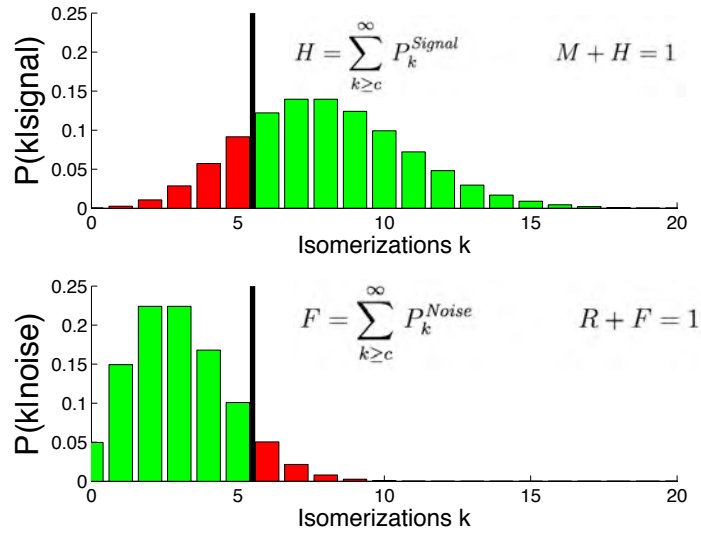


Figure 14: False alarms.

Misses & rejections

Four possible outcomes: hits, false alarms, **misses**, **rejections**.

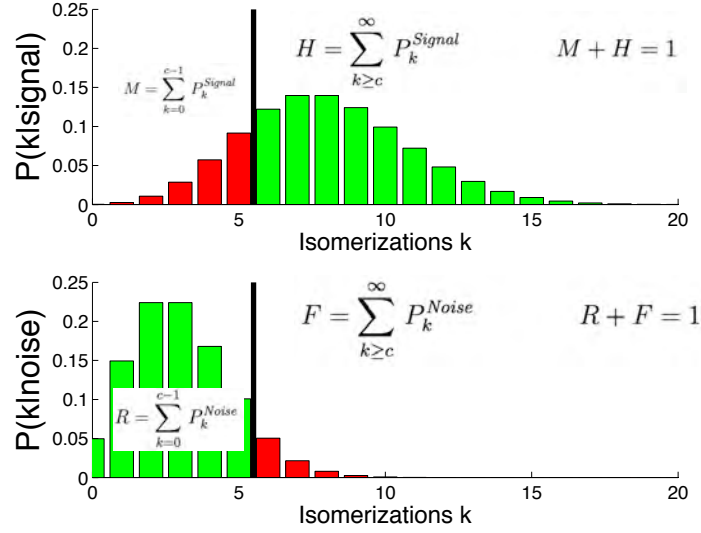


Figure 15: Misses and rejections.

The behavioral results can be fully characterized in terms of ‘hit’ rate and ‘false alarm’ rate:

$$H \equiv P(\text{‘yes’} | \text{‘signal’}) = \frac{\text{no. hits}}{\text{no. signal trials}} = \sum_{k \geq c} P_k^{Signal}$$

$$F \equiv P(\text{‘yes’} | \text{‘noise’}) = \frac{\text{no. false alarms}}{\text{no. noise trials}} = \sum_{k \geq c} P_k^{Noise}$$

The *fraction correct* is defined as

$$P_{corr} \equiv \frac{P(\text{‘yes’} | \text{‘signal’}) + P(\text{‘no’} | \text{‘noise’})}{2} = \frac{H}{2} + \frac{1 - F}{2}$$

and the fraction of ‘yes’ responses is

$$P_{yes} \equiv \frac{P(\text{‘yes’} | \text{‘signal’}) + P(\text{‘yes’} | \text{‘noise’})}{2} = \frac{H + F}{2}$$

Determinants of F and H

Note that the fraction of outcomes F and H depends on two factors:

- *Signal strength*, the physical difference between signal and noise or, in other words, the degree of overlap between the two distributions. In our example, $\Delta\lambda = \lambda_{Signal} - \lambda_{Noise} = 8 - 3 = 5$.
- *Criterion level*, the decision criterion adopted by the observer. This may reflect his free choice, the rewards/penalties associated with different responses, or many other factors. In our example, $c = 6$.

The aim of SDT is to independently measure *signal strength* and *criterion level*.

Summary second step: decision criterion

- Behavioural choices create the necessity for classifying a continuum of sensory experience.
- In our example, two distinct stimuli elicit overlapping distributions of sensory experience.
- For two stimuli and two responses, there are four possible trial outcomes: hits, misses, false alarms and correct rejections.
- *hits* and *false alarms* suffice to capture the situation:

$$H = P(\text{'yes'} | \text{'signal'})$$

$$F = P(\text{'yes'} | \text{'noise'})$$

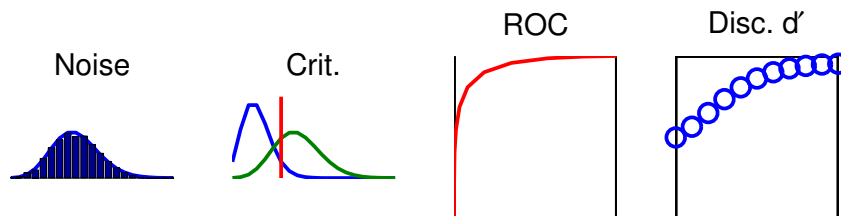


Figure 16: Four steps of SDT.

Liberal criterion

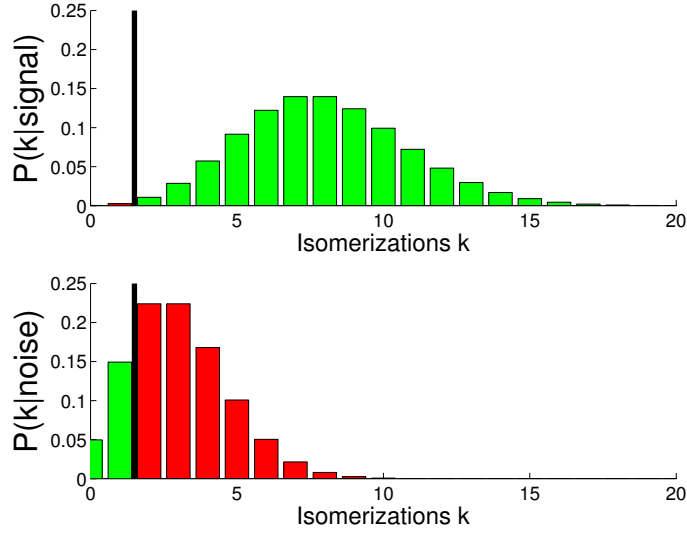


Figure 17: With a liberal criterion $c = 2$, H and F are both large.

Conservative criterion

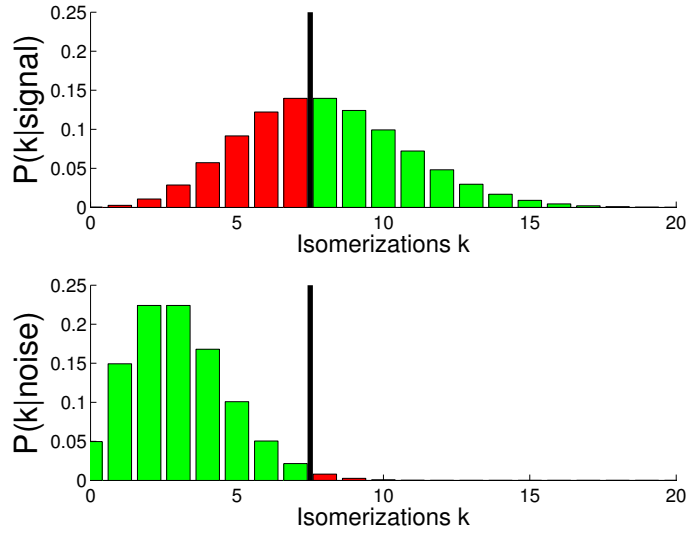


Figure 18: With a conservative criterion $c = 8$, H and F are both small.

Optimal criterion

To determine the optimal criterion, we need to know the costs and benefits associated with correct and incorrect reports. Assuming that all

incorrect reports ('misses' and 'false alarms') are equally costly, the optimal criterion is the criterion that minimizes the total number of incorrect reports.

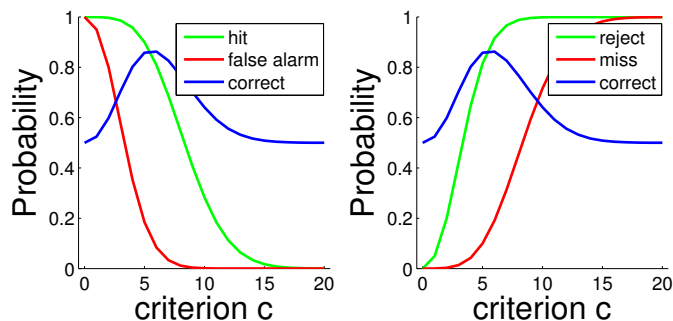


Figure 19: Evaluation of the costs and benefits for the criterion.

Optimal criterion

With an optimal criterion $c = 6$, $M + F$ is minimal:

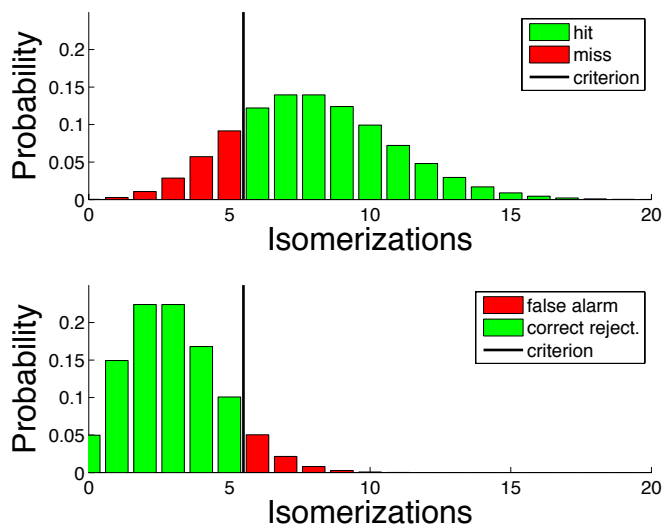


Figure 20: Optimal criterion.

Receiver-operating characteristic (ROC)

The *ROC* plots ‘hits’ against ‘false alarms’ (true positives against false positives), for different criterion levels.

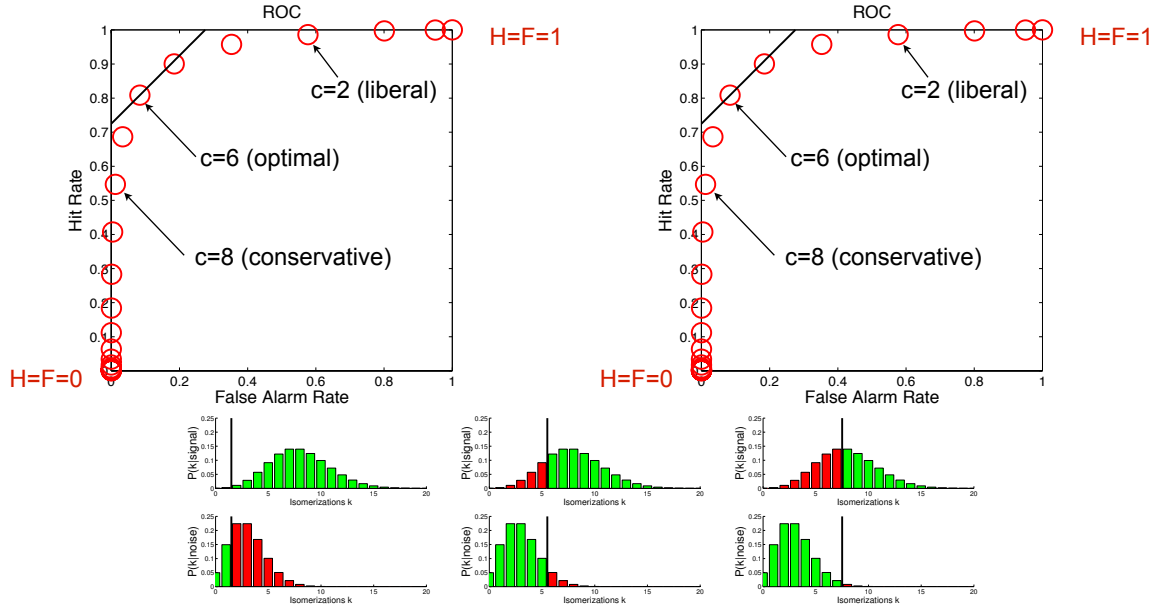


Figure 21: A Pyramidal cell. B Purkinje cell. C Stellate cell [2]

Summary third step: ROC

- Observers are free to place criterion where they see fit.
- As criterion moves from conservative to liberal, both F and H increase from 0 to 1.
- The receiver-operating characteristic (ROC) is $H = f(F)$.
- ROC reveals the optimal criterion and, thus, optimal performance.
- It quantifies reportable information about discrete stimuli, regardless of criterion.

Different signal strengths

The ROC analysis can be repeated for signals of different signal $\Delta\lambda$.

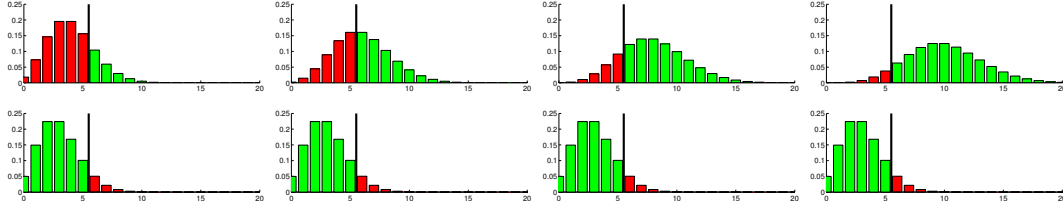


Figure 22: From left to right: $\Delta\lambda = 1$, $\Delta\lambda = 3$, $\Delta\lambda = 5$, $\Delta\lambda = 7$

Quantify signal strength

We can now quantify signal strength *independently* of decision criterion: (i) area under ROC, (ii) optimal performance.

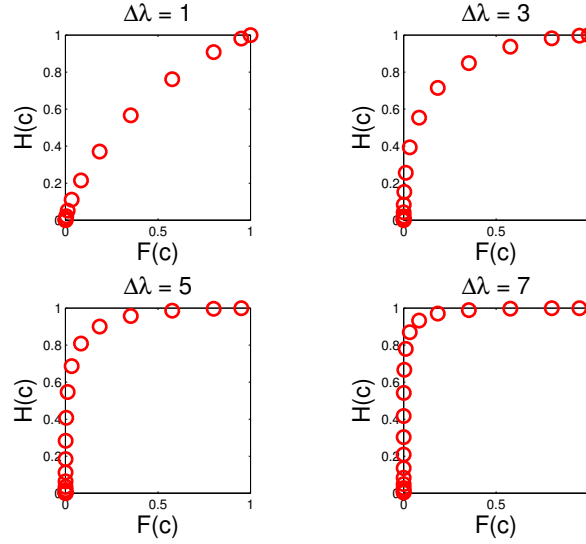


Figure 23: Quantification of signal strength.

Psychometric function I: reportable experience and signal strength

$$P_{opt}(\Delta\lambda) = \frac{1}{2} + \frac{H(\Delta\lambda, c_{opt}) - F(\Delta\lambda, c_{opt})}{2}, \quad c_{opt} = f(\Delta\lambda)$$

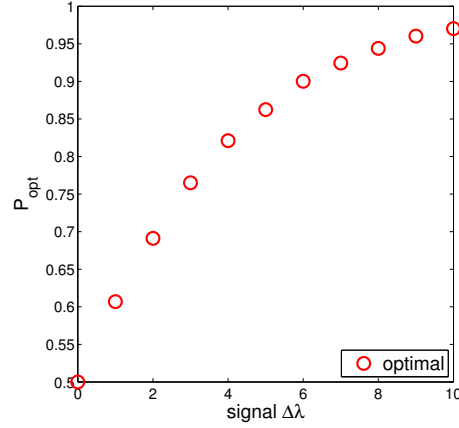


Figure 24: Optimal signal strength.

Summary fourth step: psychometric function

- ROC analysis involves H and F for different criteria c .
- Repeating ROC analysis for different $\Delta\lambda$, reveals optimal criterion $c_{opt} = f(\Delta\lambda)$ for each $\Delta\lambda$.
- In turn, this yields optimal performance $P_{opt}(\Delta\lambda)$ for each $\Delta\lambda$.
- Taken together, this determines the psychometric function.

$$P_{opt}(\Delta\lambda) = \frac{1}{2} + \frac{H(\Delta\lambda, c_{opt}) - F(\Delta\lambda, c_{opt})}{2}, \quad c_{opt} = f(\Delta\lambda)$$

Summary SDT forwards

- Given noisy neural signals associated with stimulus presence or absence (e.g., flash detection), we determined the optimal detection performance.
- We assume that choice behavior is determined by comparing noisy signal with a fixed criterion c .

- We use ROC analysis to determine optimum criterion for each stimulus strength.
- We obtain psychometric function: increase of detection performance with signal strength.

3 Signal-detection theory (backwards)

SDT is even more useful when we can observe only choice responses and have no access to neural activity.

In this situation, we may infer statistical properties of (unobserved) neural responses from the (observed) behavioural responses.

Thus, we use SDT to reason *backwards* from choice responses to *predict* a hypothetical neural response.

Gaussian assumption

Assume that the (unobserved) underlying neural signal distributions (noise only and signal plus noise) are Gaussians of equal width.

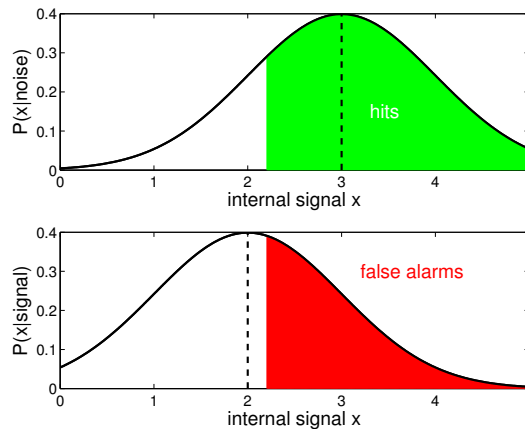


Figure 25: This assumption can be avoided with 2-alternative-forced choice experiments.

Knowns and unknowns

Presenting stimuli (signal or noise) repeatedly and observing associated choice responses, we establish the fractions H and F .

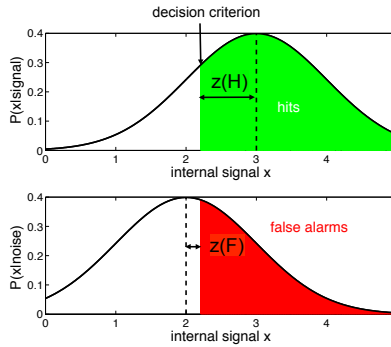


Figure 26: Fractions H and F .

How far apart are the distributions (discriminability)? Which criterion did the observer apply (bias)?

Aside: Quantiles and z-score values

Relate ‘quantiles’ and ‘z-score values’ of a signal distribution (normal distribution).

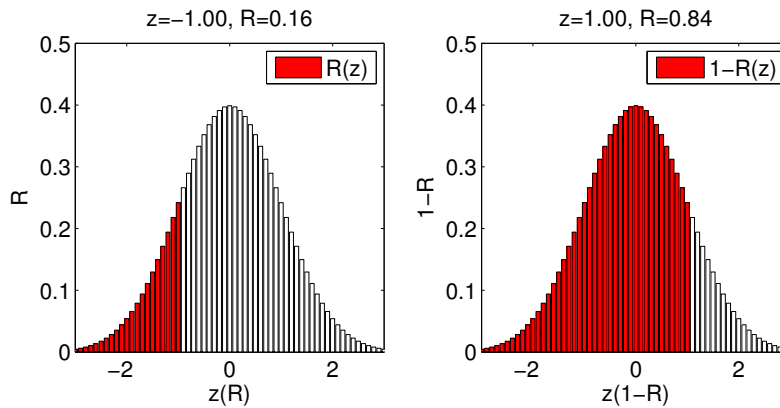


Figure 27: Quantiles R and z-score z

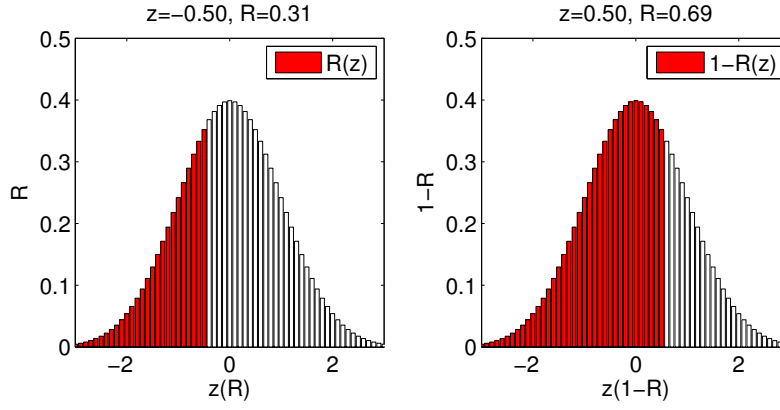


Figure 28: Quantiles R and z-score z

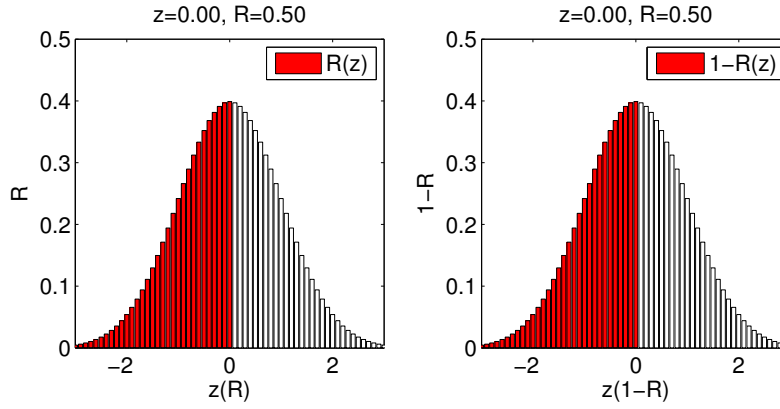


Figure 29: Quantiles R and z-score z

Useful formulas

The Z-score measures positive or negative distance *from the center* of a normal distribution:

$$R(z) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^z e^{-z'^2/2} dz' = \frac{1}{2} + \frac{1}{2} \operatorname{erf} \frac{z}{\sqrt{2}},$$

$$z(R) = \sqrt{2} \operatorname{erf}^{-1} (2R - 1)$$

$$z(1 - R) = -z(R)$$

$$\operatorname{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-x'^2} dx' \quad \xrightarrow{x=z/\sqrt{2}} \quad \frac{1}{2} \operatorname{erf}\left(\frac{z}{\sqrt{2}}\right) = \frac{1}{\sqrt{2\pi}} \int_0^z e^{-z'^2/2} dz'$$

Discriminability d' and bias c

Sensitivity d' measures signal strength in terms of the mean difference between the ‘*signal*’ and ‘*noise*’ distributions. Its unit is the standard deviation of the underlying signal distributions.

$$d' \equiv z(H) - z(F)$$

Response bias c measures the decision criterion of the observer (conservative, neutral, liberal), relative to the optimal criterion. Its unit is again the standard deviation of the underlying signal distributions.

$$c \equiv -\frac{z(H) + z(F)}{2}$$

Discriminability d'

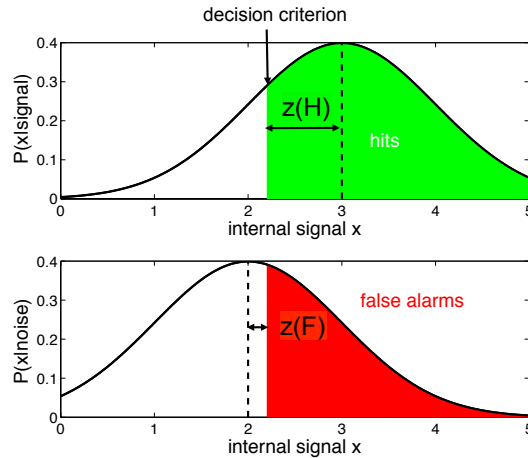


Figure 30: Discriminability d'

$$d' = z(H) - z(F)$$

$$z(1 - F) = \frac{d'}{2} + c = -z(F) \qquad z(H) = \frac{d'}{2} - c$$

Response bias c

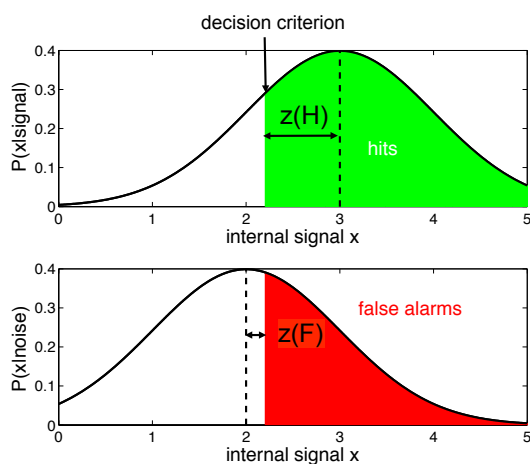


Figure 31: AResponse bias c

$$c = -\frac{z(H) + z(F)}{2}$$

$$z(1 - F) = \frac{d'}{2} + c = -z(F) \qquad z(H) = \frac{d'}{2} - c$$

Observed performance ...

Follows from from hits and false alarms:

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

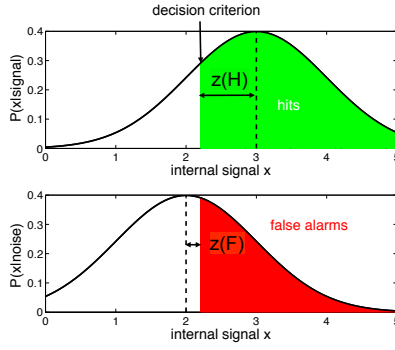


Figure 32: Observed performance.

...and optimal performance

Is the quantile of $d'/2$:

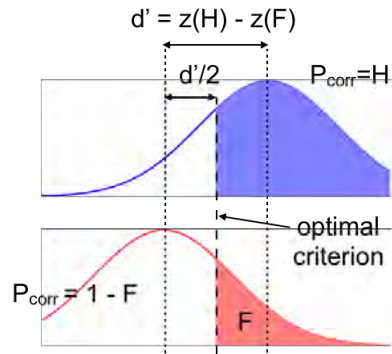


Figure 33: Optimal performance.

$$\begin{aligned}
 P_{opt} &= R(d'/2) = \frac{1}{2} + \frac{1}{2} \operatorname{erf} \frac{d'/2}{\sqrt{2}} = \frac{1}{2} + \frac{1}{2} \operatorname{erf} \frac{d'}{\sqrt{8}} = \\
 &= \frac{1}{2} + \frac{1}{2} \operatorname{erf} \frac{z(H) - z(F)}{\sqrt{8}}
 \end{aligned}$$

Psychometric function I:

discriminability d' and physical signal strength

Choose physical signal strength s , observe H and F , compute discriminability d'

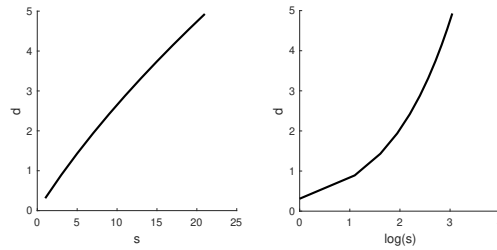


Figure 34: Discriminability d' and physical signal strength.

Psychometric function II: optimal performance and physical signal strength

Choose physical signal strength s , observe H and F , compute optimal performance P_{corr}

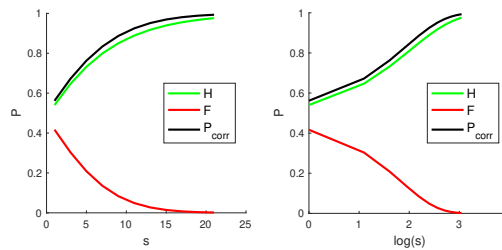


Figure 35: Optimal performance and physical signal strength.

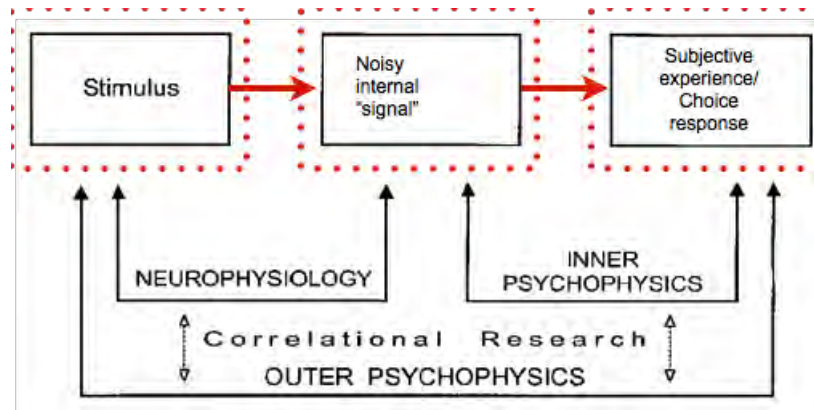
Summary SDT backwards

- With the Gaussian assumption, F and H may be converted to $z(F)$ and $z(H)$.

- Discriminability $d' = z(H) - z(F)$ quantifies sensory difficulty (distribution overlap), independently of decision criterion.
- Response bias $c = -\frac{z(H)+z(F)}{2}$ quantifies placement of decision criterion, independently of sensory difficulty.
- Optimal performance P_{opt} is

$$P_{opt} = \frac{1}{2} \left[1 + \operatorname{erf} \left(\frac{z(H) - z(F)}{\sqrt{8}} \right) \right]$$

4 Big picture



Importance of psychophysics

Psychophysics quantifies reportable information about discrete stimulus classes within subjective experience.

Reveals ‘behaviorally available’ information encoded by a sensory system.

Sets ‘lower limit’ for information encoded by candidate neural populations.

Predicts response characteristics of candidate neural populations (rel. distribution widths & distances).

Psychophysics and related behavioural paradigms are an indispensable part of *integrative* neuroscience.

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