Cognitive Neural Systems and Behaviour

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from molecules to mind

Cognition

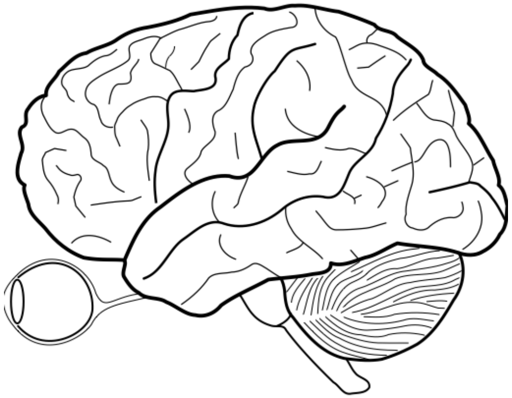
Language

Perception

Planning

Decision-making

Reasoning



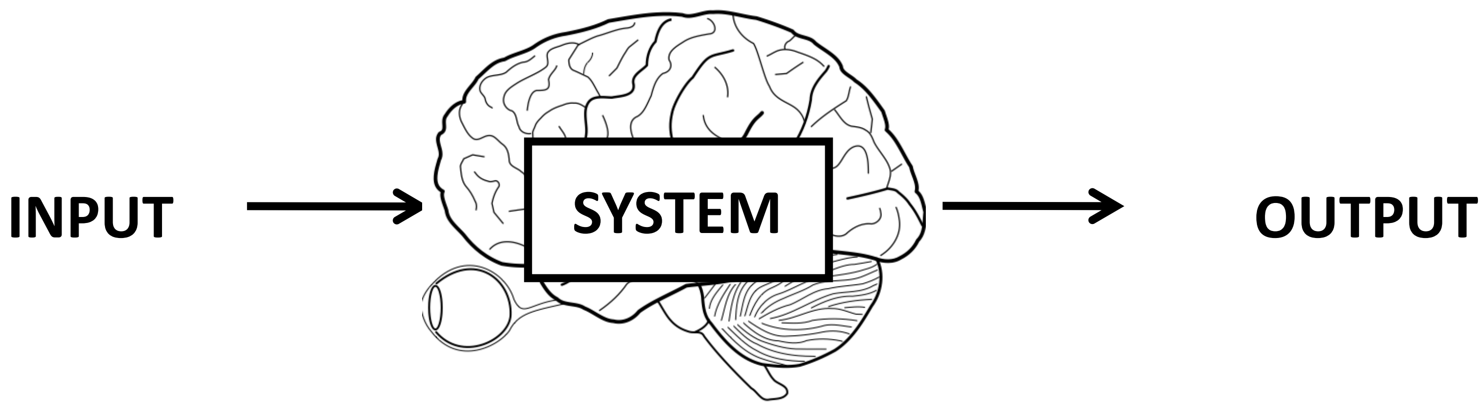
Attention

Memory

Emotion

Learning

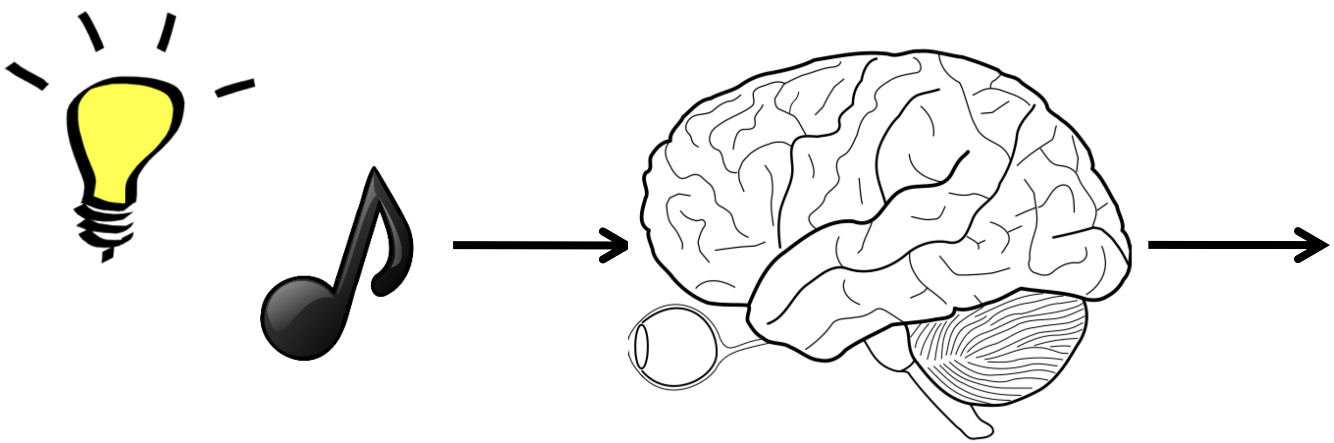
Cognitive Neuroscience as a system identification problem



Cognitive Neuroscience as a system identification problem

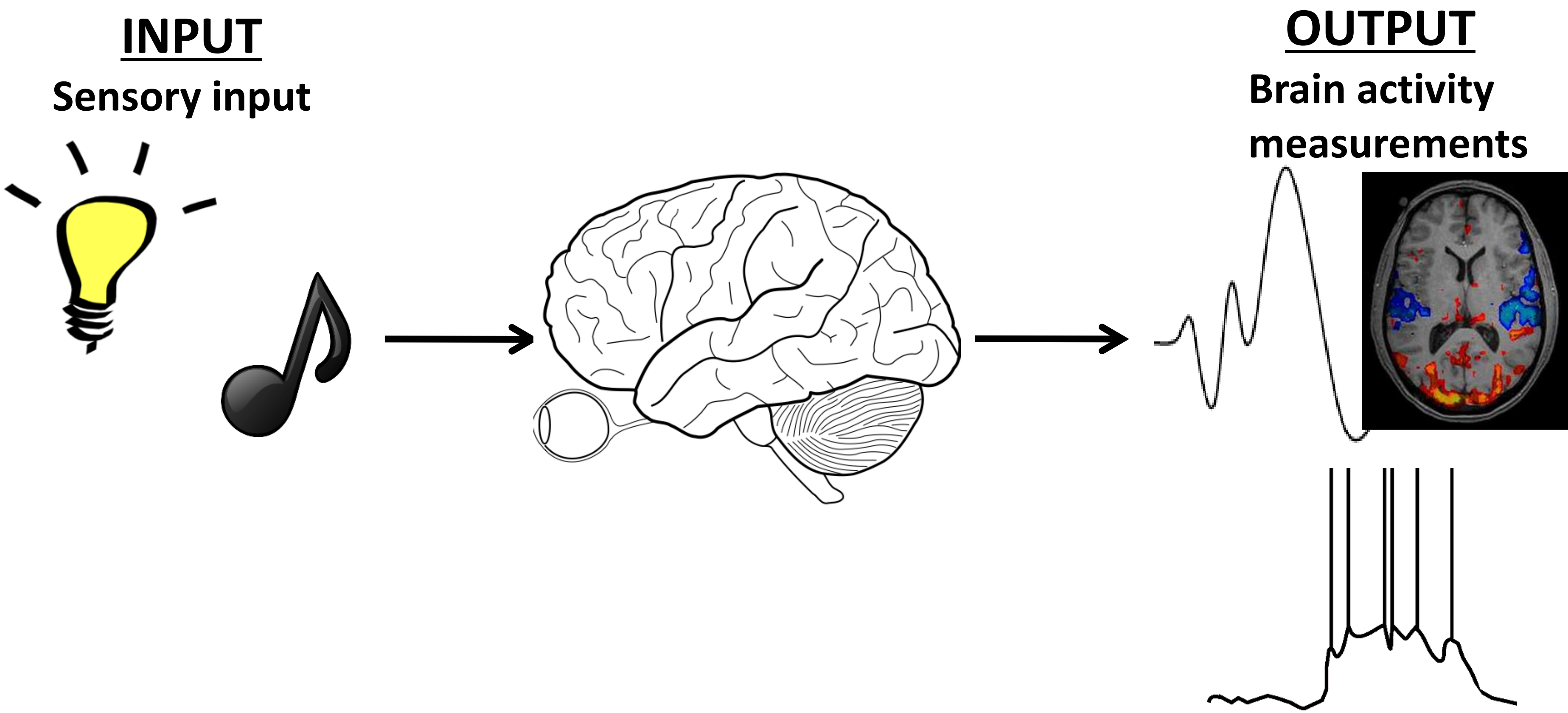
INPUT

Sensory input



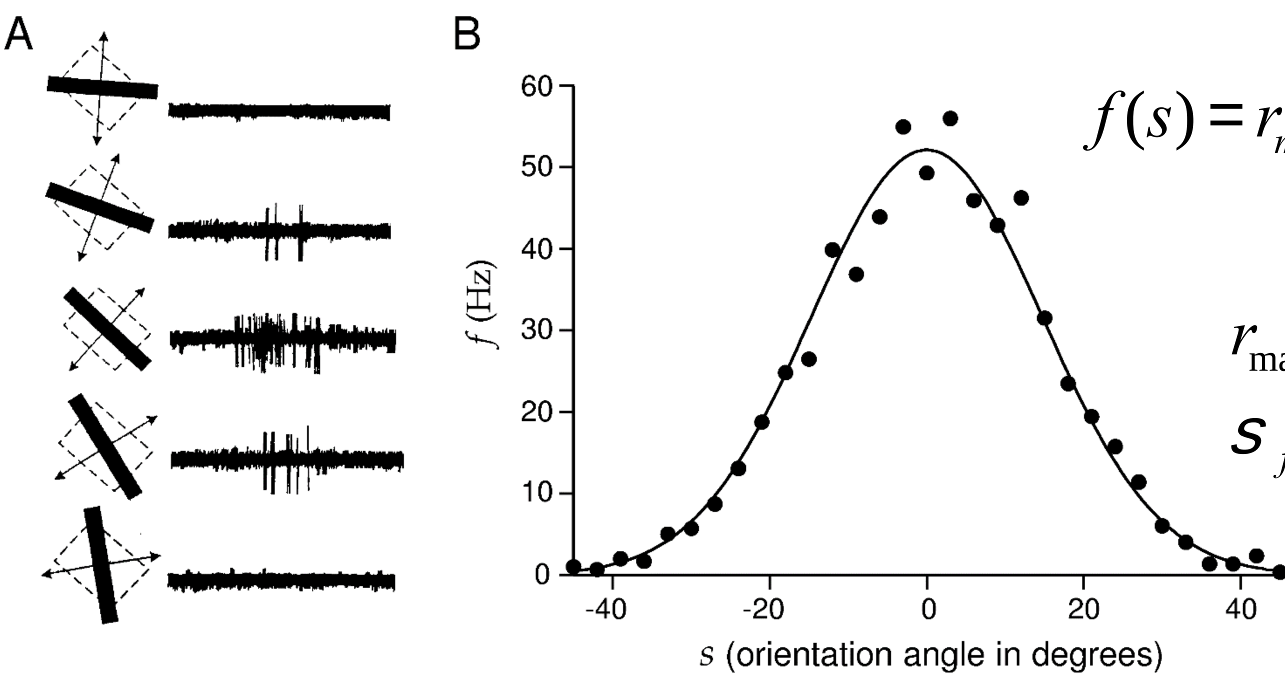
OUTPUT

Cognitive Neuroscience as a system identification problem



Encoding: Tuning Curve

- A tuning curve describes how a neuronal response such as the spike count in a certain post-stimulus window varies as a function of a single stimulus attribute ***s***
- Average firing rate can be mathematically described as a function of *s*: <*r*>=*f*(*s*). (whose functional form depends on neuron and stimulus)
- Example: extracellular recordings from monkey V1 neuron as bar passed over receptive field (Hubel & Wiesel)



$$f(s) = r_{max}\exp\left(-\frac{1}{2}\left(\frac{s - s_{\max}}{\sigma_f}\right)^2\right)$$

$$r_{\max} = 52.14 \text{ Hz},\ s_{\max} = 0°,$$

$$\sigma_f = 14.73°$$

s_{max} the “preferred orientation”

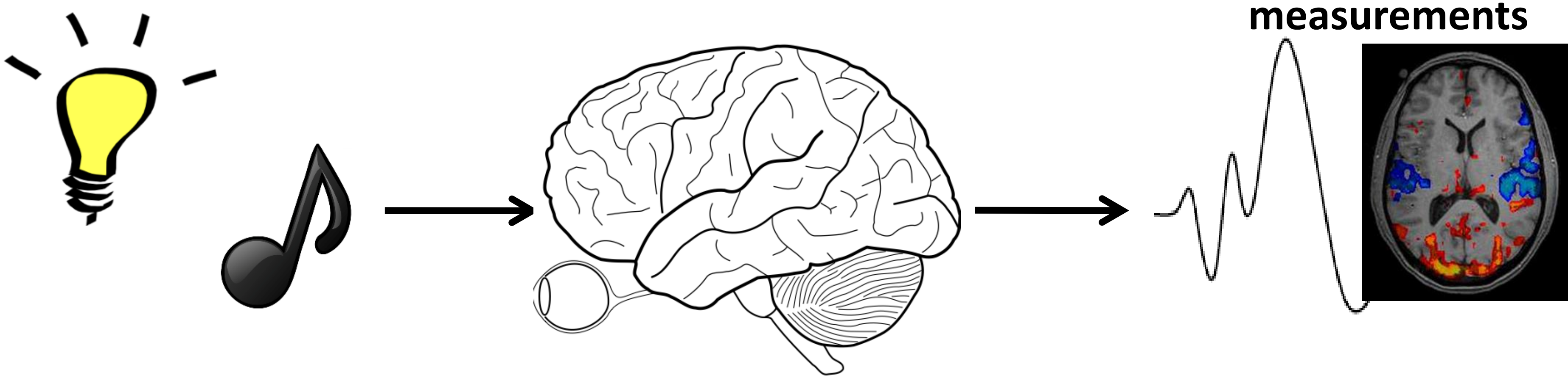
Cognitive Neuroscience as a system identification problem

INPUT

Sensory input

OUTPUT

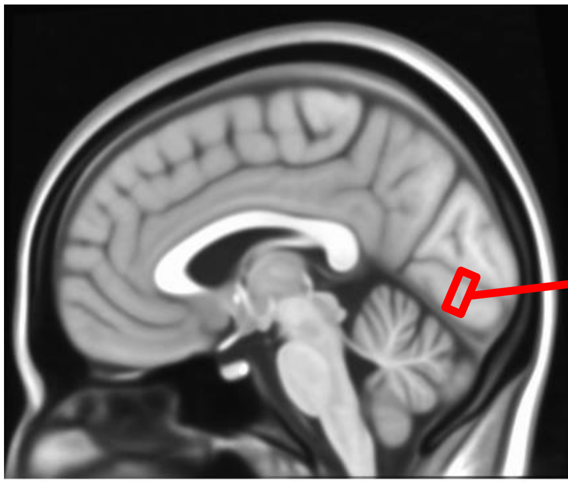
Brain activity measurements



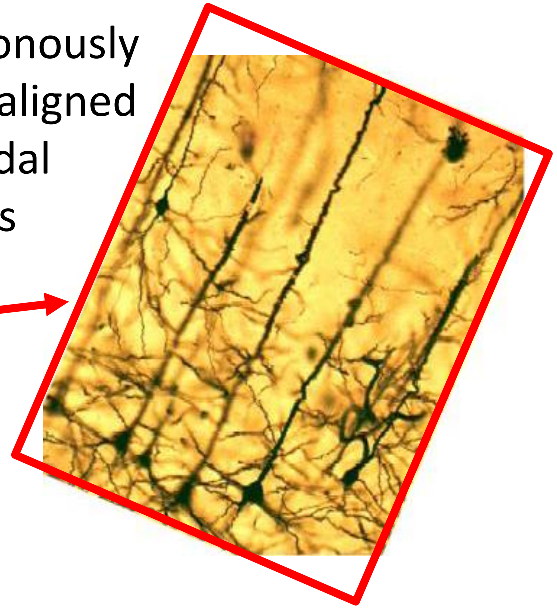
BUT

- How do these signals participate in cognition?
- Limited insights when using noninvasive measures

Electroencephalography (**EEG**)



Synchronously active, aligned pyramidal neurons



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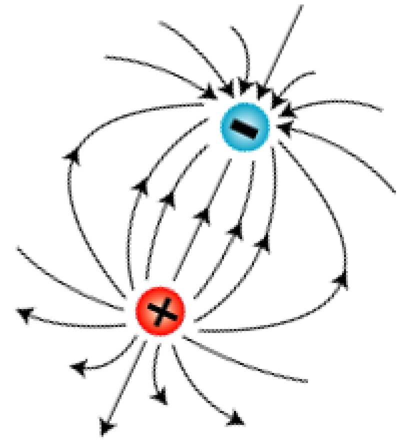

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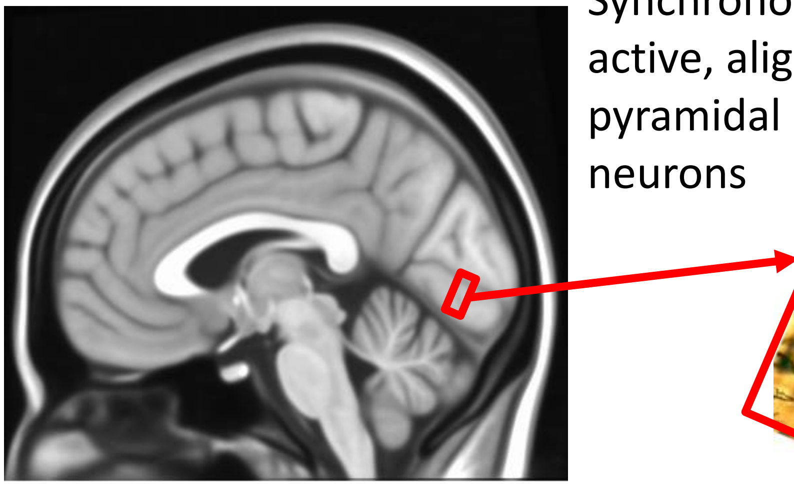

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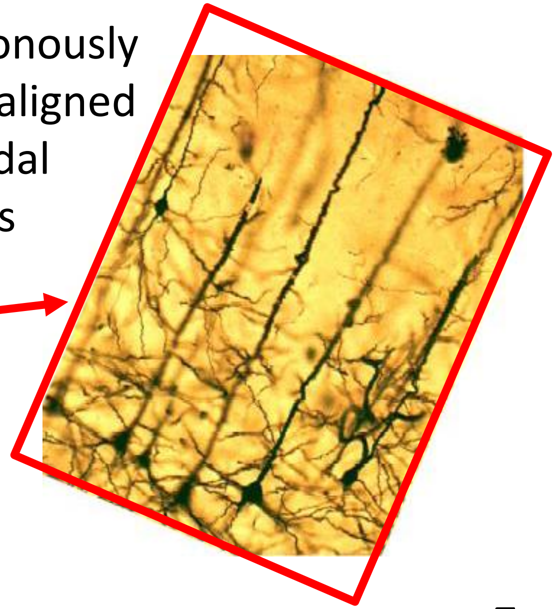

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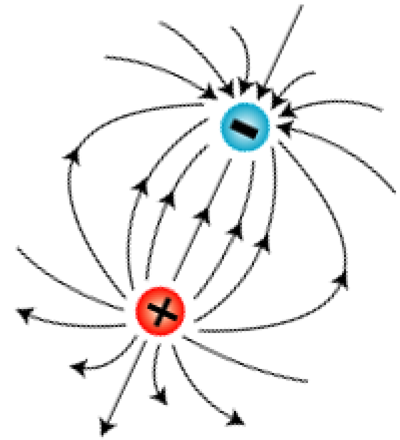
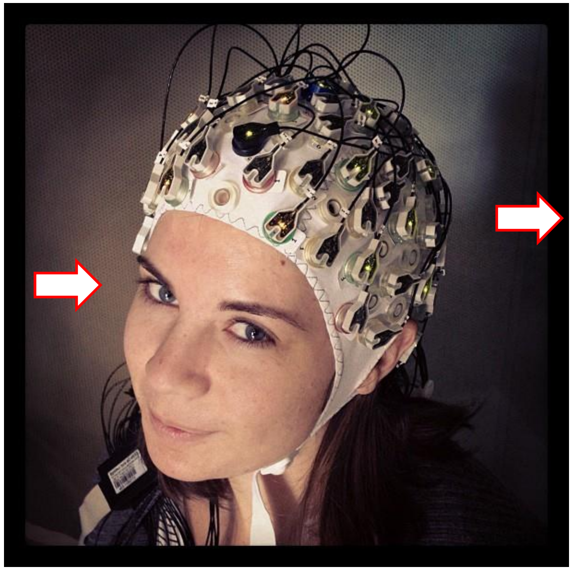
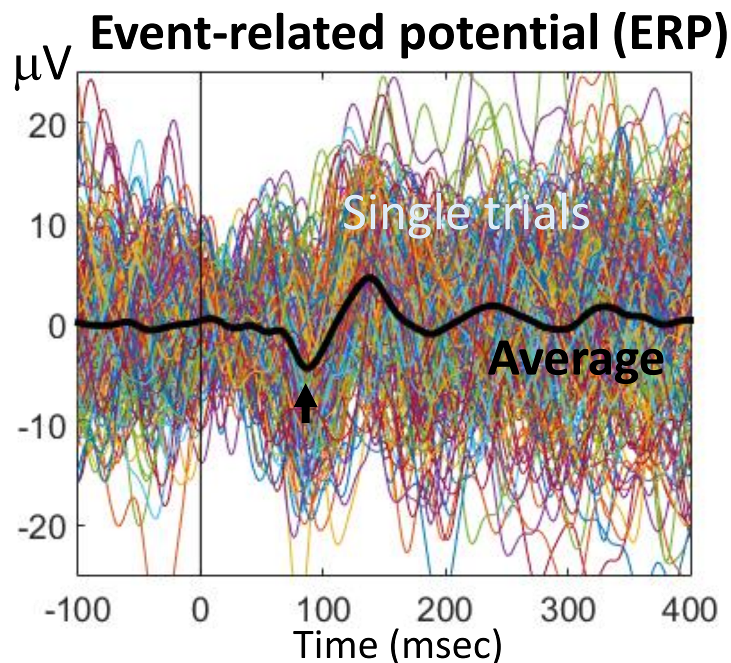


Sensory stimulus





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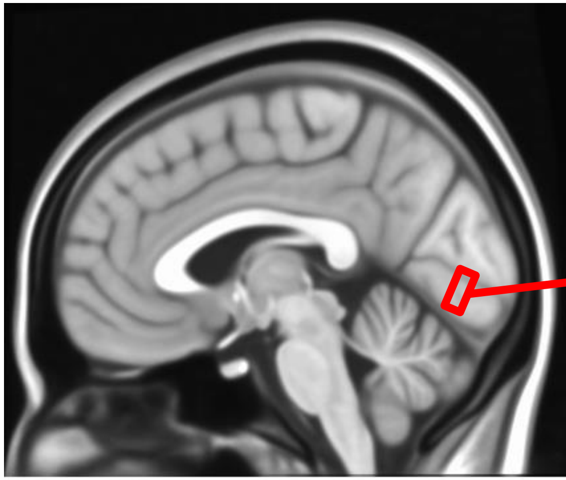
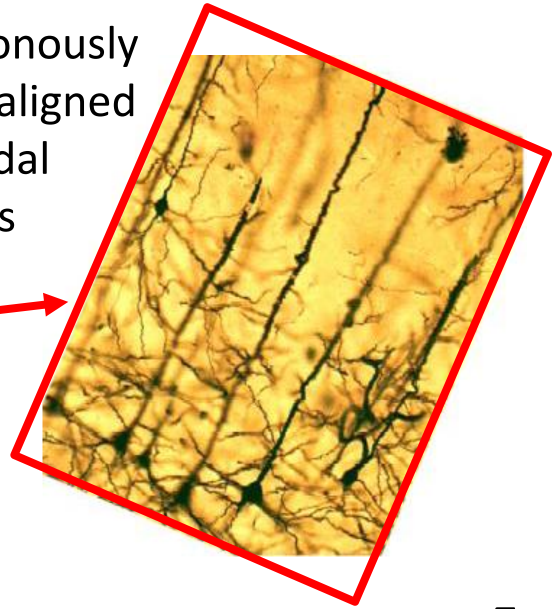


Synchronously active, aligned pyramidal neurons



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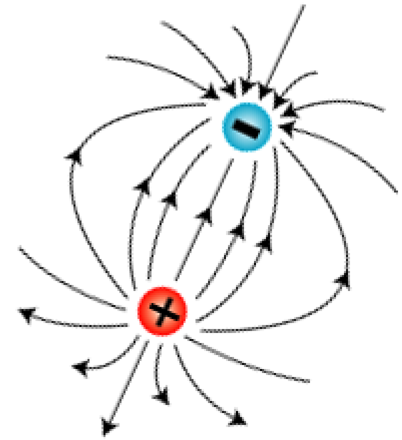
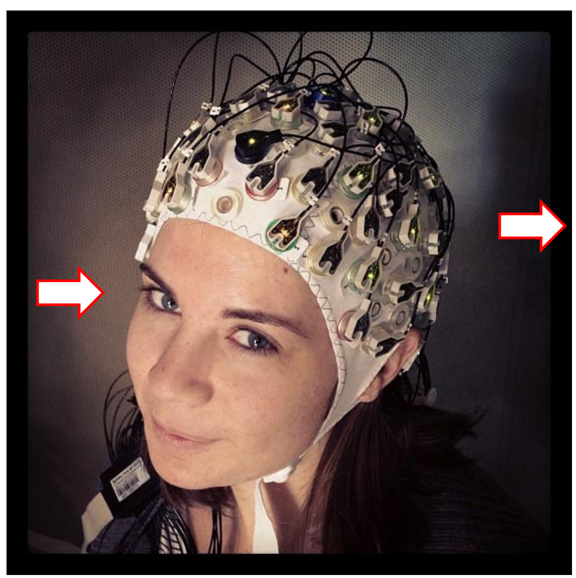
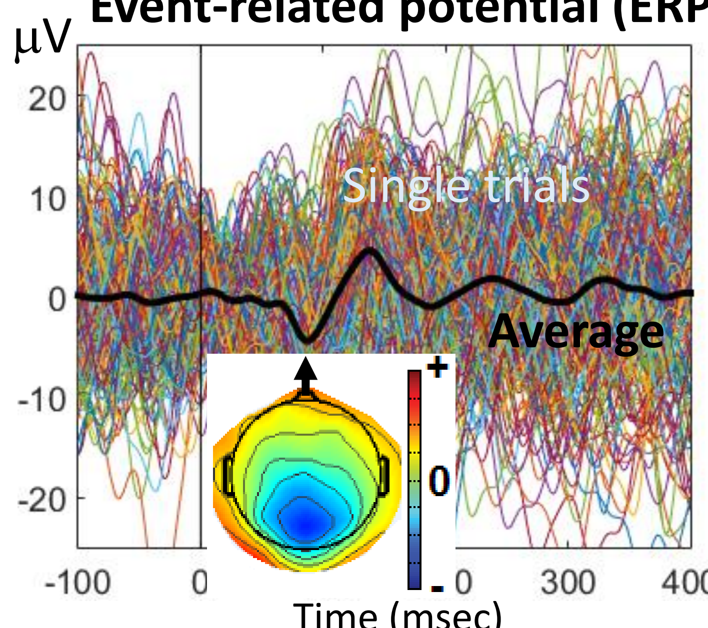


Sensory stimulus



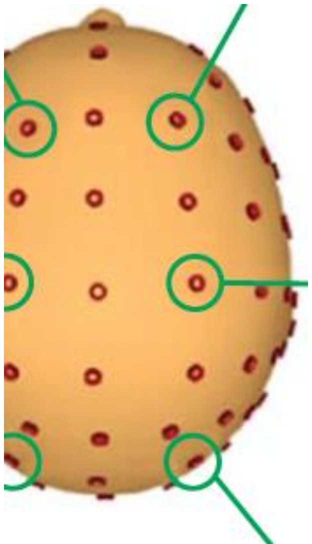
Event-related potential (ERP)



Human ERP indices of neural processing:

- diagnostic value?

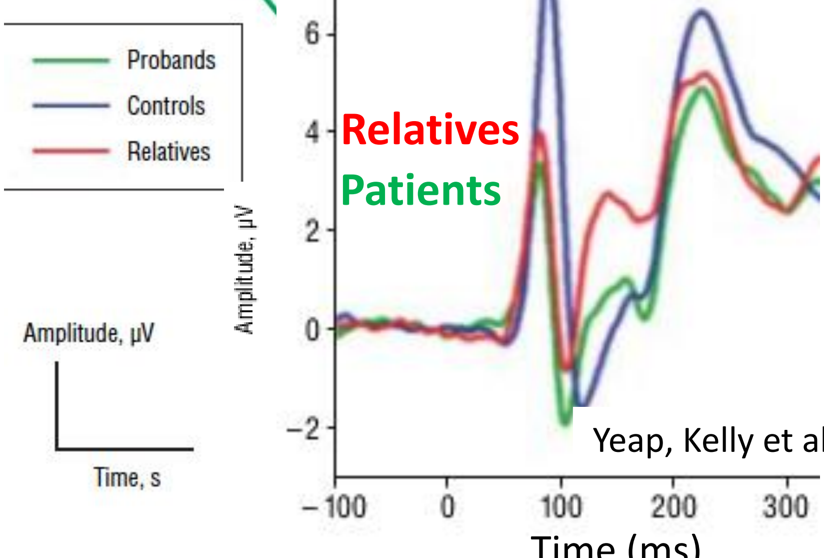
- “direct,” but how interpretable?



Endophenotypic “P1” deficit in schizophrenia

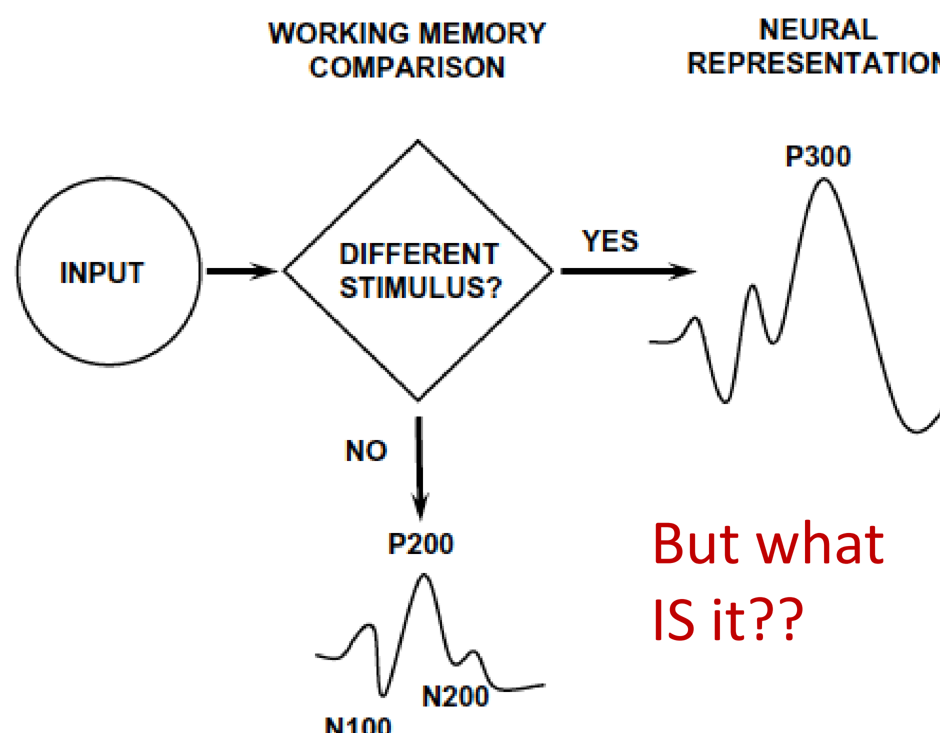
-a problem with basic sensory processing?

- But WHAT exactly?



Yeap, Kelly et al (2006)

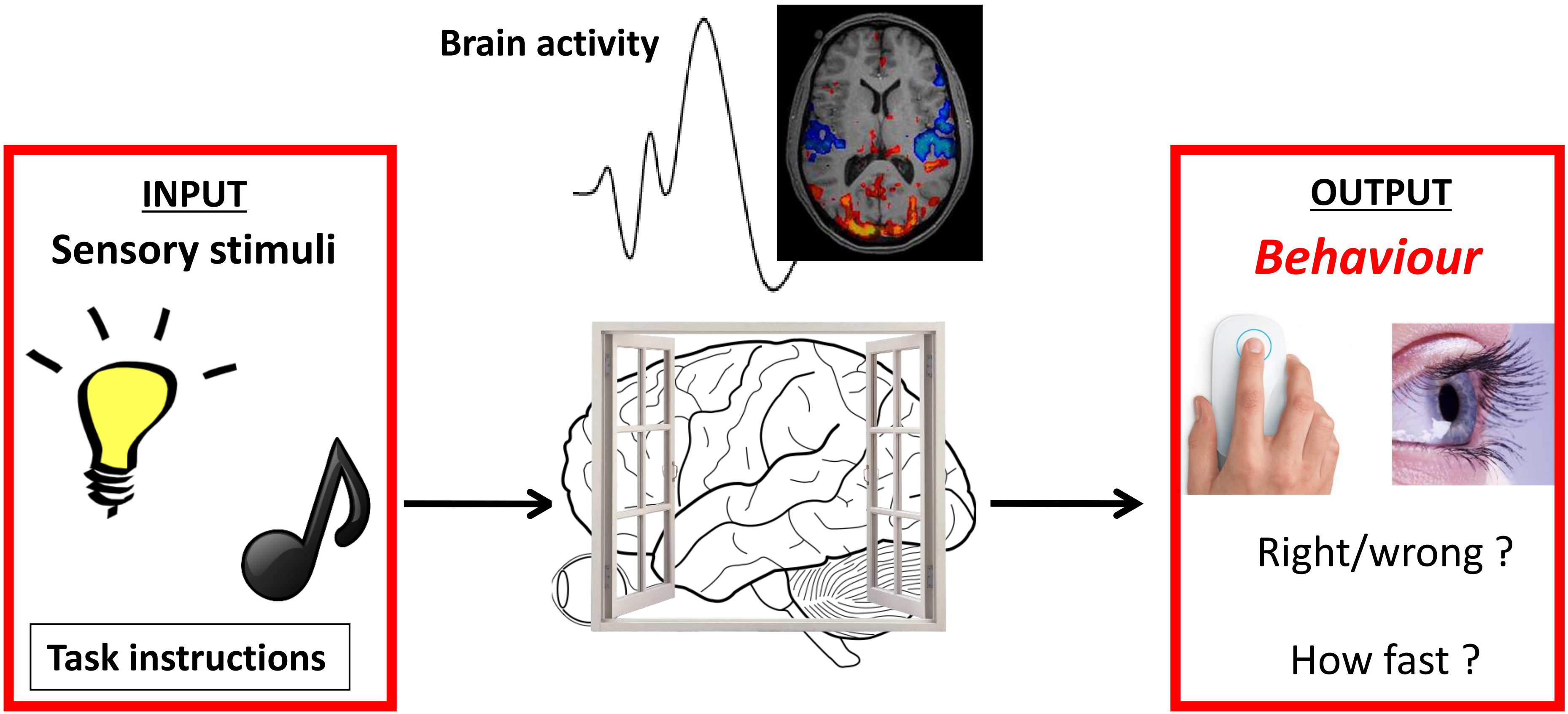
CONTEXT UPDATING THEORY OF P300



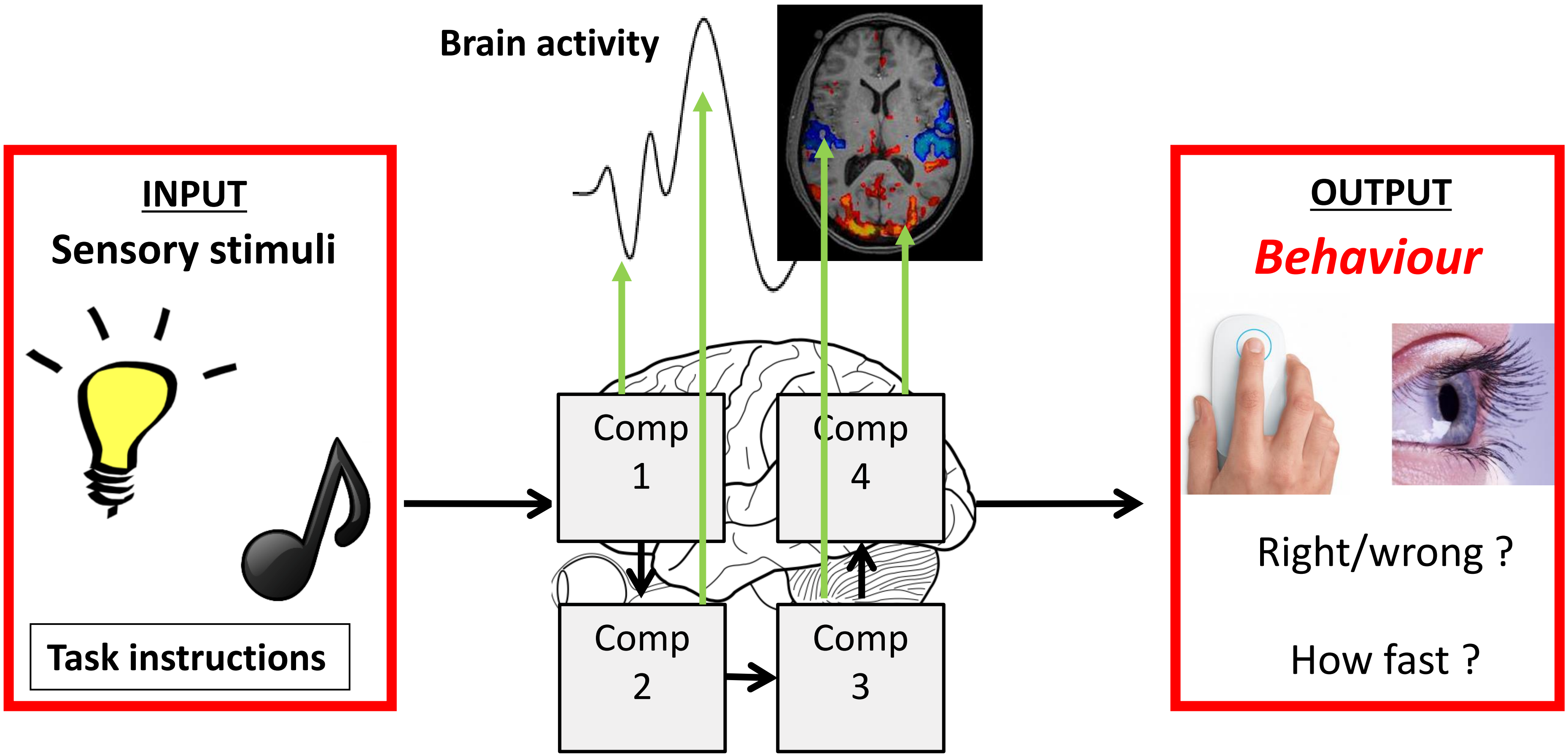
But what IS it??

Polich (2007)

Cognitive Neuroscience as a system identification problem



A system identification problem
and a design problem



Problem:
Design a task (= stimuli + instructions) that can be broken down into **computational building blocks** that can be mapped onto measured brain signals.

Overview

- Intro to **Psychophysics**
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- Applying SDT to understand the neural basis of perceptual **detection**
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Psychophysics

- The scientific study of the relationships between

Stimuli		Sensations
Φ	$\longleftrightarrow$	Ψ
physical domain		psychological domain

- Landmarks:
- Wilhelm Wundt (1879): first Experimental Psychology lab
- G. T. Fechner (1860): *Elements of Psychophysics* published
- Signal Detection Theory – Green & Swets (1966)

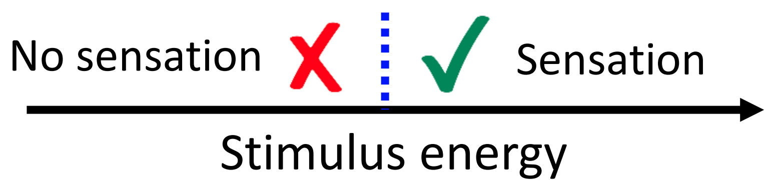
- Broader modern usage: the systematic measurement of behaviour in relation to experimental events

Source: Gescheider GA, Psychophysics: The Fundamentals (1997)

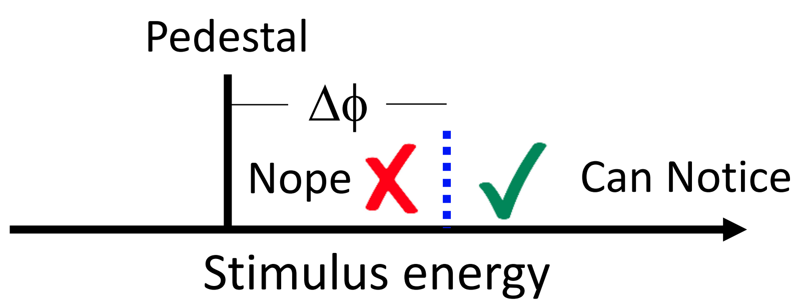
Sensory Threshold

- Herbart (1824): mental events have to be stronger than some critical amount in order to be consciously experienced.
- E.H. Weber & G.T. Fechner: can *measure* that critical amount

- *Absolute threshold* (smallest amount to produce a sensation).



- *Difference threshold* (smallest change $\Delta\phi$ to produce a just noticeable difference (jnd) in the sensation).



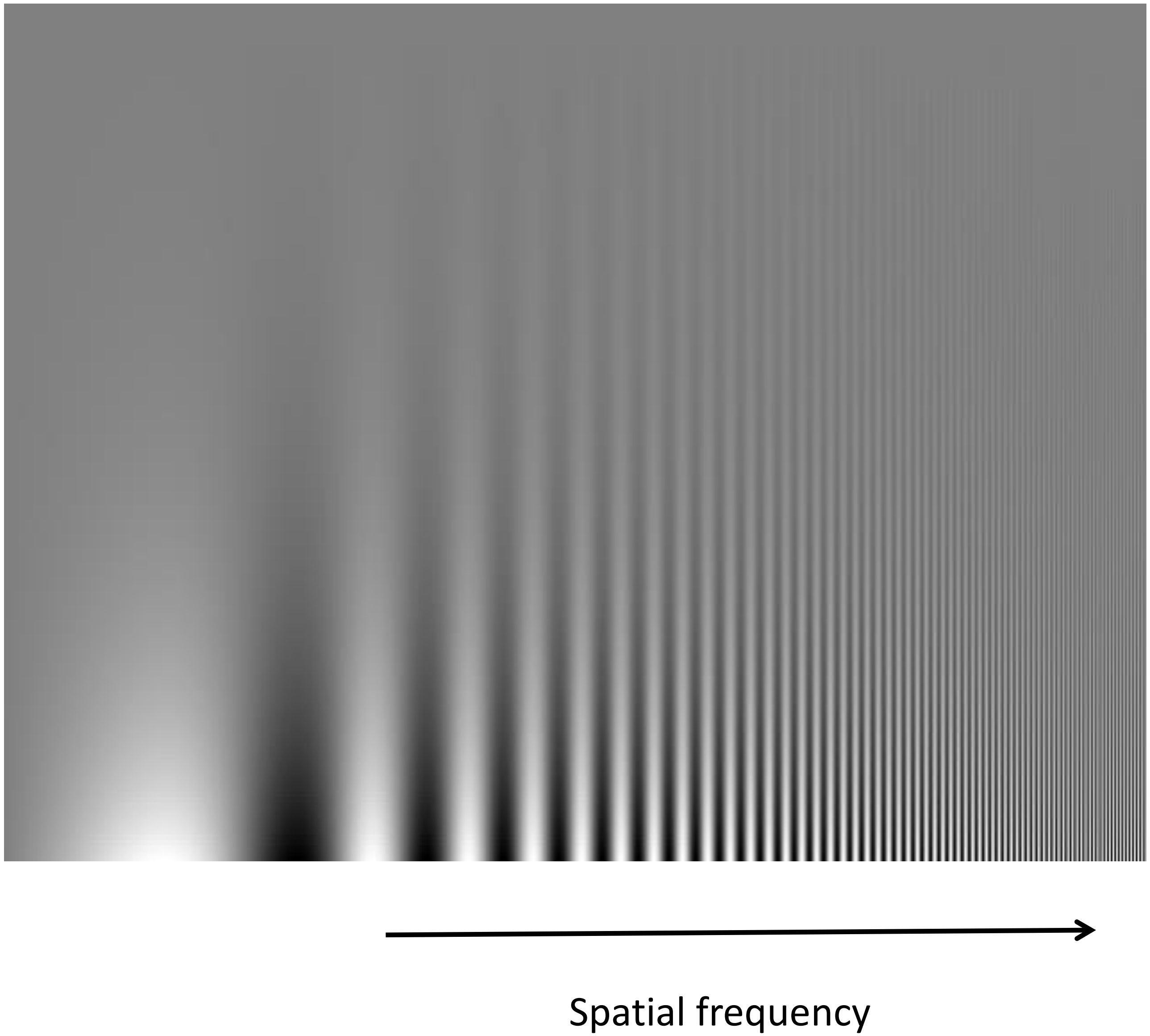
Two goals of psychophysics

- **Descriptive** – specification of sensory capacities.

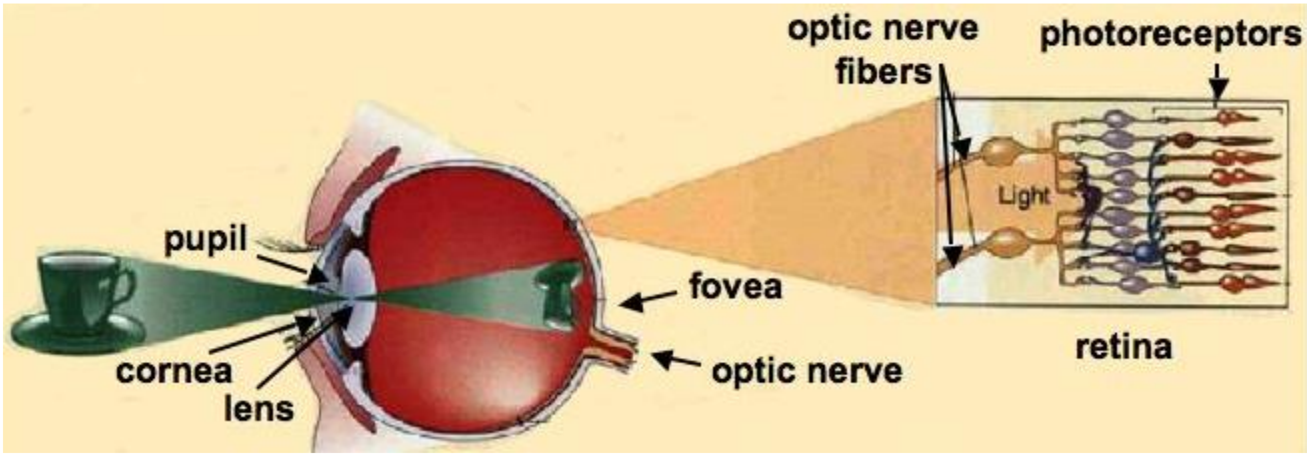
- **Analytical** – the testing of hypotheses about underlying biological mechanisms that determine sensory capacity

- Sensory capacities vary systematically across many dimensions other than intensity:
  - Extension (how big)
  - Duration (how long exposed)
  - Quality (e.g. light wavelength (color/hue), sound pitch, orientation of visual or cutaneous stimulus, modality itself)

Example: contrast detection threshold as a function of spatial frequency

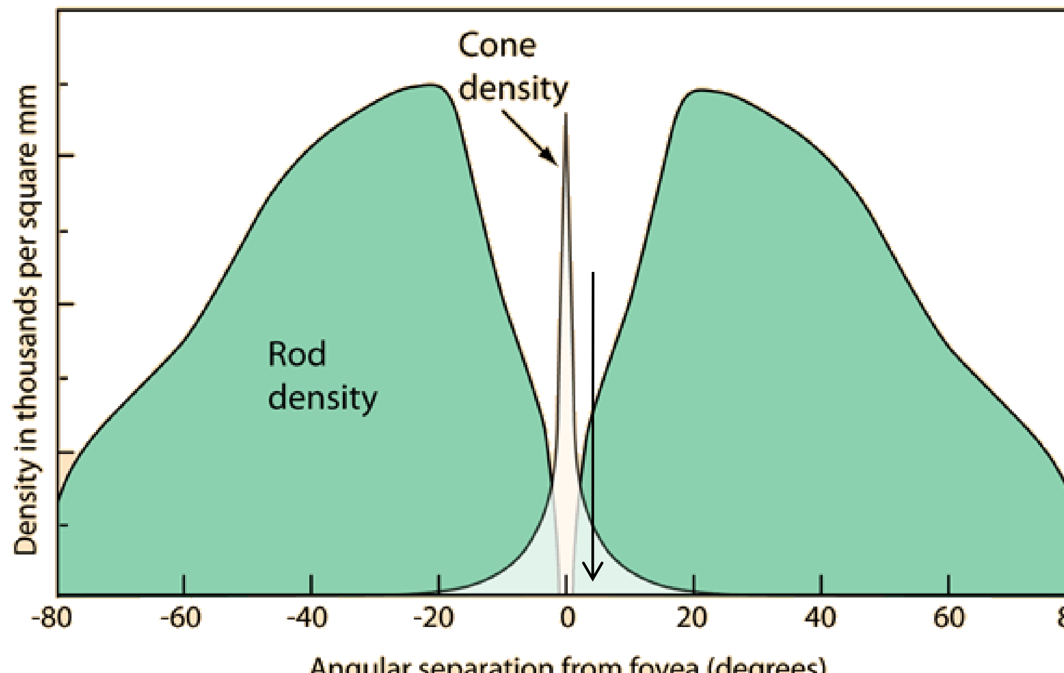


Psychophysical insights into eye physiology



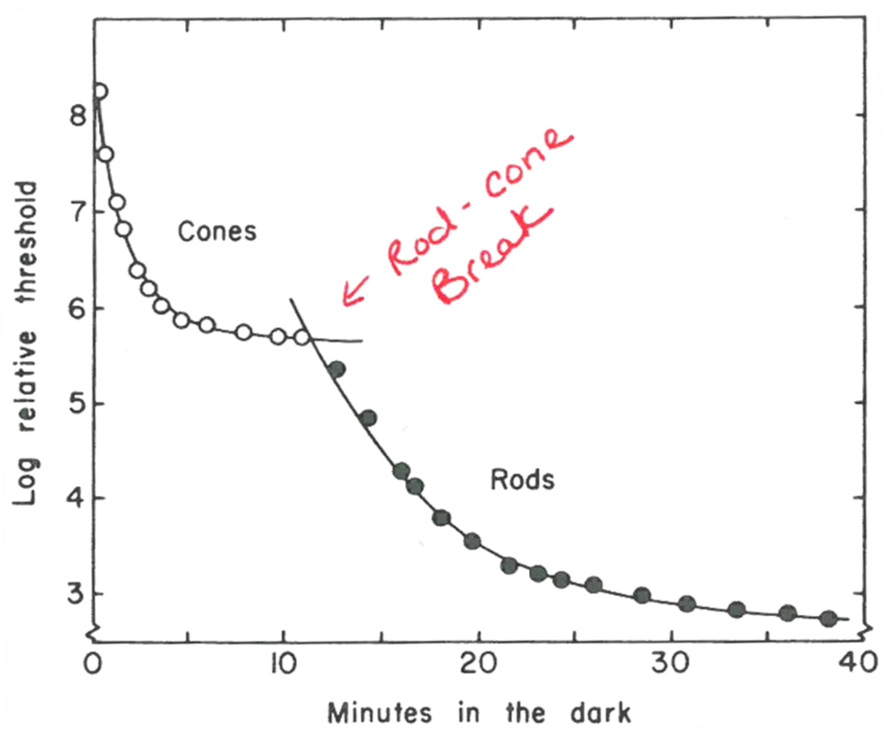
Rods are responsible for **scotopic vision** (low light $10^{-2} – 10^{-6}$ cd/m^2)

Cones are responsible for **photopic vision** (normal light $1 – 10^{6}$ cd/m^2, high acuity, color perception)



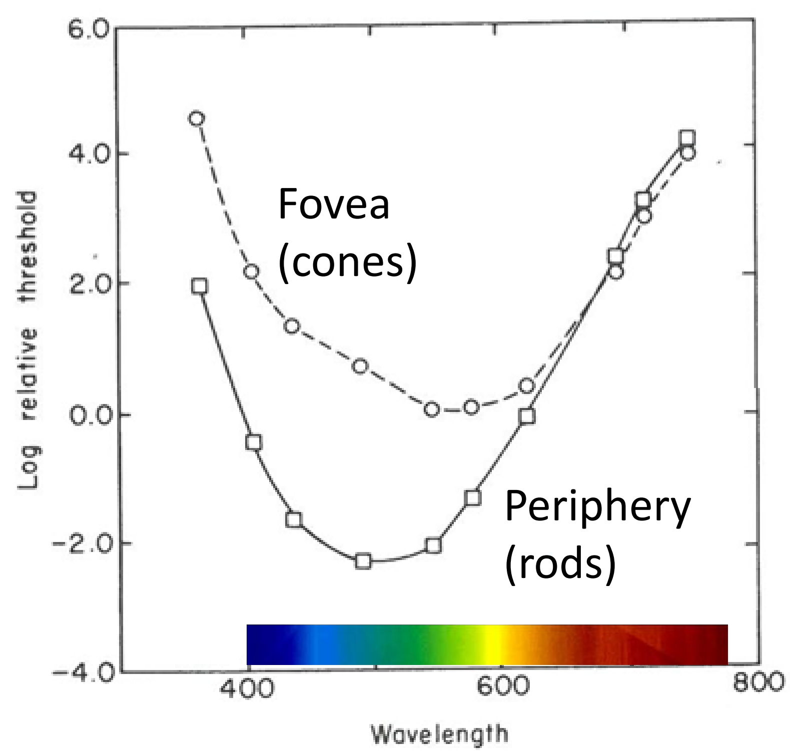
Psychophysical insights into eye physiology

Dark adaptation – recovery of detection threshold after intense light



Rods recover later, and take over ultimate sensitivity

Spectral sensitivity curves – absolute threshold vs colour (Wald 1945)



At threshold, colour perceived at fovea but not at periphery

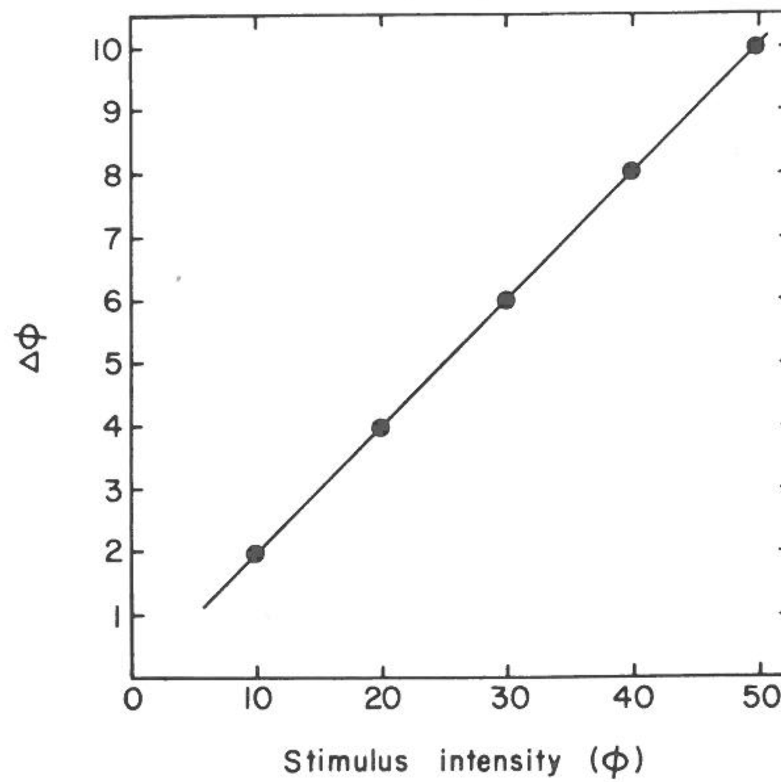
Difference Thresholds: Weber's Law

- Weber discovered that the heavier the weight, the bigger the weight difference required to tell it was heavier.
- i.e., difference threshold scales linearly with stimulus intensity.

$$\Delta\phi = c\phi \quad \text{or} \quad \Delta\phi / \phi = c$$

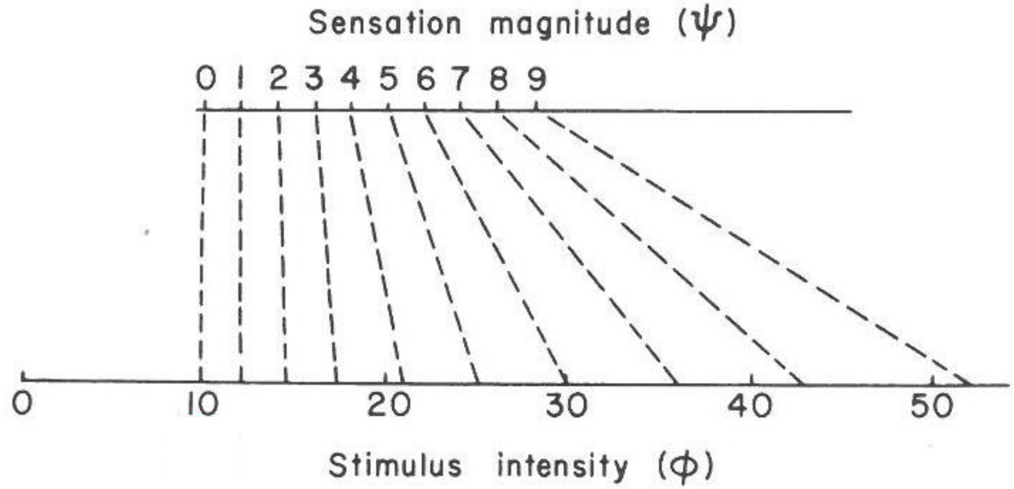
- Applies to wide range of stimuli applied to eye, ear, skin, nose, tongue, …

Weight judgments – which heavier?



Fechner's psychophysics

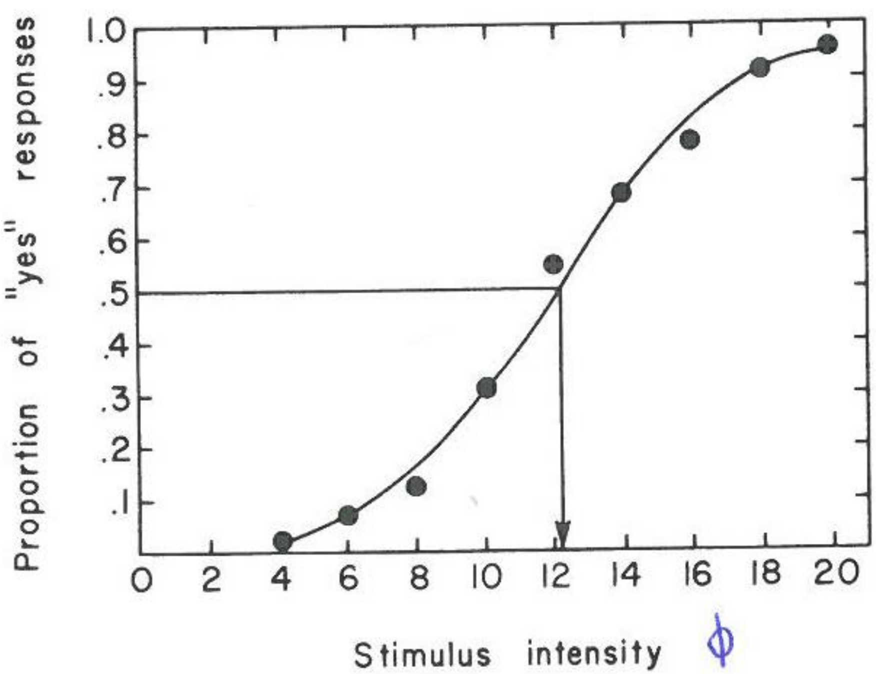
- Idea similar to Weber's law: arithmetic series of mental intensities correspond to a geometric series of physical energies.



- Proposed that just noticeable differences (jnd) are equal psychological increments in sensation magnitude, which correspond to values of $\Delta\phi$ on the physical scale that increase with ϕ.

Measuring psychophysical thresholds: *Method of Constant Stimuli*

- ***Absolute Threshold:*** Present set of stimulus intensities repeatedly in random order, then plot proportion "yes" response for each level:
- Gives ***Psychometric function***



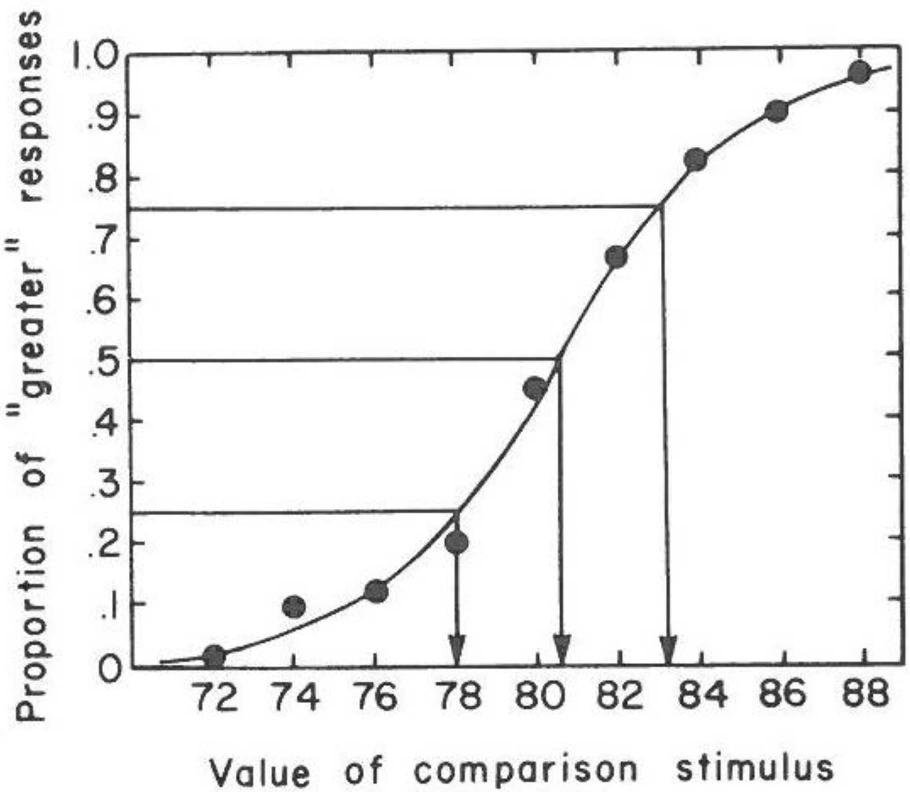
Define **threshold** as intensity producing e.g. 50% "yes"

Usually a **sigmoidal** relation that can be fit using cumulative Gaussian function or similar

center μ of Gaussian gives absolute detection threshold

Measuring psychophysical thresholds: *Method of Constant Stimuli*

- ***Difference Threshold:*** observer reports which of a pair of stimuli produces a sensation that is greater in magnitude – a standard (St; fixed) vs a comparison (Co; varying)
- Again randomize levels, but also order to eliminate space/time error

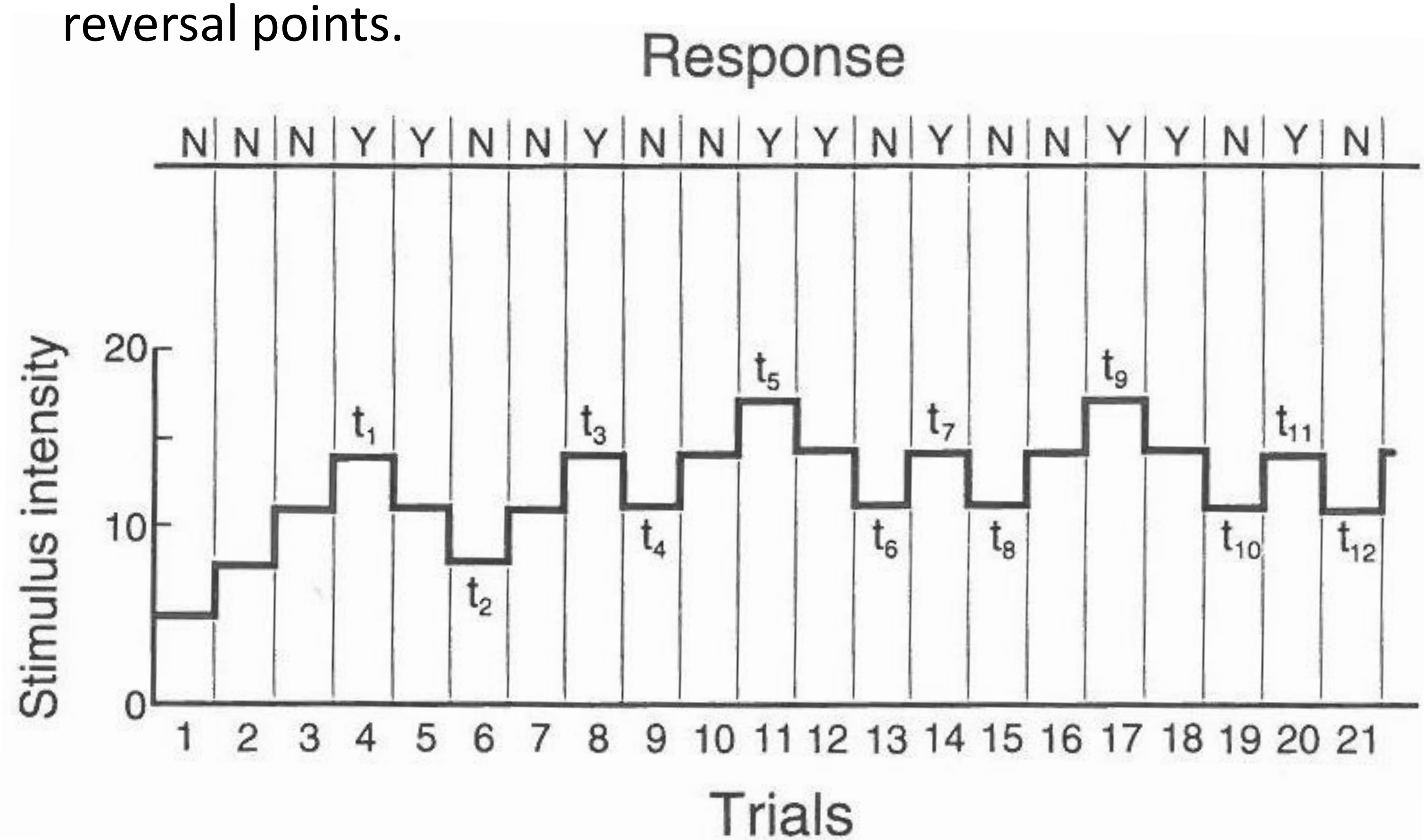


- e.g. Is weight of Co greater or less than St=80g?
- Again **sigmoidal**

- Point of subjective equality (PSE) is value of Co that the observer judges to be greater 0.5 of time.
  - μ of cumulative Gaussian fit.
- Difference Threshold = σ, or Steepness of curve at PSE

Staircase methods

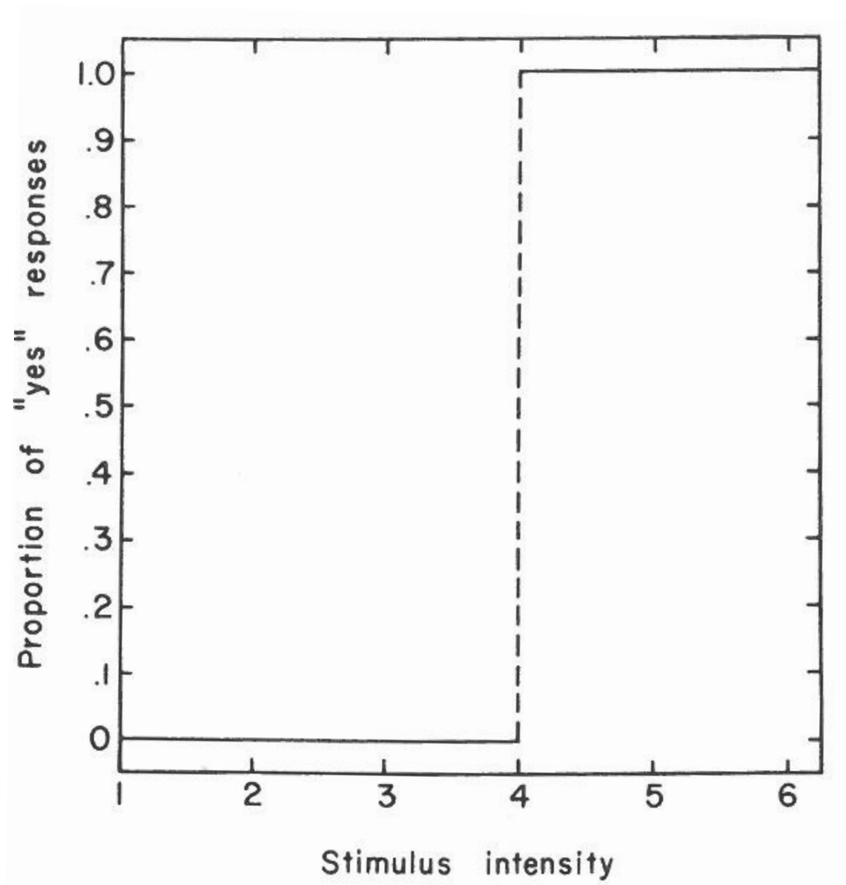
- More efficient
- intensity proceeds upward or downward until there is a change in response, and reverses. The threshold is the average of the reversal points.



step size is critical!

Wait!

- Why are psychometric functions not like this?



Stimulus Noise

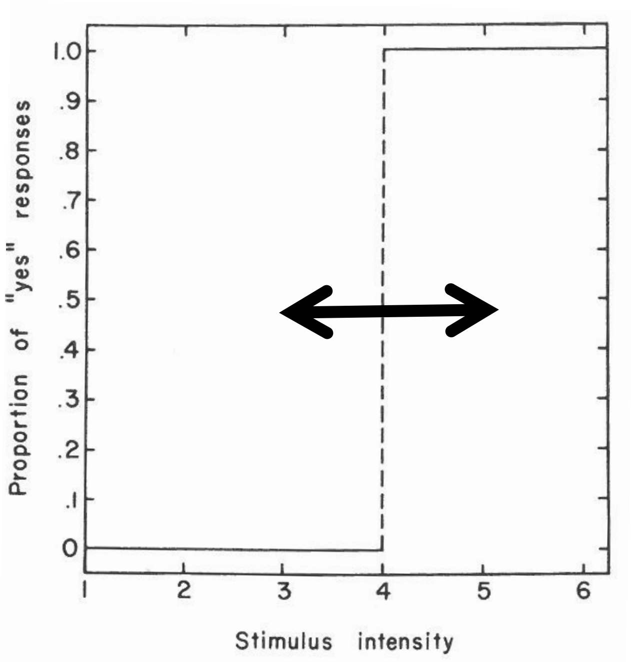
- Noise in psychophysical measurements can come from variability or noisiness in the physical stimulus for a given condition
- Sometimes this is on purpose and controlled: (e.g. face detection in phase-scrambled noise)

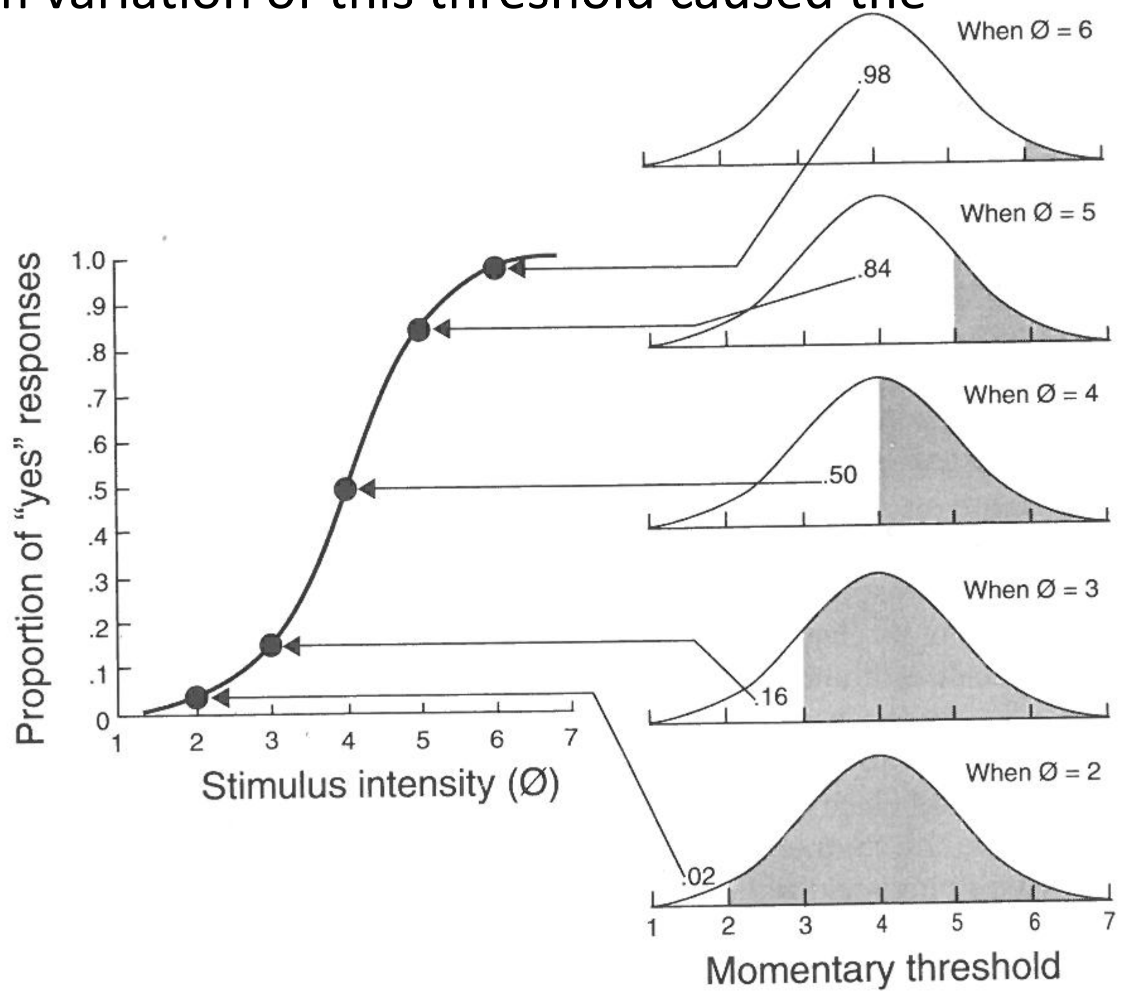
- Sometimes it’s uncontrolled: (e.g. odorant detection; some escapes!)

- Can lead to overestimation of thresholds!
- But that’s not all – PMFs are sigmoidal even with zero stimulus variation.

Perceptual variability

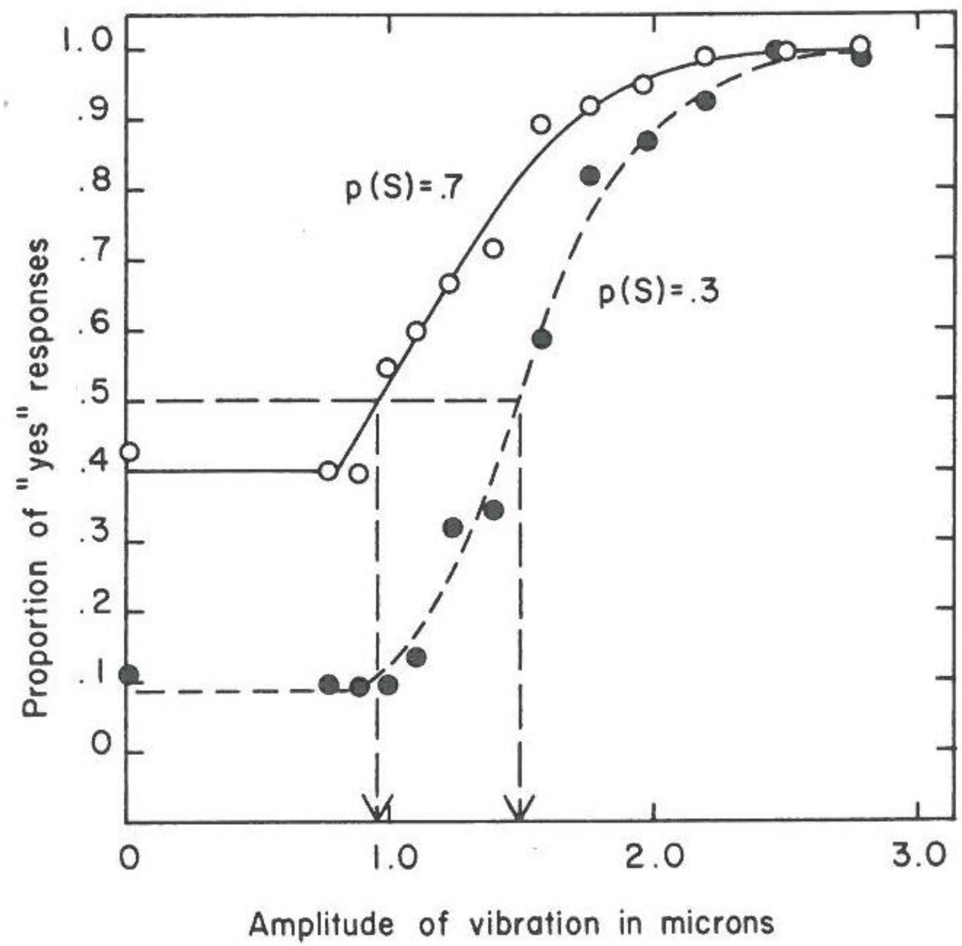
- Early theorists: neural threshold for sensation – sharp transition from no sensation to sensation at critical amount of neural activity
- Initial idea was that random variation of this threshold caused the sigmoidal shape of PMF





PMF also varies with nonsensory factors!

- E.g. Probability of stimulus occurrence, p(S)
- "Catch trials" reveal response bias
- Training helps only so much
- Similar effect of costs and benefits of outcomes



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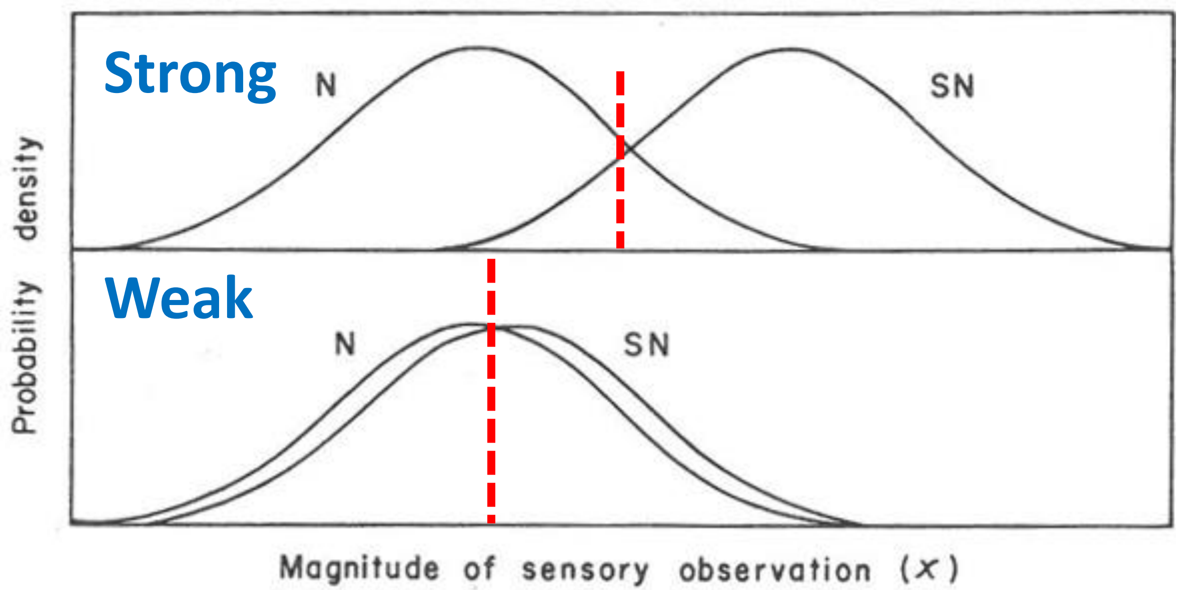
Signal Detection Theory

- Tanner & Swets (1954): human detection is same problem as electronic signal-detecting devices hampered by noise
- **The internally represented *observation* (*x*) is what is noisy** – not the threshold.
- Subject makes a decision from that observation: is it noise alone (N), or signal + noise (SN)? This is done by comparing to a **criterion**.



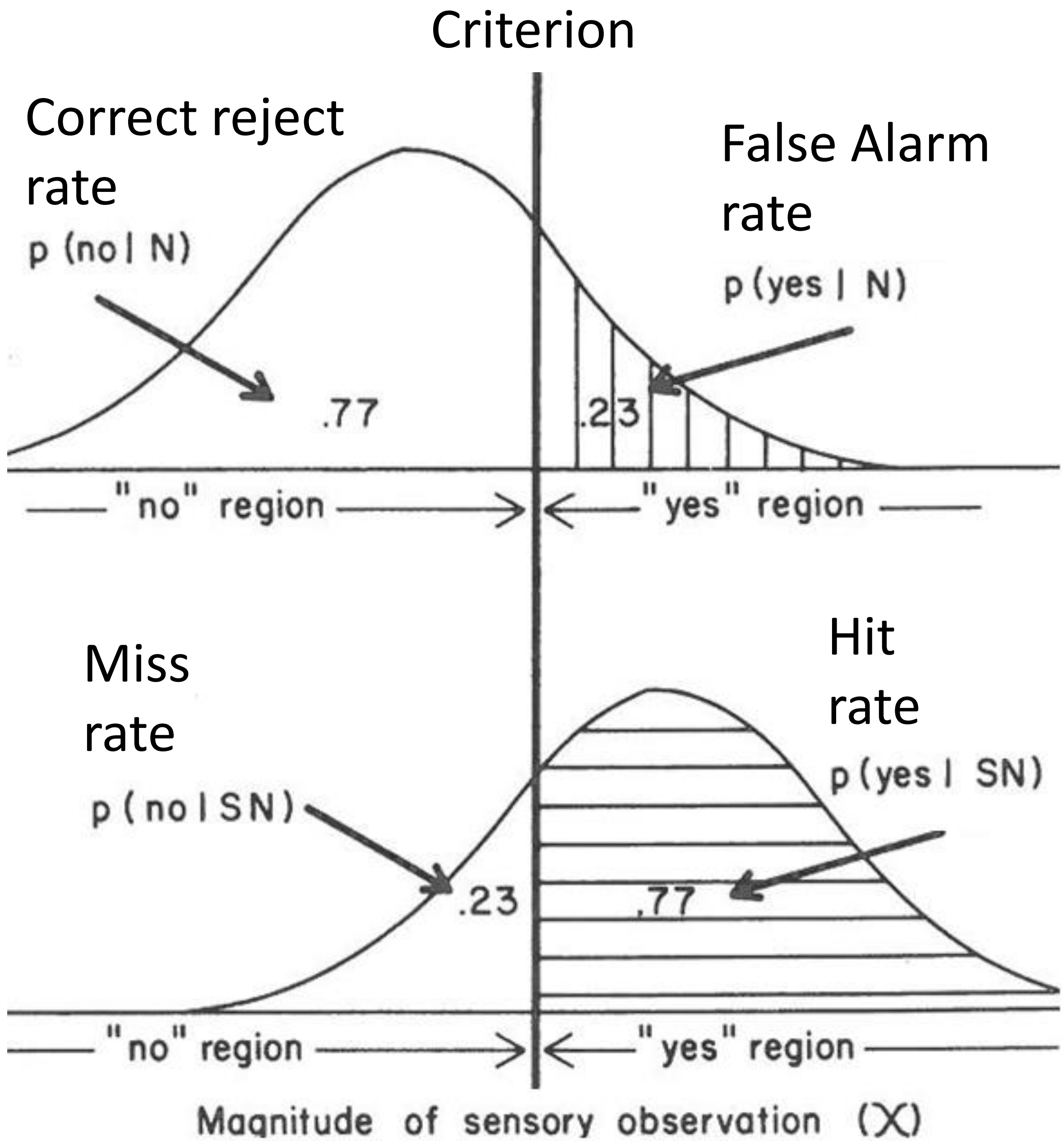
Likelihood distributions determined by stimuli and neural encoding noise

Criterion set strategically!

Criterion determines outcomes

In detection, 4 classes of trial:

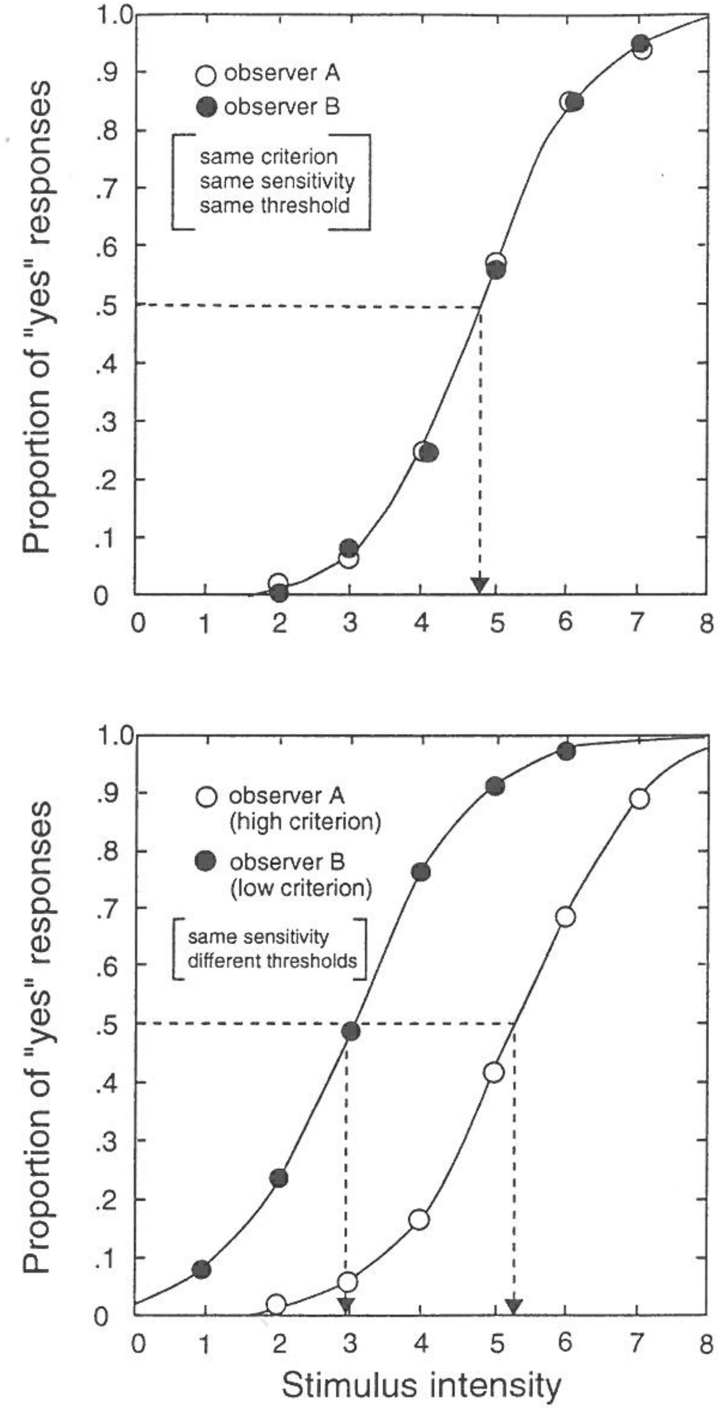
	Report "yes"	Report "no"
Stimulus **present**	**HITS**	**MISSES**
Stimulus **absent**	FALSE ALARM	CORRECT REJECTION



OPTIMAL setting depends on expected costs/benefits of each possible outcome!

Measuring Sensitivity

- In classical psychophysics the measurements of threshold were a function of both stimulus detectability and the observer's criterion.
- Thus, differences in threshold across observers or conditions may be contaminated by changes in criterion, leading to false conclusions about changes in sensitivity.
- In the bottom, observer B is equally sensitive to observer A but has a lower criterion, i.e. is more inclined to say "yes" ...

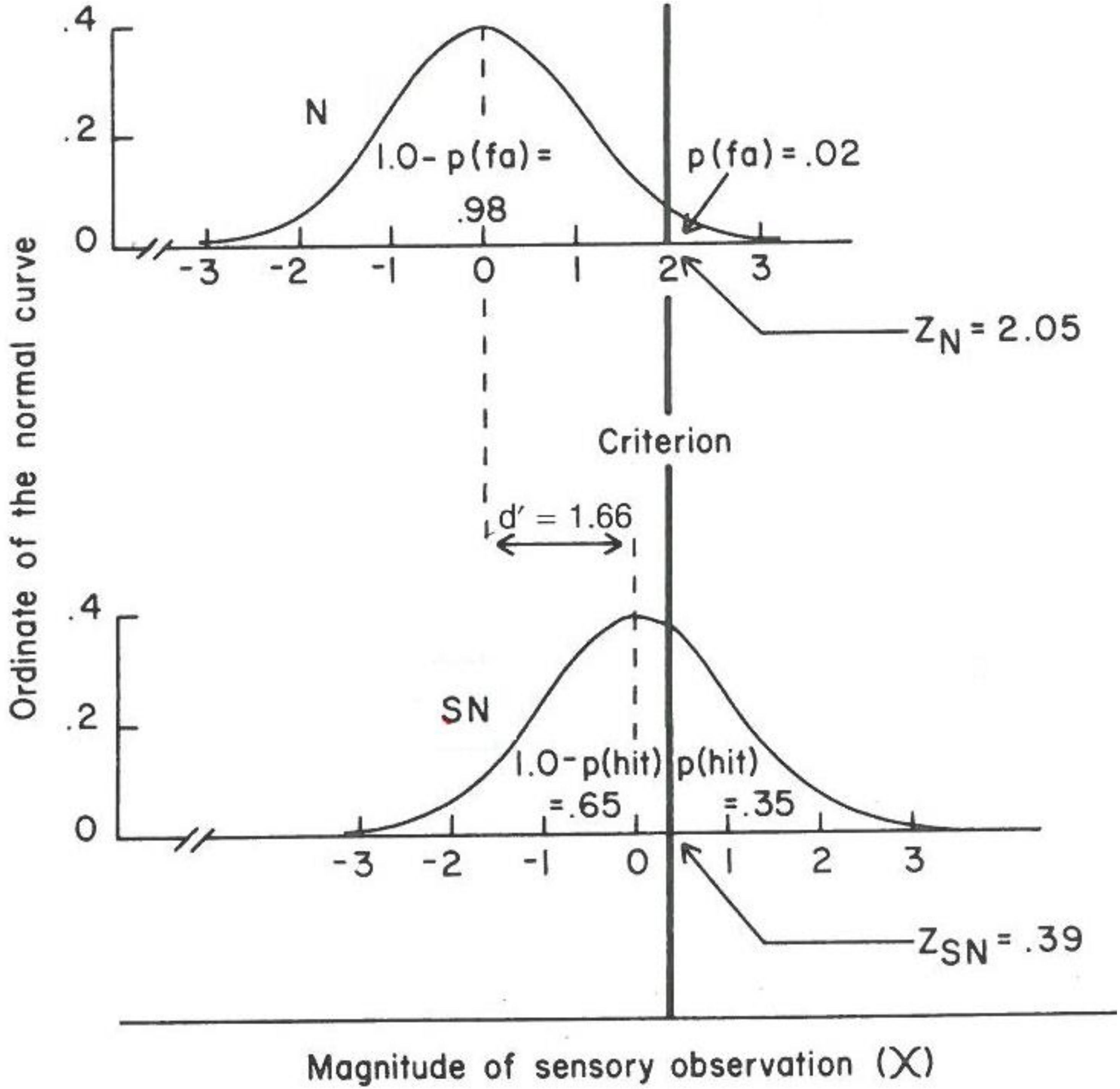


Sensitivity: **d’**

- Signal Detection Theory provides a way to independently measure sensitivity and criterion location. It proposes a sensitivity or detectability measure d’ :

$$d' = \frac{M_{SN} - M_N}{s_N}$$

- where M_{SN} and M_N are the means of the SN and N distributions and σ_N is the standard deviation of the noise distribution.
- Entirely independent of criterion.
- Computed using z-score transformations of observed false alarm and hit rates, p(fa) and p(hit)
- First find criterion as a z-score relative to the N and SN distributions:
- Zn = norminv(1-p(fa))
- Zsn = norminv(1-p(hit))
- Then subtract to give d’:   d’ = Zn - Zsn



Ordinate of the normal curve
.4
.2
0
N
1.0- p(fa) =
.98
p(fa) = .02
-3 -2 -1 0 1 2 3
Z_N = 2.05
Criterion
d′ = 1.66
SN
1.0- p(hit)
=.65
p(hit)
=.35
Z_SN = .39
Magnitude of sensory observation (X)

Response Bias

- Response bias is the tendency of an observer to set a liberal versus conservative criterion in responding “yes” over “no” due to factors other than signal intensity.
- One measure is:

$$C = 0.5[Z_{SN} + Z_N]$$

- When the false alarm rate and miss rate are equal, the hit rate and correct rejection rate are also equal and the value of C is zero.
- C=0 represents no bias – it’s the point where the N and SN distribution cross. The total number of “yes” responses will be the same as the total number of “no” responses.
- Negative C reflects a bias toward saying “yes,” and positive C reflects a bias toward saying “no.”
- Like d’, C is expressed in standard deviation units (z-score).

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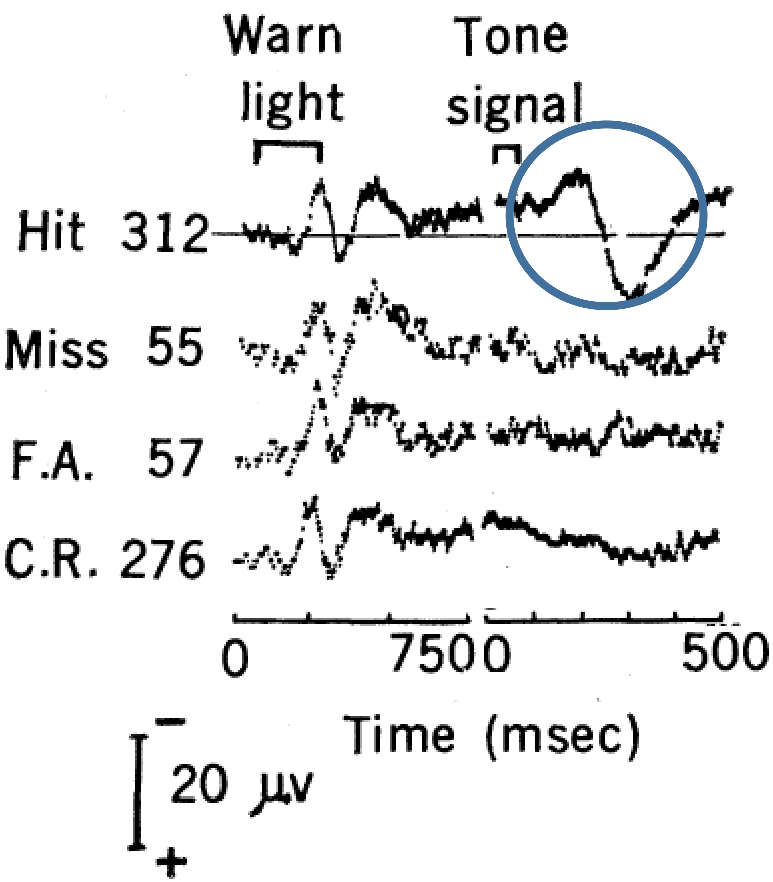
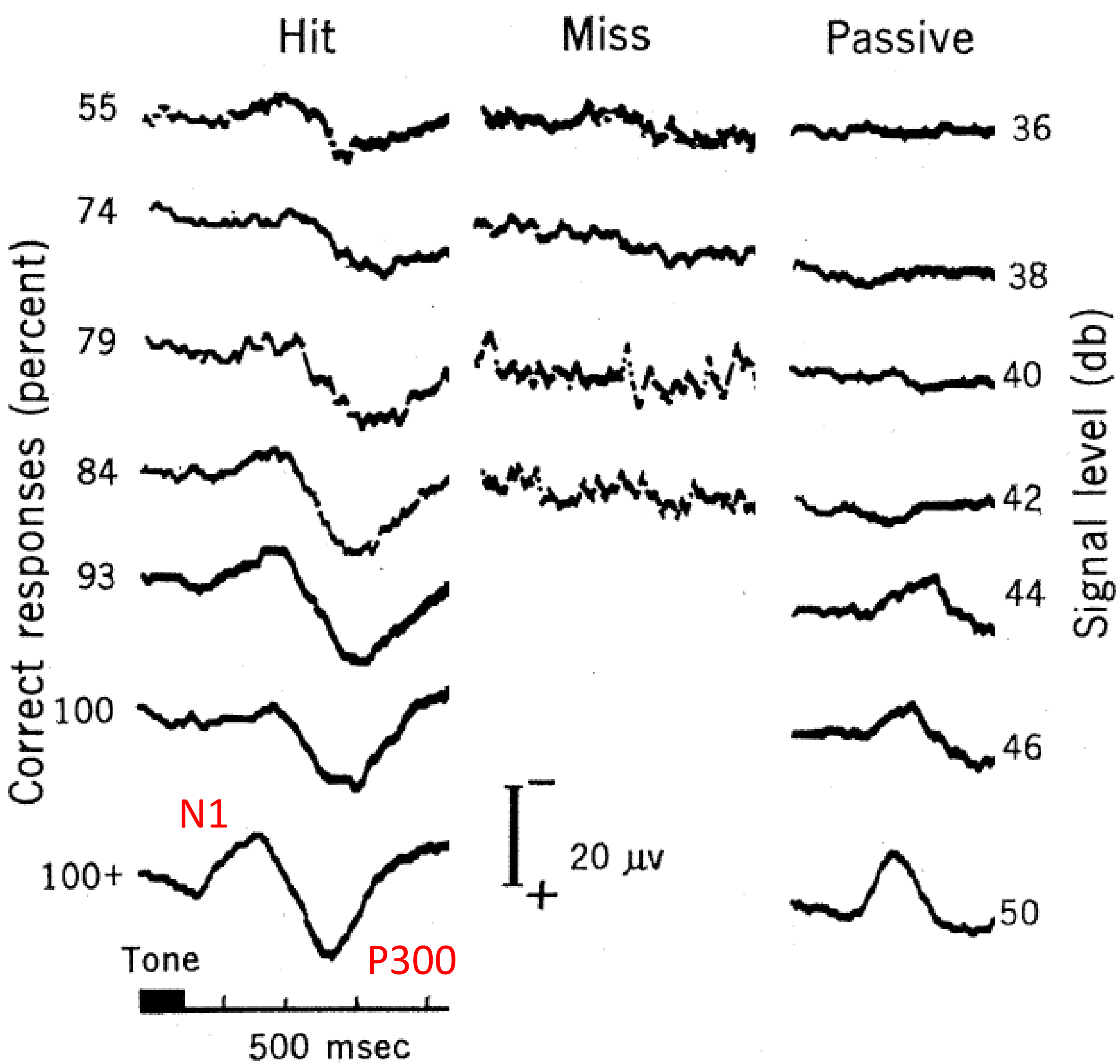
Hillyard et al, Science (1971)



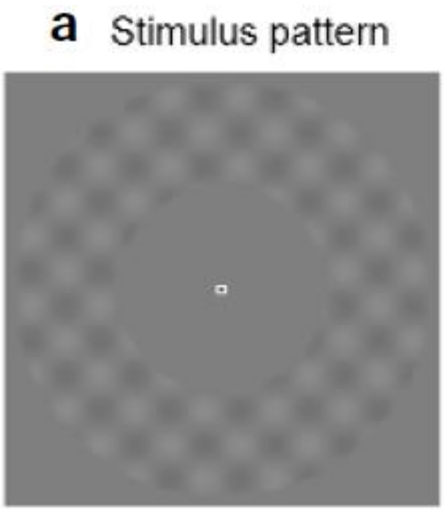
- Human EEG, one electrode at vertex
- Task: 500 ms after visual warning, tone pip presented or not (50-50), in background noise
- Different sound levels in different blocks
- Question: Does the Auditory Evoked Potential (AEP) play a role in “determining perceptual reactions?”

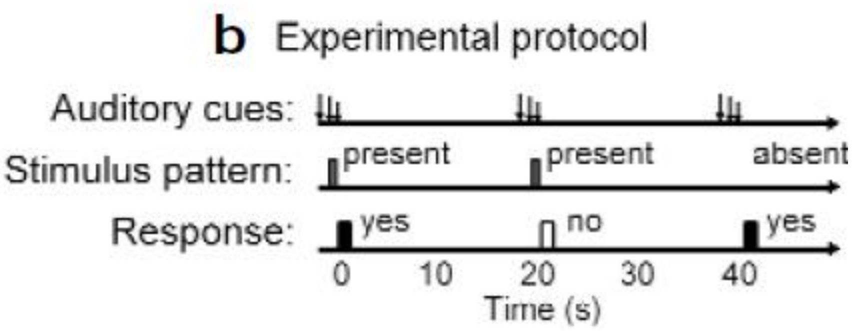
Hillyard et al, Science (1971)

- Across blocks with different difficulty
- N1 rises with stimulus strength even when passively heard
- P300 absent in passive condition

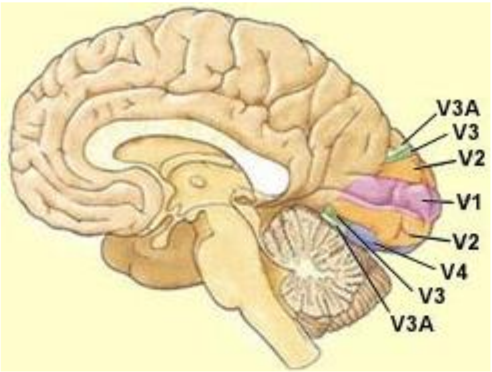


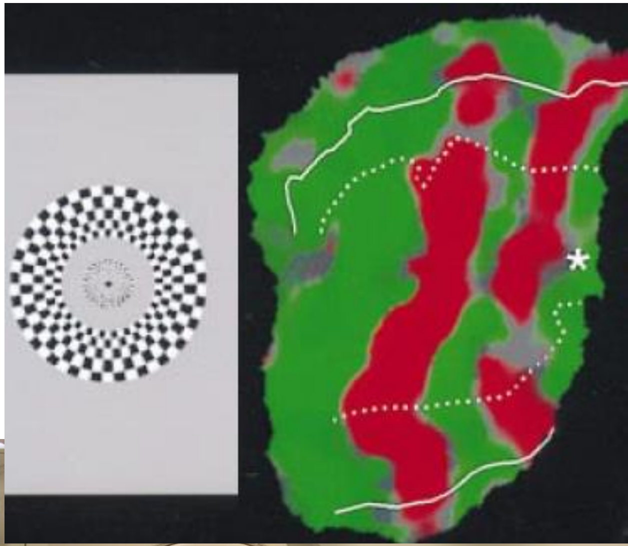
Ress & Heeger, Nat Neurosci (2000, 2003)

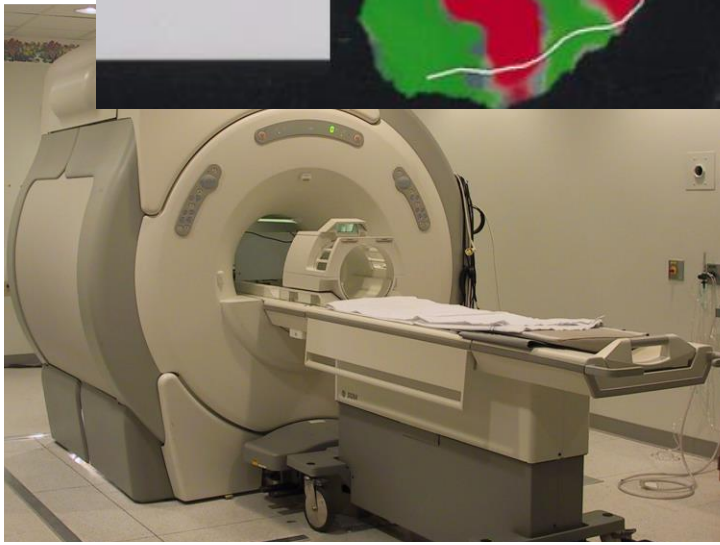


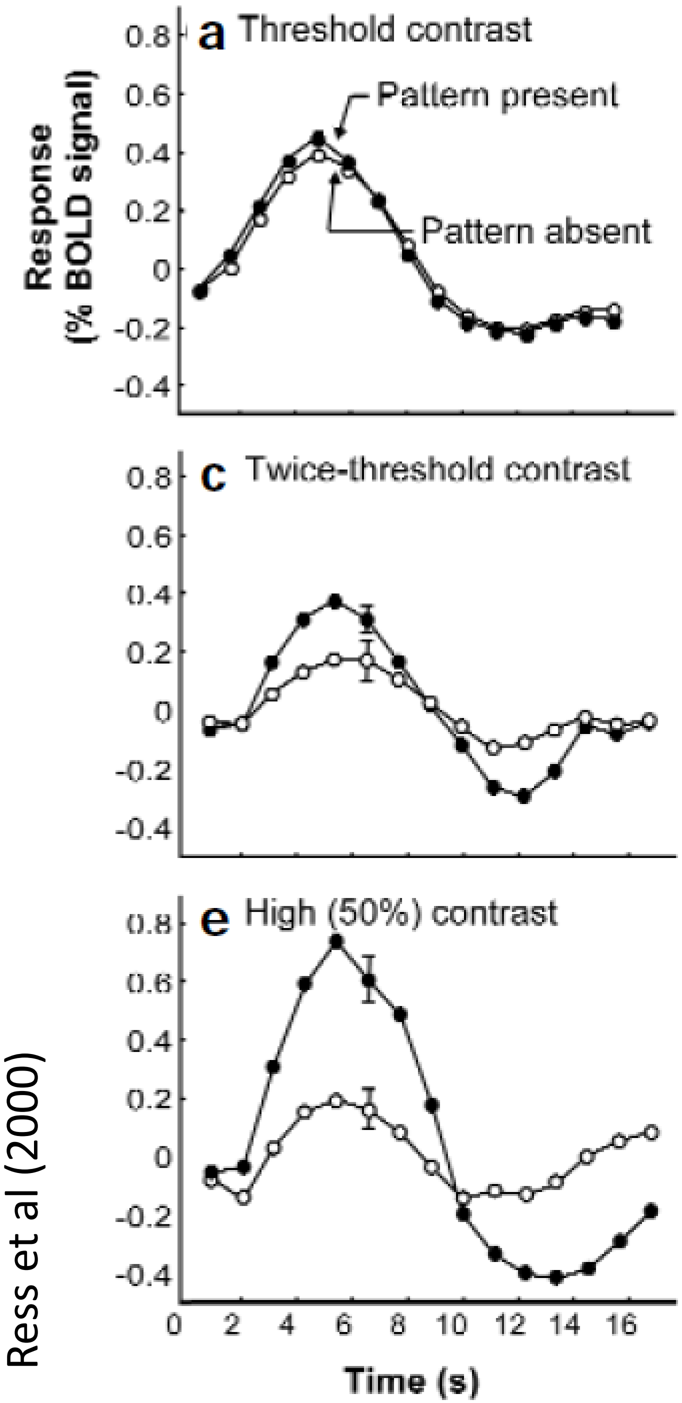


- fMRI: hemodynamic BOLD response in 3-mm voxels. Focus on areas V1, V2, V3





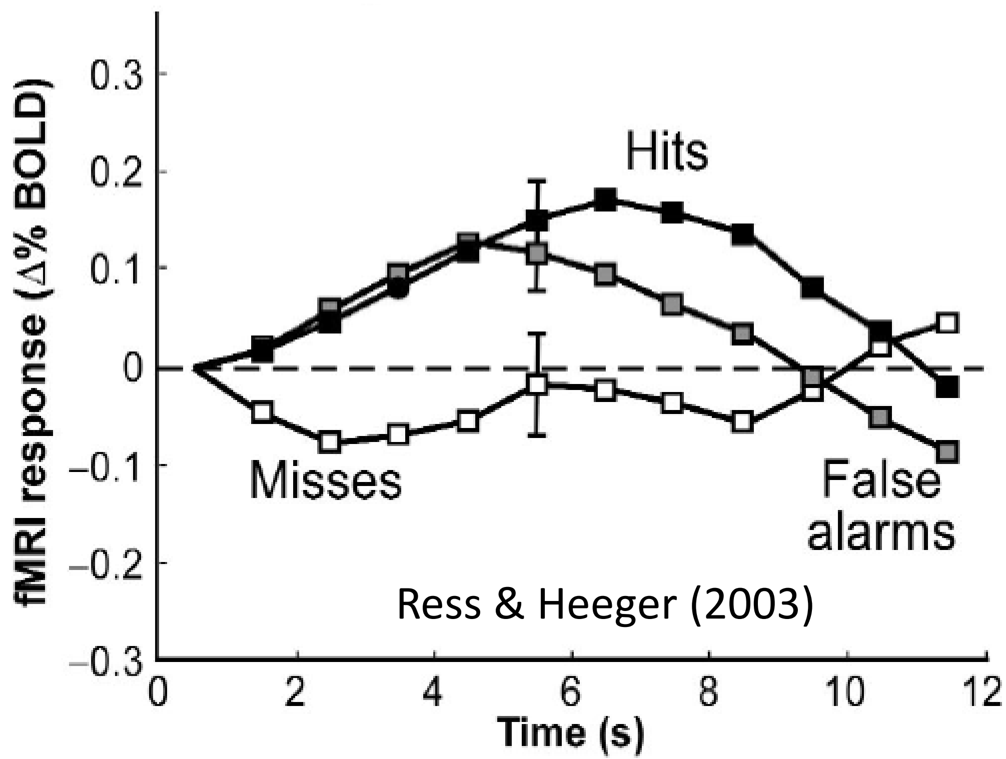




Ress et al (2000)

- V1 activity, and its modulation by stimulus presence, increased with pattern contrast

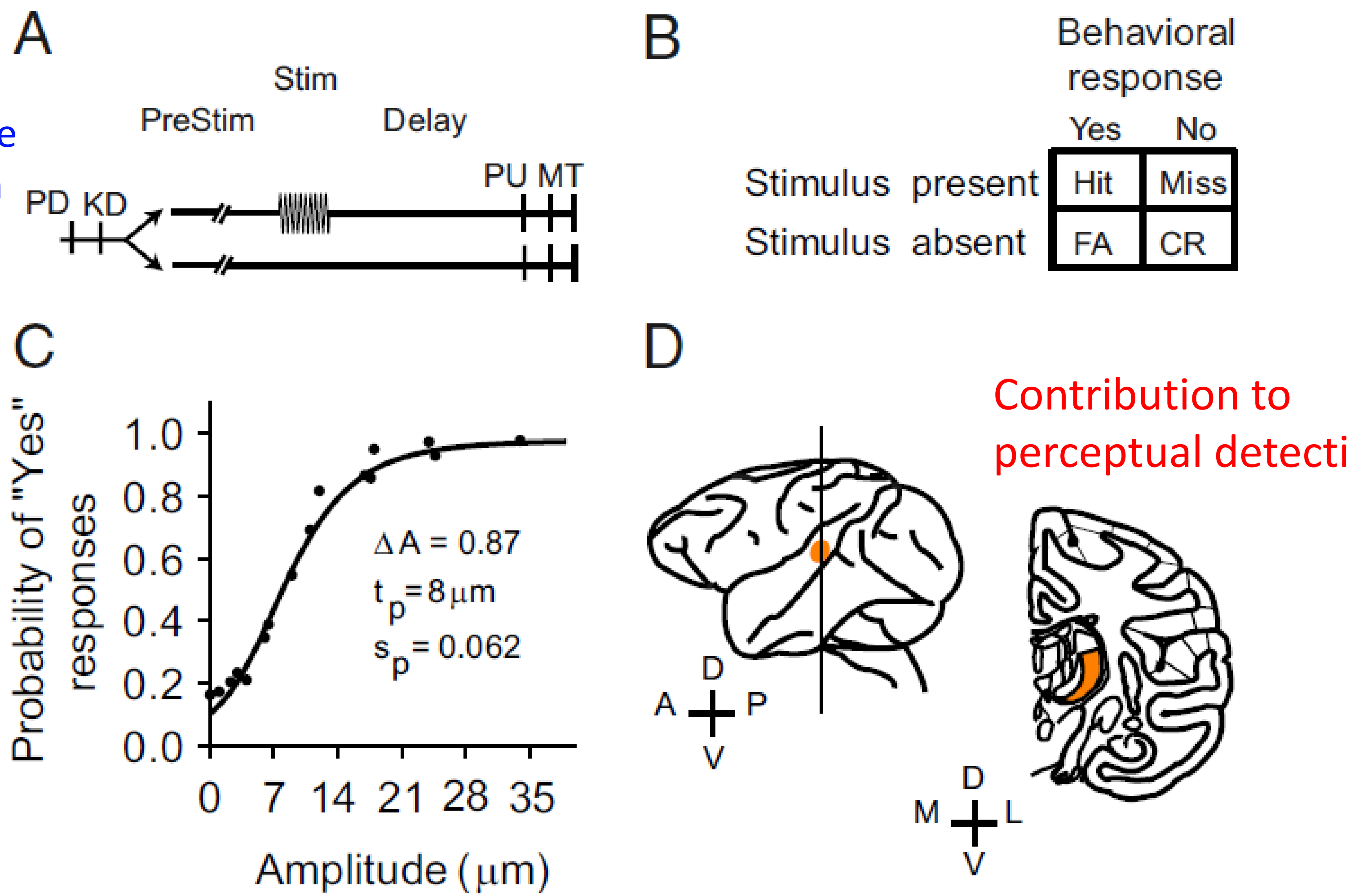
- Greater activation for False alarms than Misses – modulated with perception, not with physical reality!



Vazquez et al., PNAS (2012)

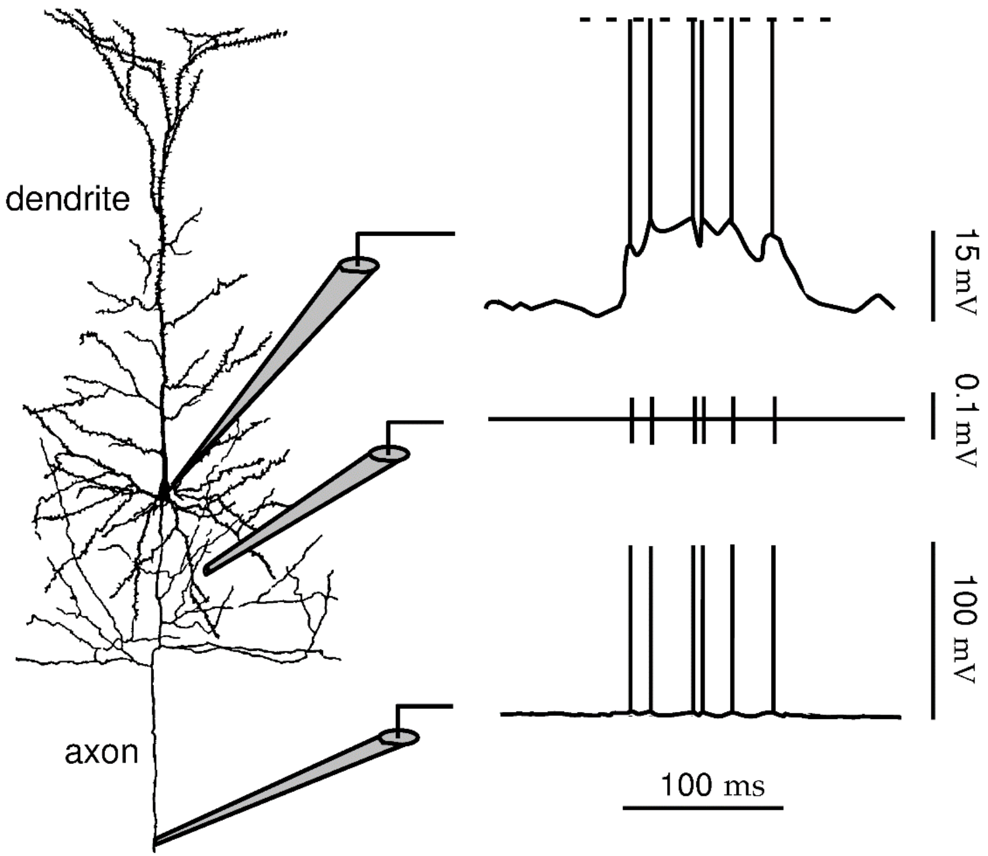
- Single-unit spiking activity of neurons in ventral posterior lateral (VPL) nucleus of somatosensory thalamus in monkeys

Vibtrotactile stimulus on fingertip



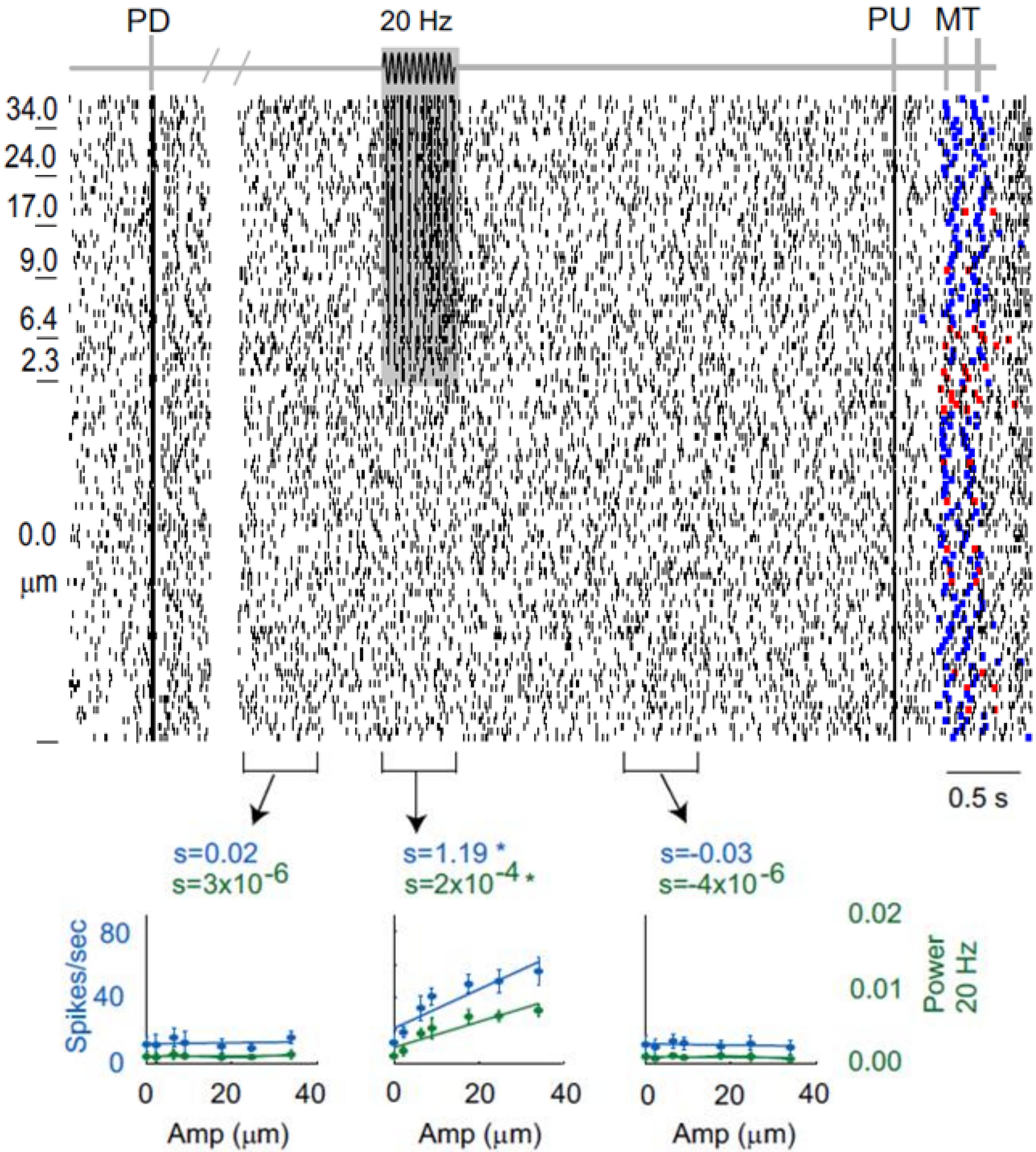
Contribution to perceptual detection?

Recording neuronal responses: Electrophysiology



Dayan & Abbot (2001)

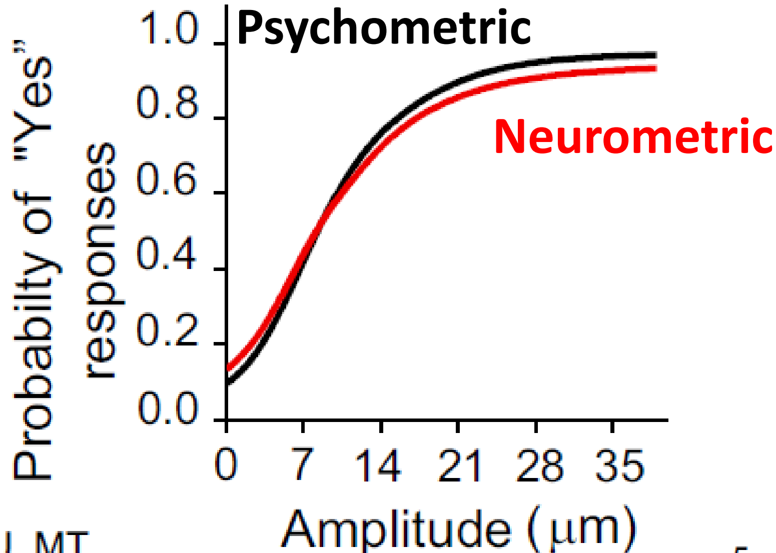
- intracellular – by inserting sharp glass electrode filled with conducting electrolyte into the cell, or "patch clamp"
- extracellular – electrode placed *near* a neuron (usually by ear)
- intracellular measures subthreshold membrane potential variations as well as action potentials, while extracellular provides just the action potentials.
- Extracellular much easier to do in vivo / awake behaving.
- A LOT of ongoing methods innovation



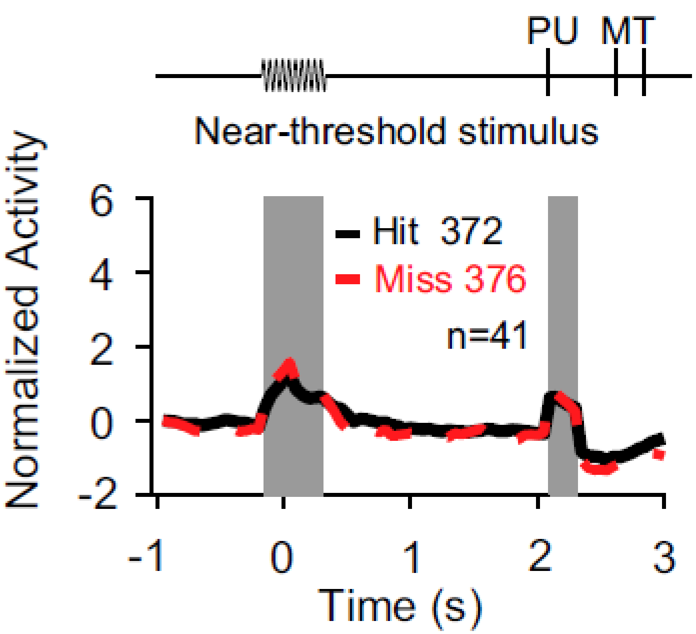
- "Raster" plot – individual spike times
- Firing rate during stimulus increased with amplitude of vibrotactile stimulus
- (so did spectral component at stimulus frequency)

Vazquez et al., PNAS (2012)

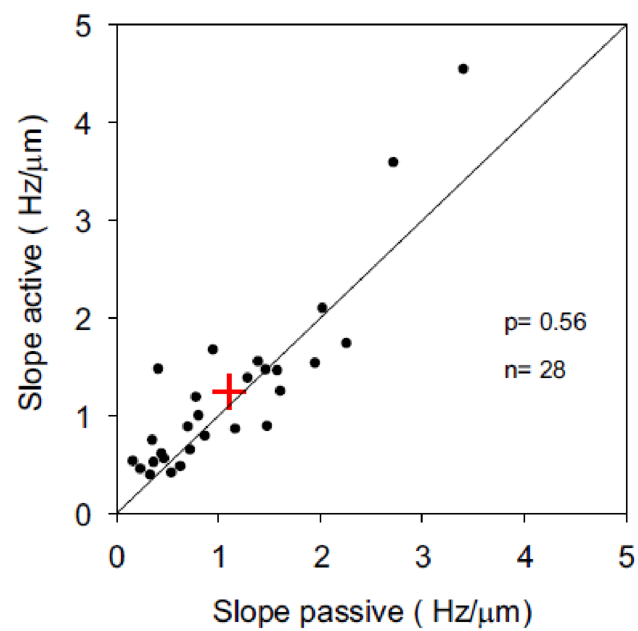
Vazquez et al., PNAS (2012)



Individual thalamic neurons almost as good as the monkey!

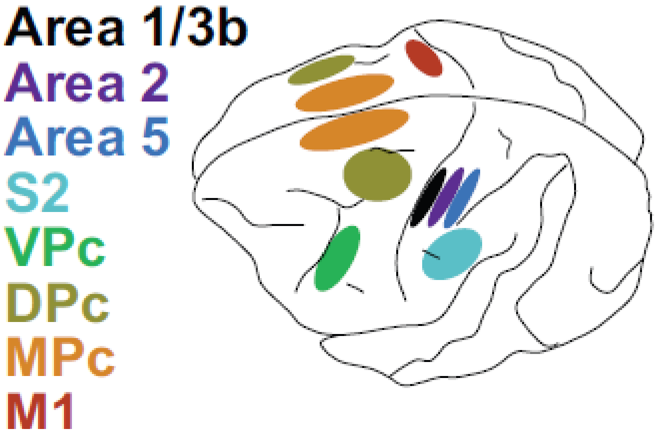


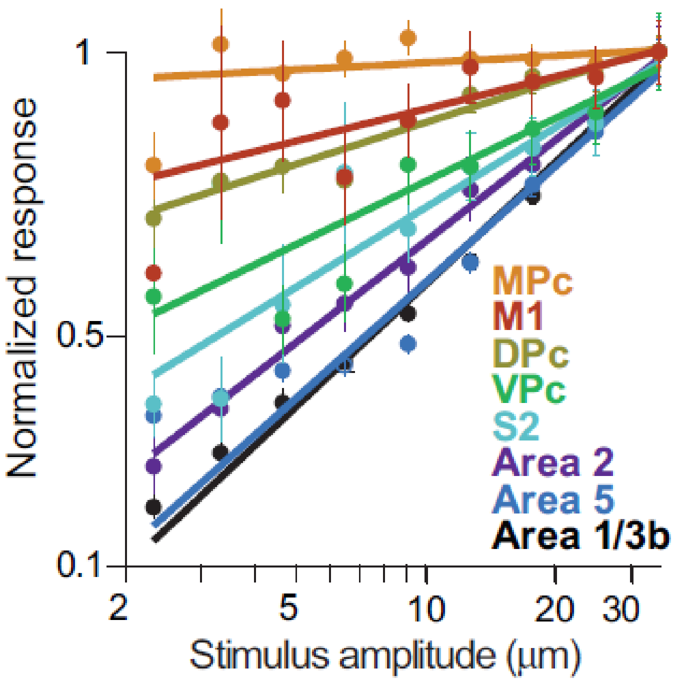
…but bore no relationship to perceptual outcome at a given stimulus level!



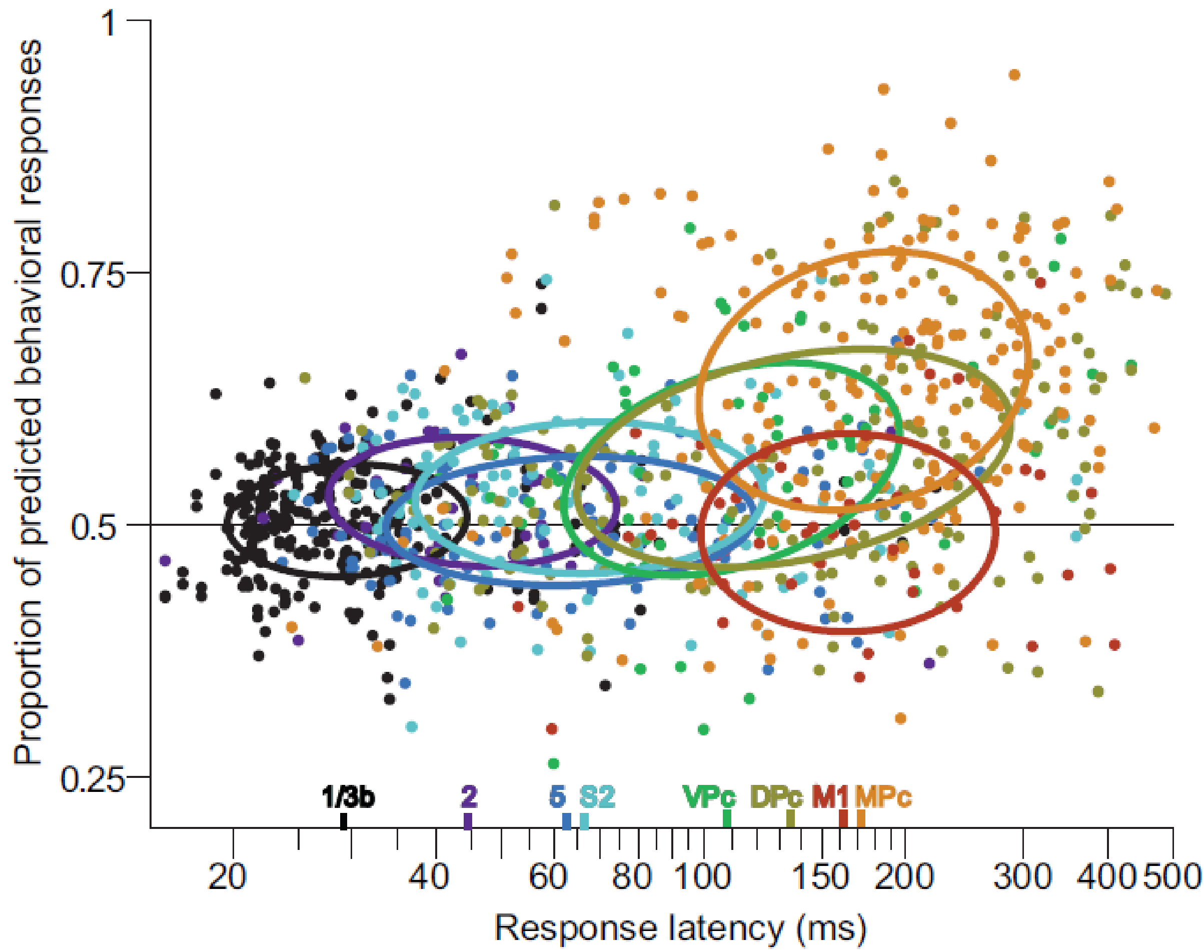
De Lafuente et al., PNAS (2006)

Recorded areas:



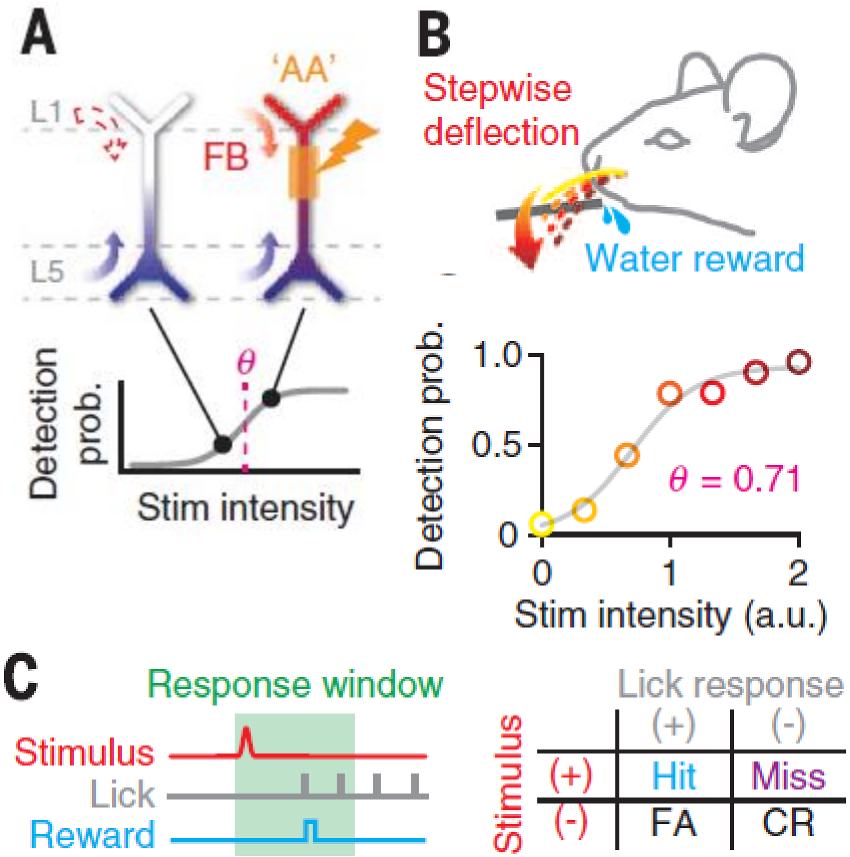


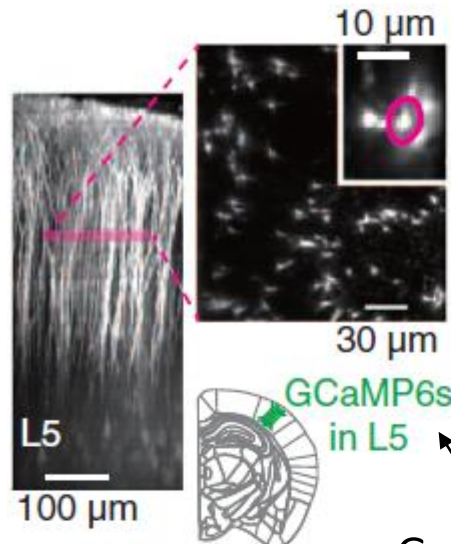
Across the sensory-motor pathway, neurons became less coupled to stimuli, and gradually more coupled to perceptual outcome



Takahashi et al, Science (2016)

- **Apical amplification hypothesis**: dendritic Ca^{2+} activity in Layer-5 cortical pyramidal neurons amplifies the effects of feedback inputs to superficial layers… and gives rise to conscious perception!

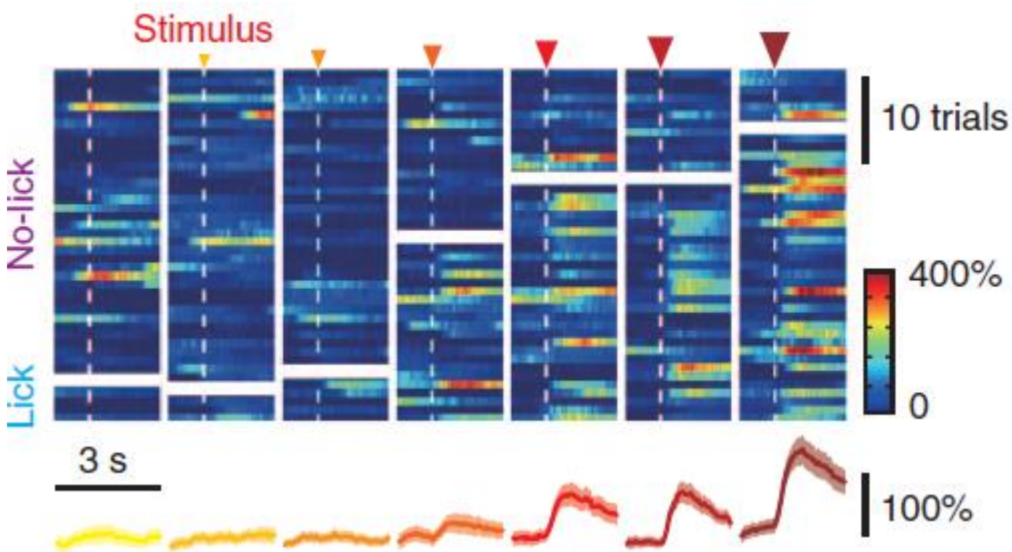




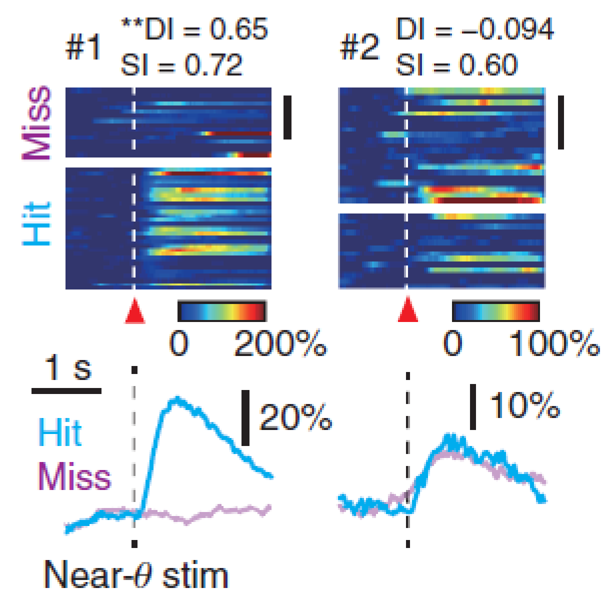
Fast-scanning two-photon **calcium imaging** from apical dendrites of L5 neurons in the C2 barrel column in primary somatosensory cortex (S1)

Genetically-encoded indicator of intracellular calcium – fluoresces green when Ca^{2+} binds to it. This is captured by a two-photon microscope

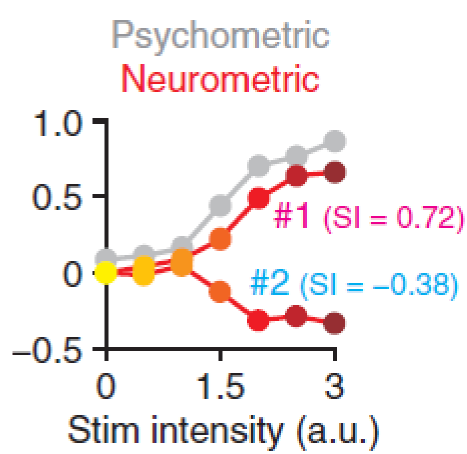
Takahashi et al, Science (2016)



- Relationship with perception?
- Diverse response types across neurons:
- Some strongly distinguished perceptual outcome, others not at all

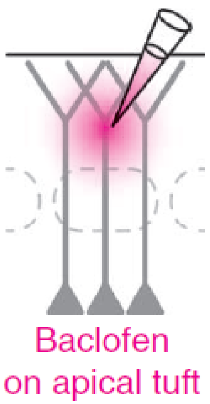


- Ca^{2+} response increased with stimulus strength for some neurons
- Decreased for others



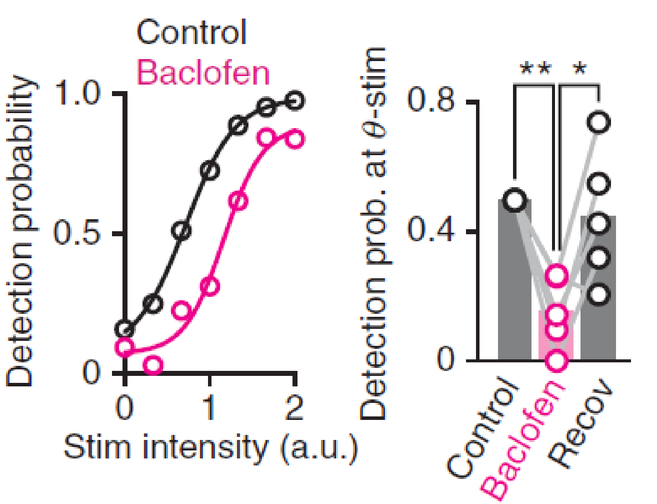
Takahashi et al, Science (2016)

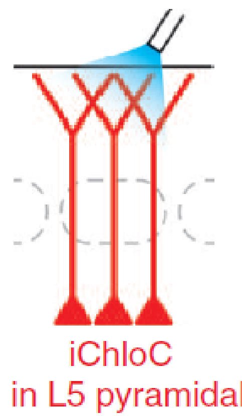
- Dendritic Ca^{2+} activity causally linked to perceptual detection



Pharmacological manipulation:

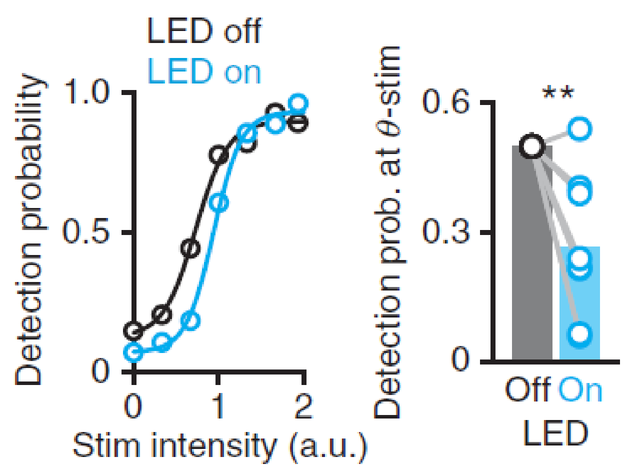
Baclofen, a $GABA_B$-receptor agonist, suppresses dendritic Ca^{2+} spikes

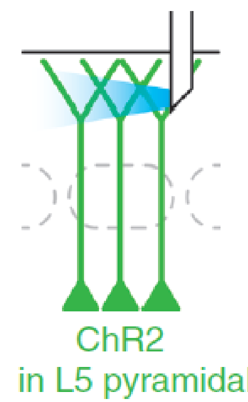




Optogenetic Inactivation:

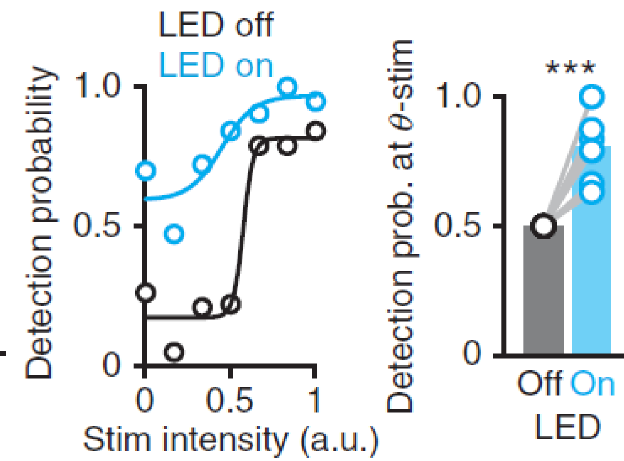
Blue-light on iChLoc suppresses dendritic Ca^{2+} activity





Optogenetic Activation:

Blue-light on ChR2 up-regulates dendritic Ca^{2+} activity



Observations

Signal Detection Theory applied:

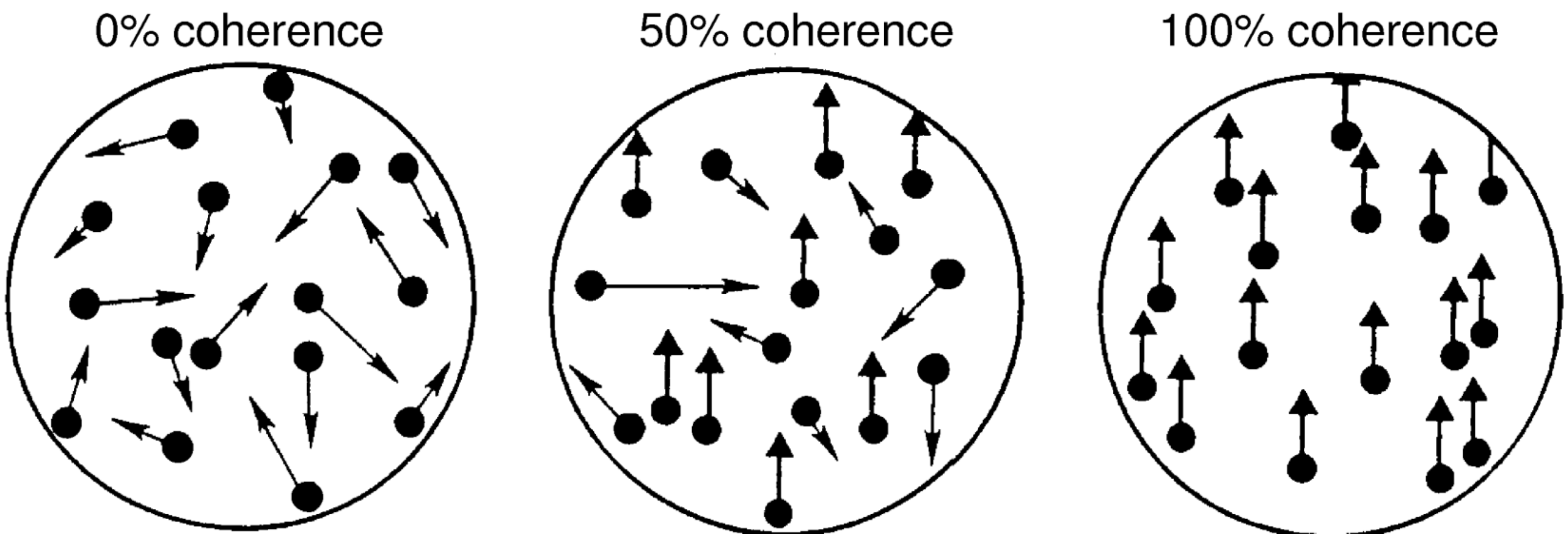
- Across many levels of analysis
  - whole-brain electrophysiology
  - individual-area hemodynamics
  - single cell spiking
  - calcium signalling in cell substructures
- Across many species
  - Human
  - Monkey
  - Mouse
- Across many sensory modalities
  - Auditory
  - Visual
  - Somatosensory
- Role of cortical feedback

Overview

- Intro to **Psychophysics**
- Signal detection theory
- Applying SDT to understand the neural basis of perceptual **detection**
- Perceptual **discrimination** and its sensory neural correlates
- Perceptual **decision making**: neurally-informed modelling
- **Attention**: Perceptual and neural effects
- Behavioural paradigms for other cognitive functions, e.g. memory and learning

Discrimination

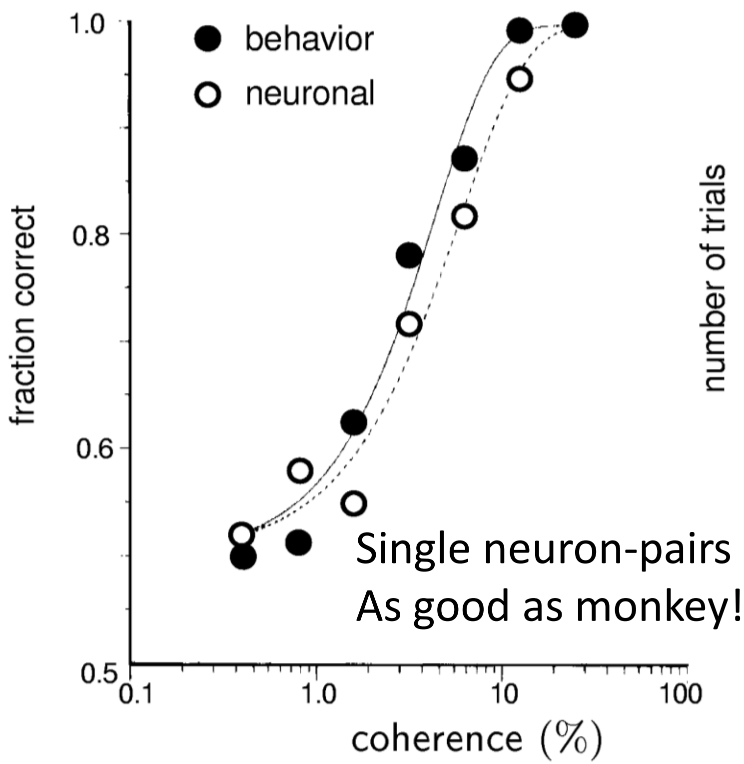
- Discrimination is deciding between a finite set of possible stimulus values.
- Motion discrimination (e.g. Britten et al 1992) provides an example:



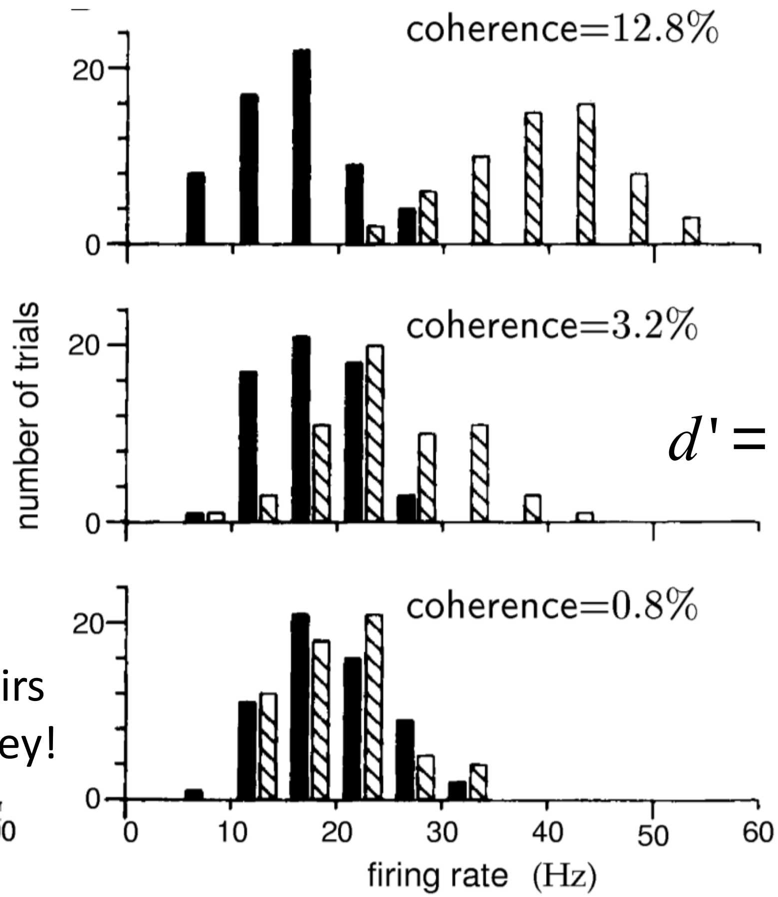
- Task: report whether the net motion is up or down.
- Coherence refers to the percentage of dots moving together in one direction, while all other dots reappear at totally random places.
- The higher the coherence, the easier the task is.

Neurometric discrimination

- Britten et al (1992) recorded spiking from single neurons in medial temporal area (MT) while monkeys performed motion task.
- MT neurons are each tuned to a direction. They presented this preferred direction versus the opposite.



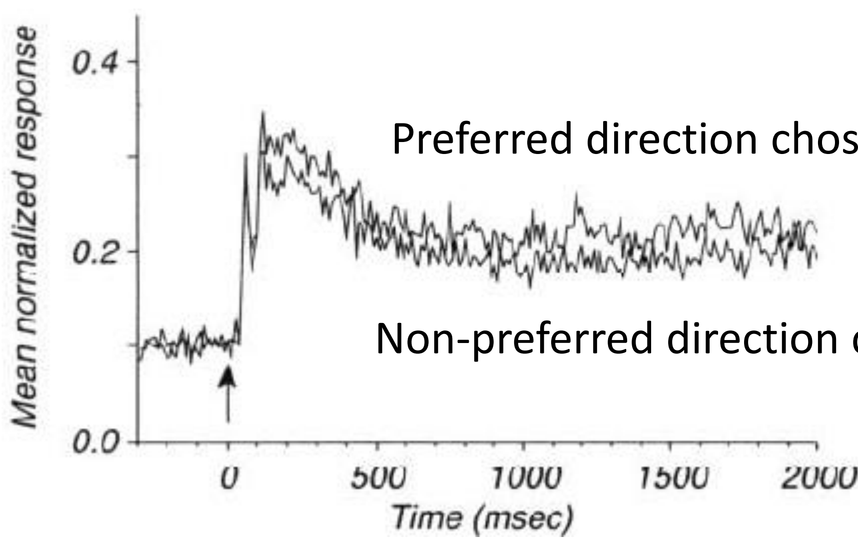
Unpreferred (-) Preferred (+)

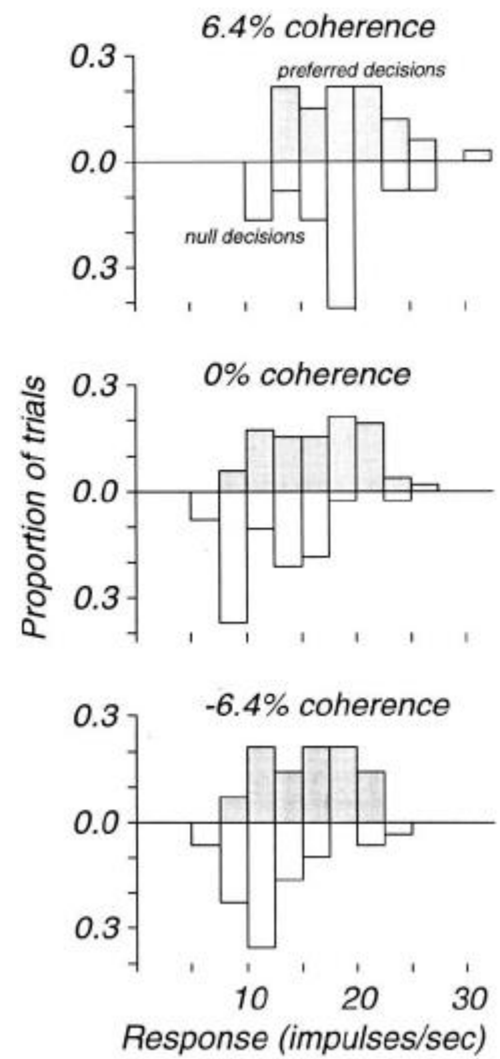


$$d' = \frac{\langle r \rangle_+ - \langle r \rangle_-}{s_r}$$

Choice Probability

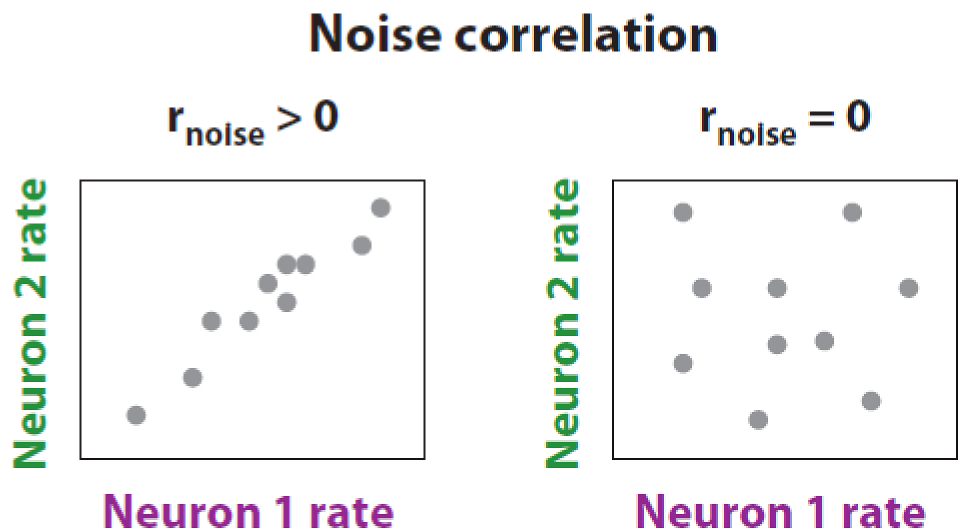
- CP: The trial to trial correlations between the activity of sensory neurons and the decisions reported by subjects
- Britten et al (1996) quantified the degree to which a monkey's choice could be discriminated from the spiking activity of single MT neurons performing the motion task.





Noise correlations

- How can a single neuron have such good discriminating ability, and be significantly correlated with behaviour, when it is only one of so many?
- Ans: They are not independent



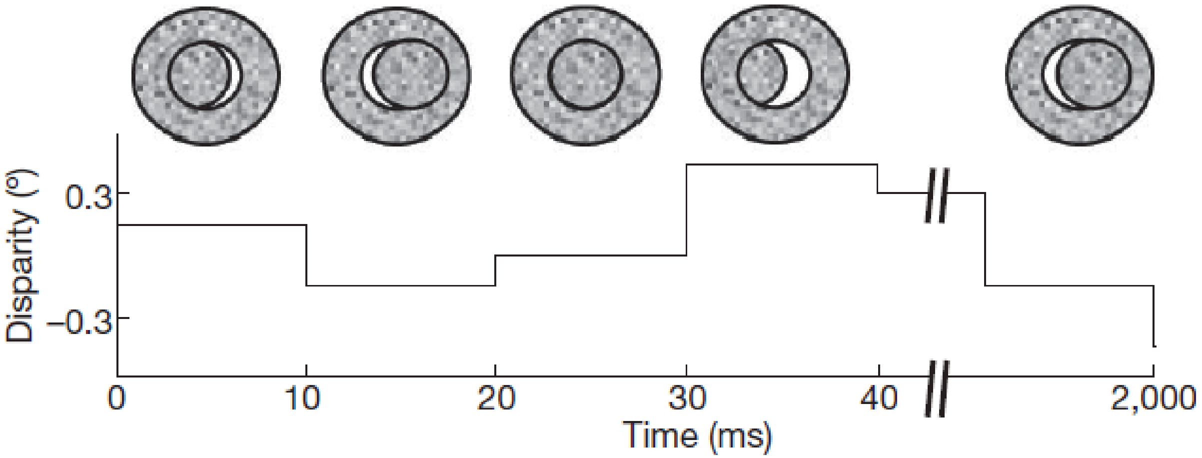
- Ongoing research examining source of noise correlations – e.g. horizontal connectivity or top-down fluctuations?

Nienborg & Cumming (2012)

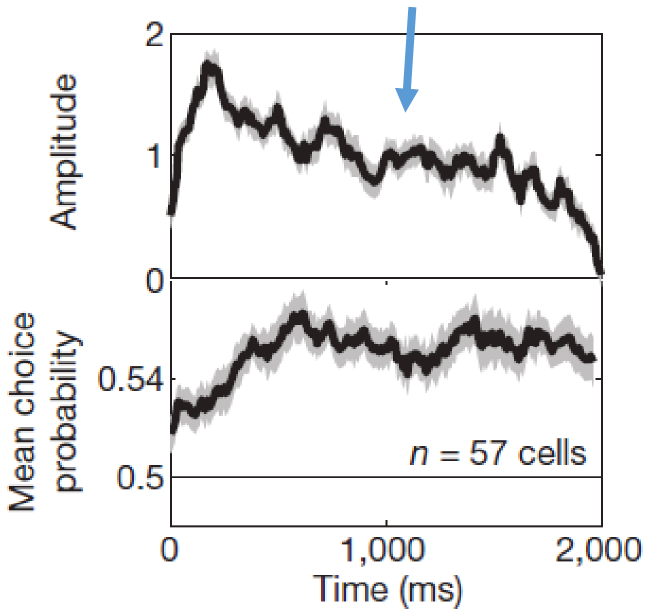
Choice Probability

- Where does CP come from?
- Random noise in sensory neurons which are read from to make decisions?
- Top-down signals (like attention) can also mediate choice probability

White-noise stimulus variations



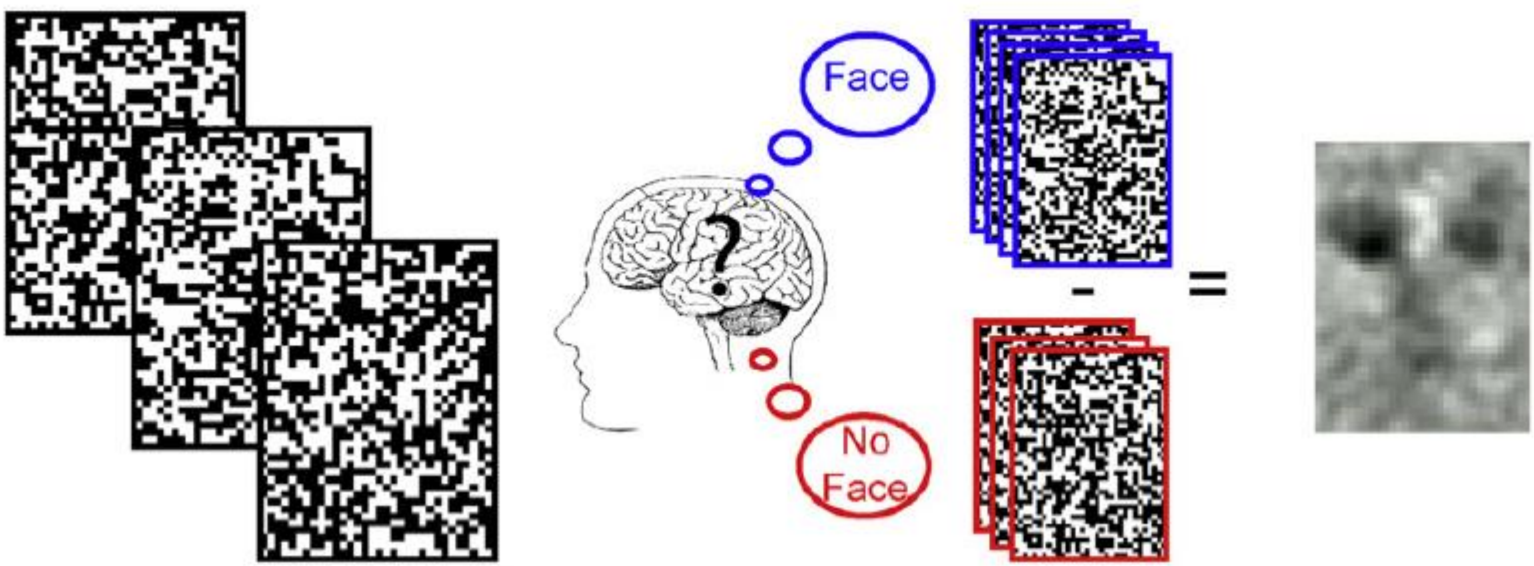
"Psychophysical kernel"



Nienborg Cumming (2009)

Psychophysical Reverse correlation

- Average a stochastically varying stimulus with respect to different perceptual outcomes
- Broader applications in e.g. face perception



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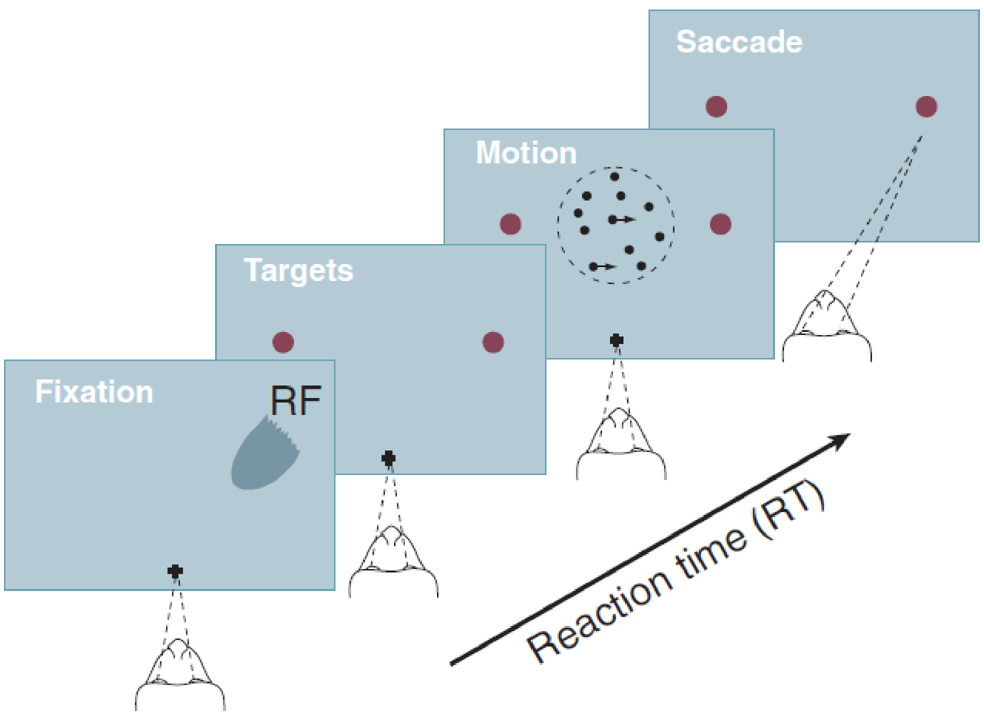
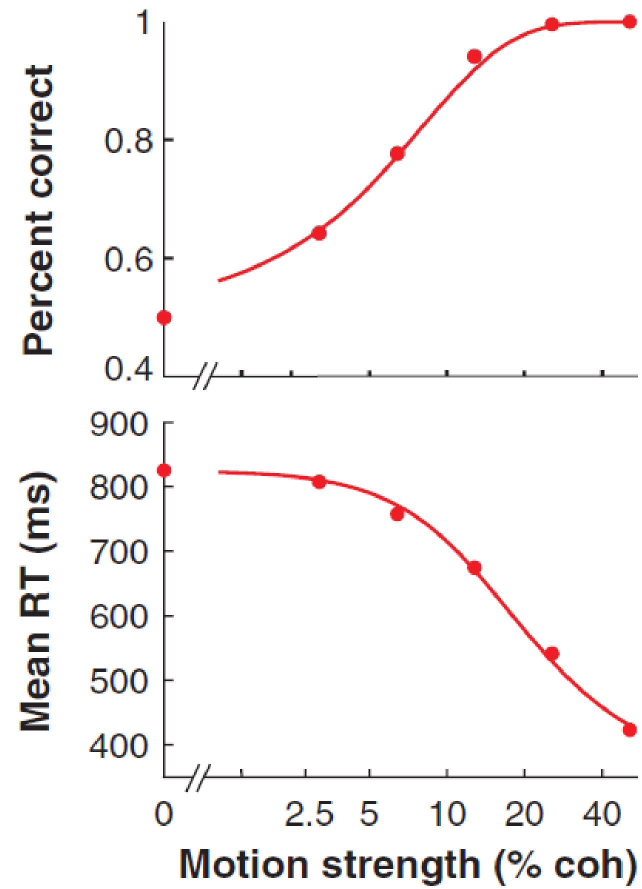
Immediate sensorimotor decisions

- Most tasks in the above involved delayed reports
- Allowing immediate decision reports provides richer data
- Effects on RT as well as accuracy





Gold & Shadlen (2007)

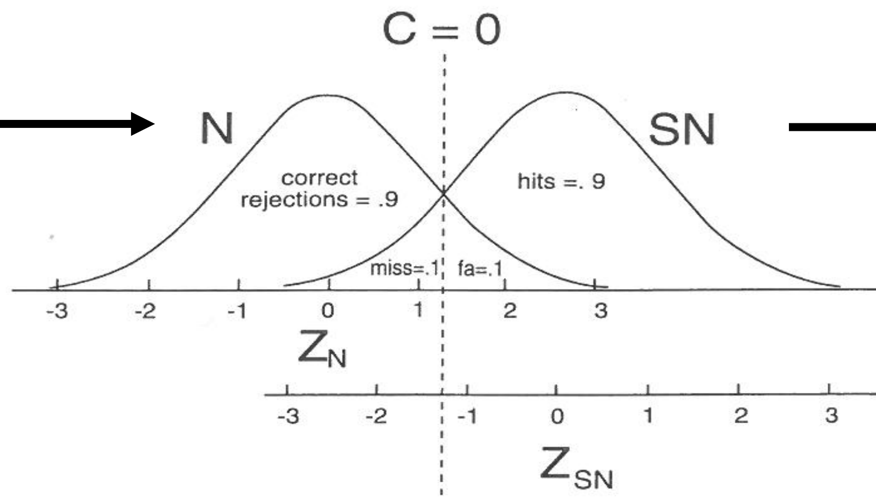
From Sensation to Action

Sensory Encoding → Decision Formation → Action Planning

Signal Detection Theory

Encode Sensory Information

Decision rule = set a criterion C



Plan & Execute Action

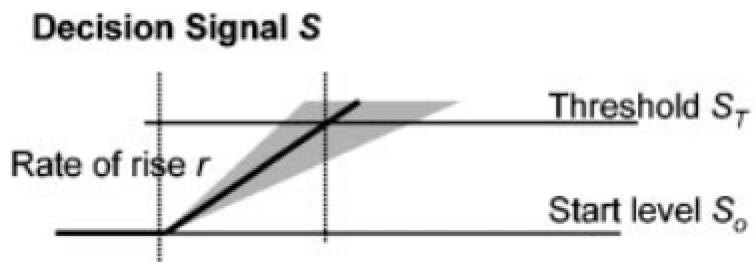
"Magnitude of sensory observation"

Provides a quantitative account of behavioral choice – the observers' decision reports.

But what about the **TIMING** of decisions??

Linear Approach-to-Threshold model

Encode Sensory Information



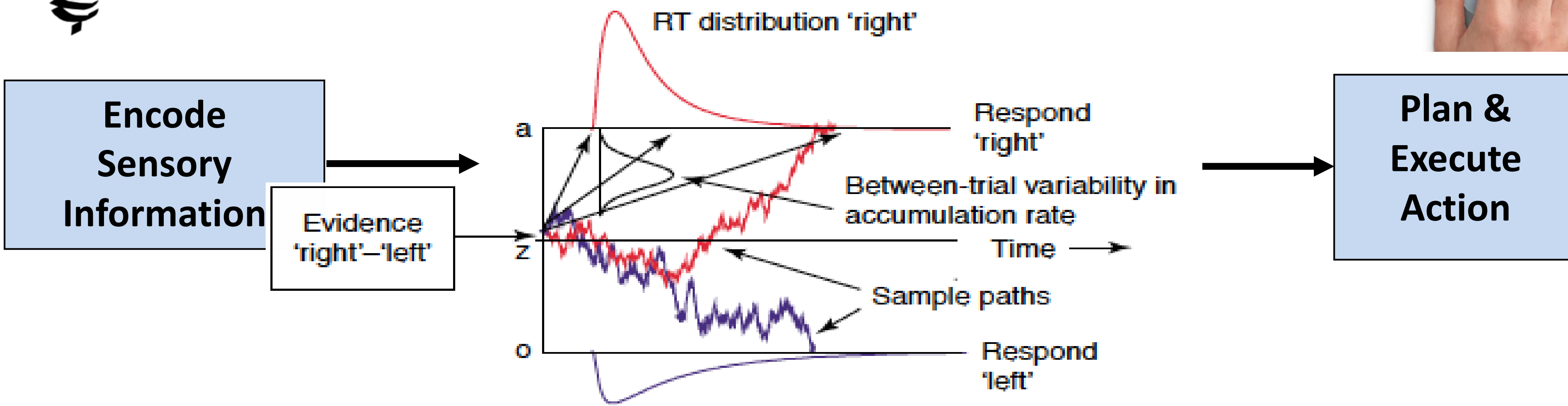
Plan & Execute Action

- A “ballistic” decision signal rises linearly in response to information about a target to a threshold at which a response is initiated.
- Rate of linear increase varies from trial to trial with a Gaussian distribution.
-

Carpenter & Williams(1995), Reddi et al (2003)

- Provides a quantitative account of **reaction time distributions**

Drift Diffusion model
(for two-alternative decisions)

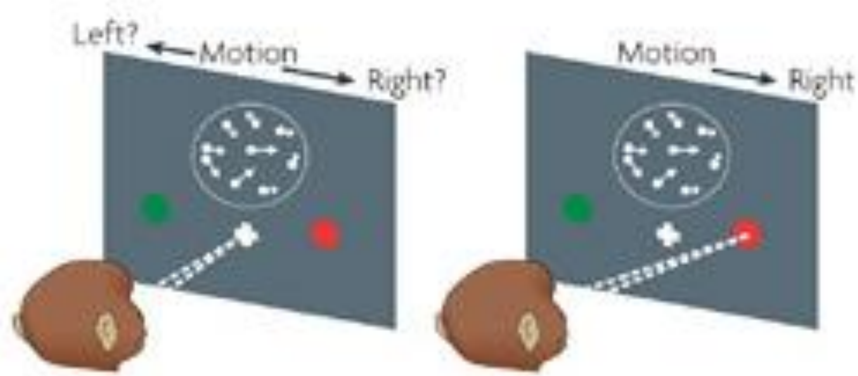


Smith & Ratcliff 04

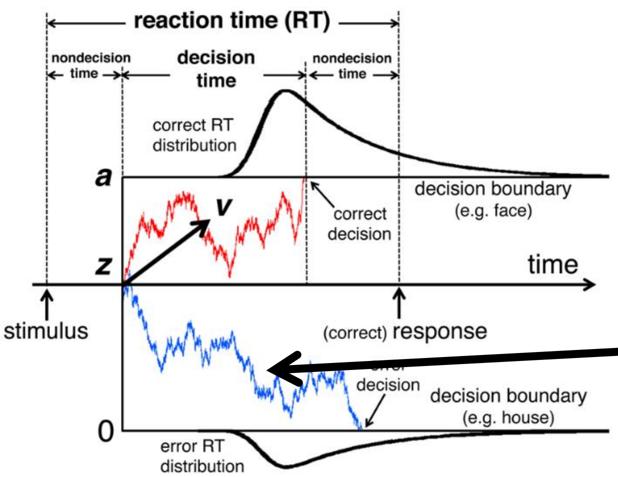
- Based on bounded accumulation of noisy sensory evidence
- Can capture both timing and accuracy of choices
- With additional parameters can capture diverse effects - very versatile!

Drift Diffusion model
(for two-alternative decisions)

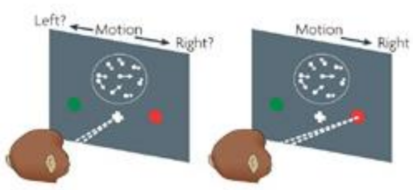
Consider a decision about noisy visual information



Drift Diffusion model
(for two-alternative decisions)



"Decision variable"



Drift Diffusion model
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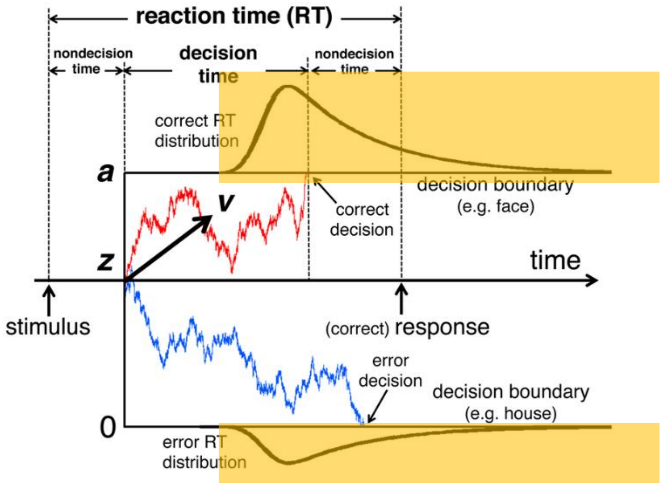
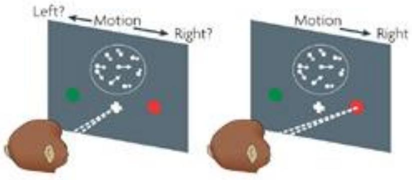


Joint distribution of response time and accuracy



Drift Diffusion model
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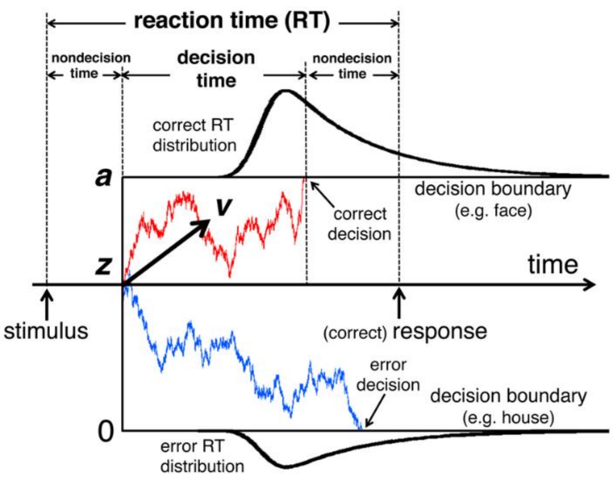
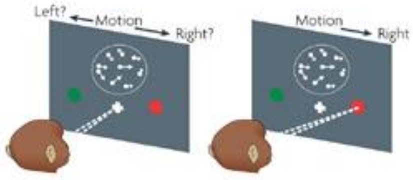


$$dX = vdt + cdW$$

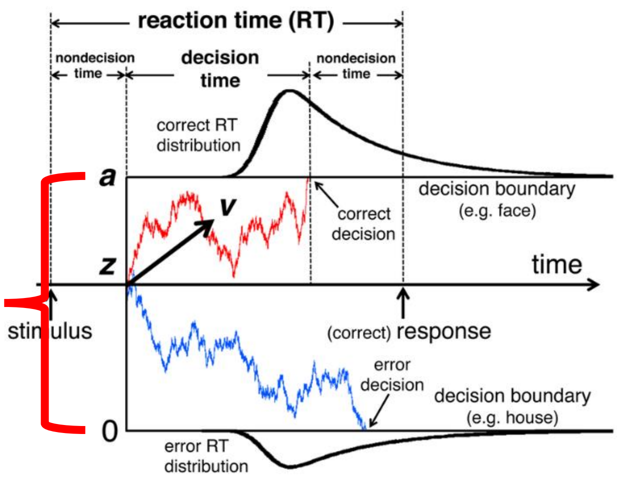
$$X(0) = z$$

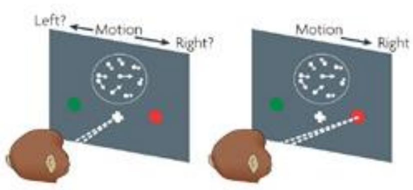


Parameters

a – decision bound
z – Starting point (no bias when z=a/2)
v – evidence accumulation (drift rate)
ndt – non-decision time

Drift Diffusion model
(for two-alternative decisions)





$$dX = vdt + cdW$$
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Parameters

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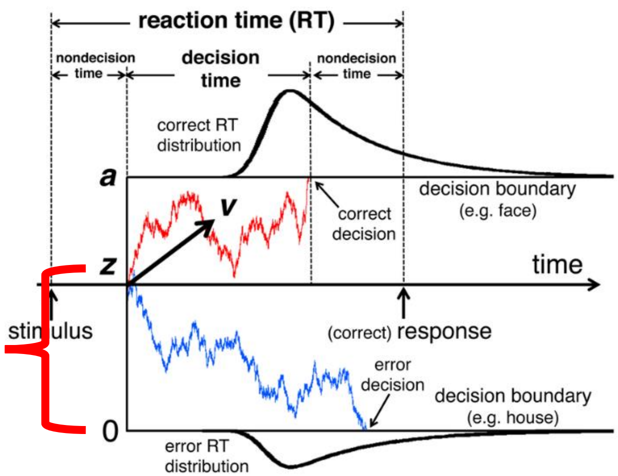
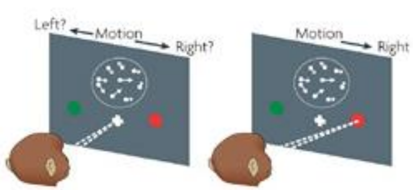
How cautious? (Speed-accuracy tradeoff)

Drift Diffusion model
(for two-alternative decisions)



$$dX = vdt + cdW$$
$$X(0) = z$$



Parameters

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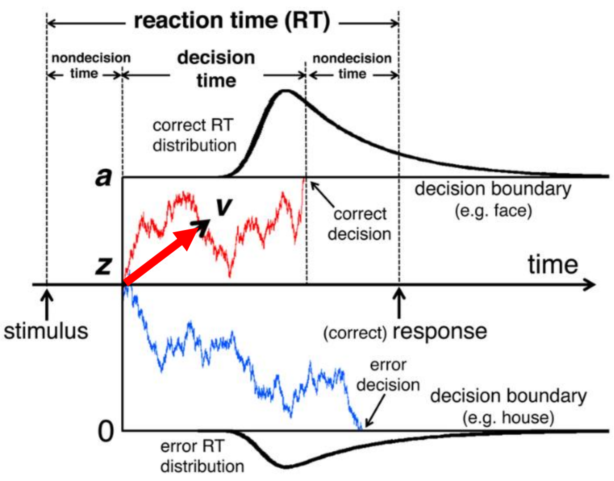
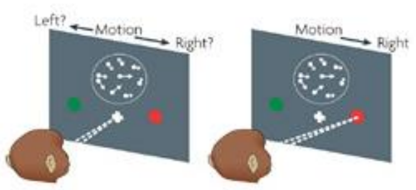
Decision bias, e.g. prior/payoff

Drift Diffusion model
(for two-alternative decisions)





$$dX = vdt + cdW$$

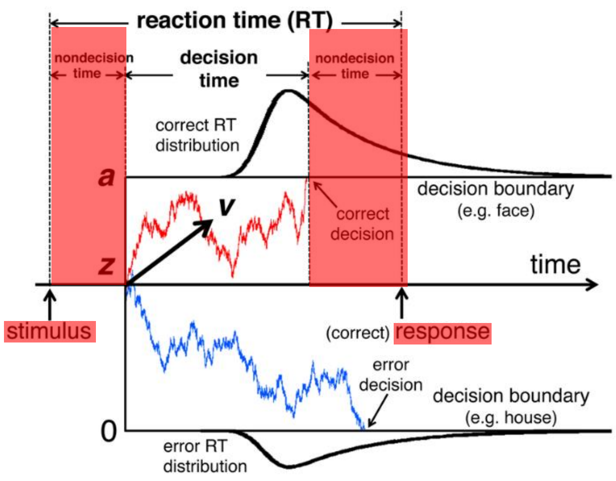
$$X(0) = z$$

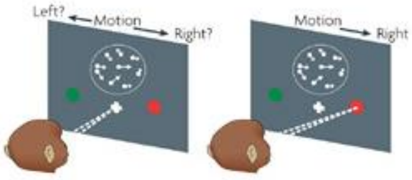
Parameters

a – decision bound
z – Starting point (no bias when z=a/2)
v – evidence accumulation (drift rate)
ndt – non-decision time

Expectation of the noisy evidence (i.e. mean)
-> average rate of rise of D.V.

Drift Diffusion model
(for two-alternative decisions)





$$dX = vdt + cdW$$
$$X(0) = z$$

Parameters

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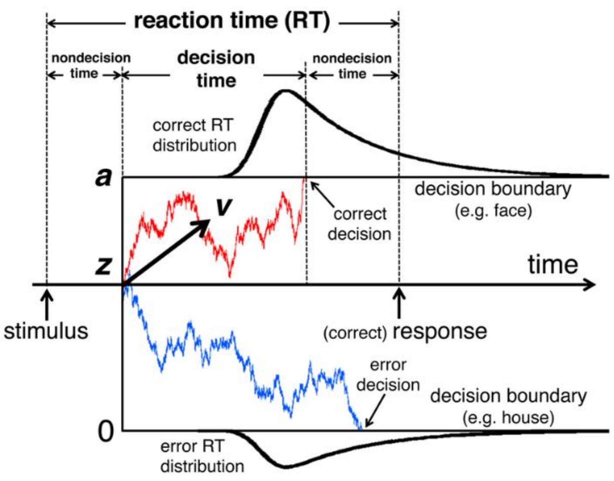
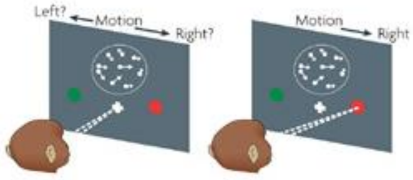
v – evidence accumulation (drift rate)
ndt – non-decision time

Additive delays due to things other than the deliberative decision process

Drift Diffusion model
(for two-alternative decisions)





$$dX = vdt + cdW$$

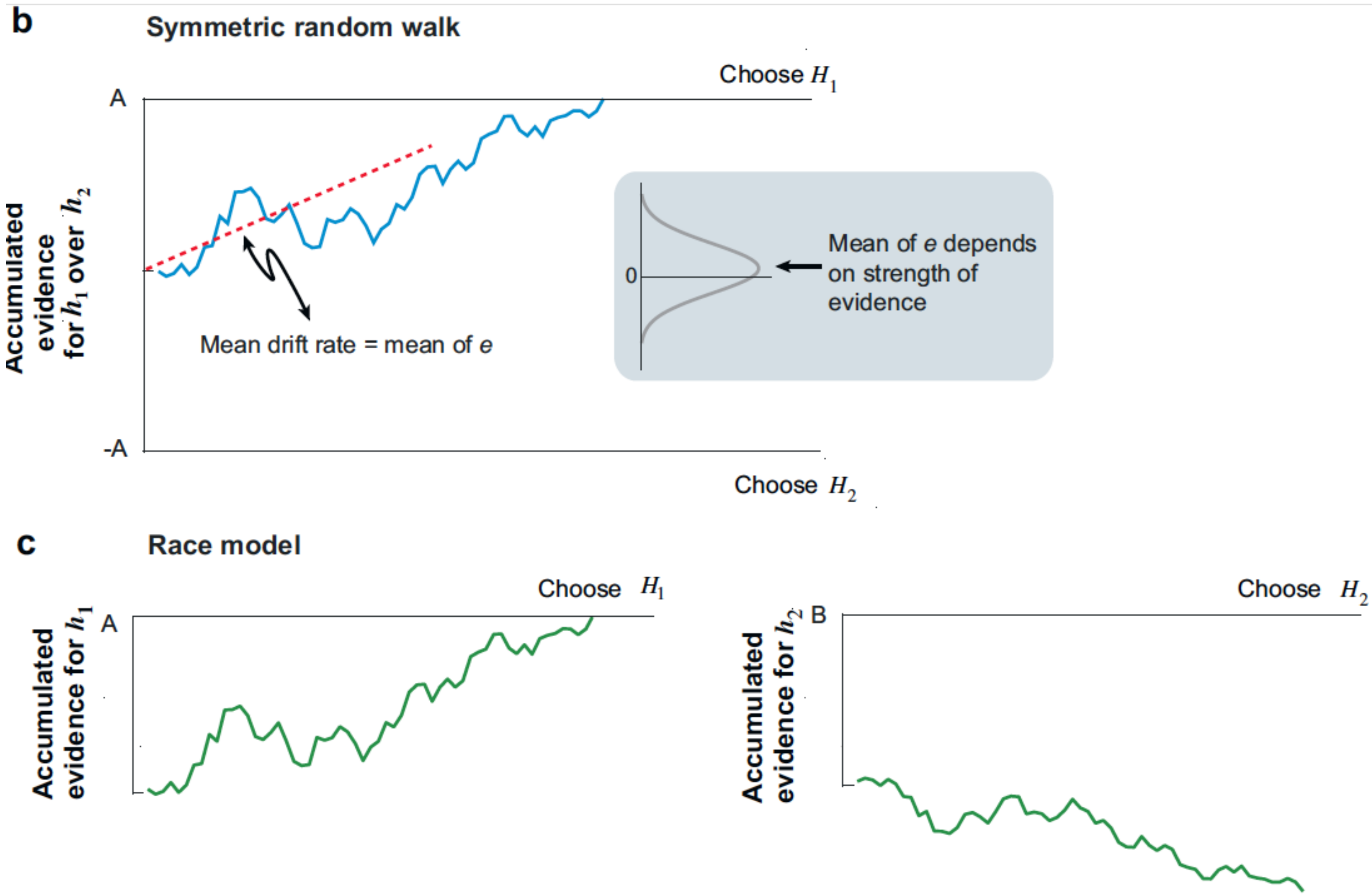
$$X(0) = z$$

Parameters

a – decision bound
z – Starting point (no bias when z=a/2)
v – evidence accumulation (drift rate)
ndt – non-decision time

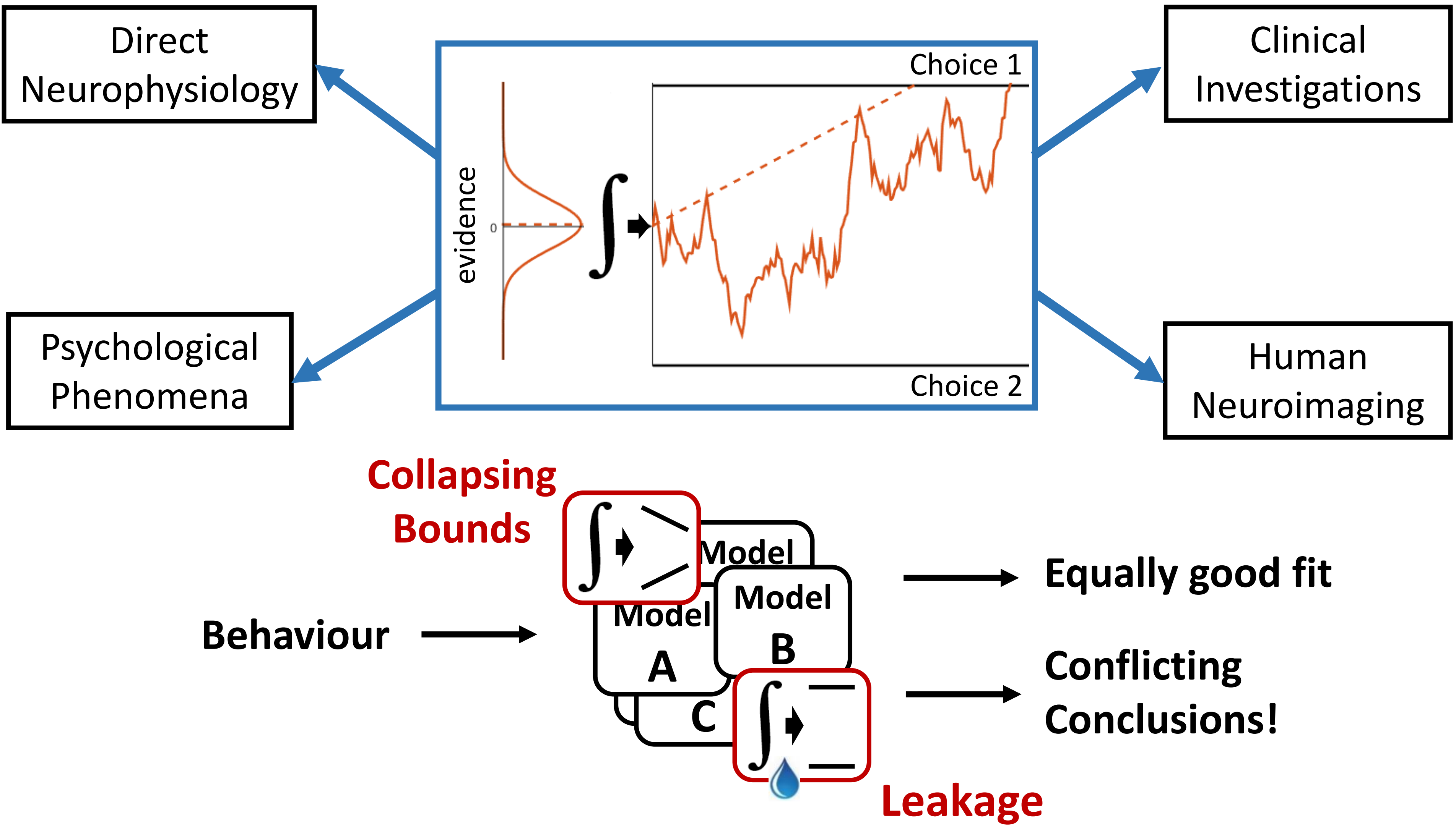
Can also add parameters for trial-to-trial variability in:
- starting point (produces fast errors)
- drift rate (produces slow errors)
- nondecision time (shape of RT dist.)

Drift Diffusion model
- easily re-cast as a RACE



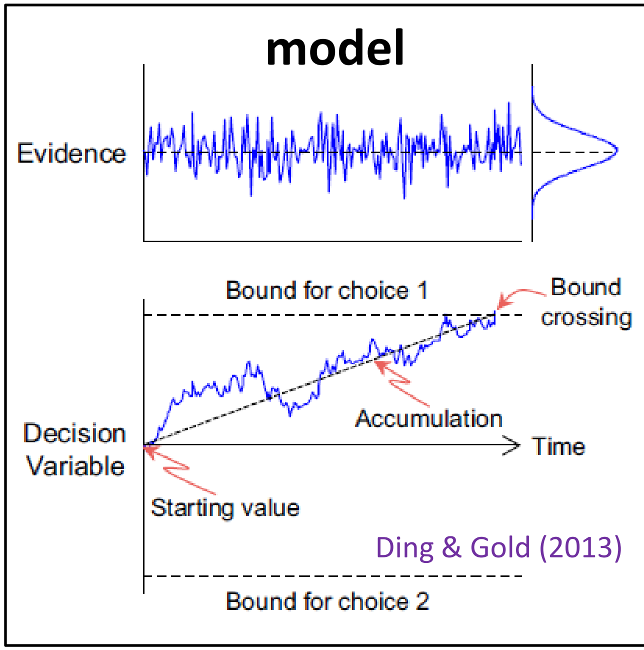
Gold & Shadlen (2007)

Models of perceptual decision making



WHEN and WHY do we employ these strategies ?

Neural correlates of a decision variable



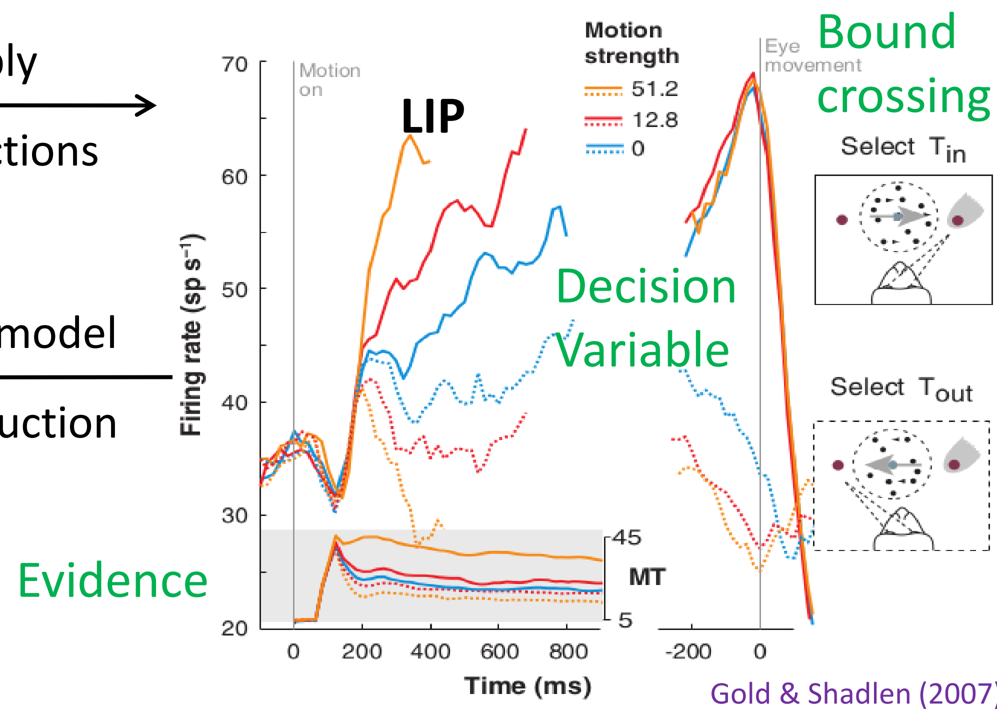
apply

predictions

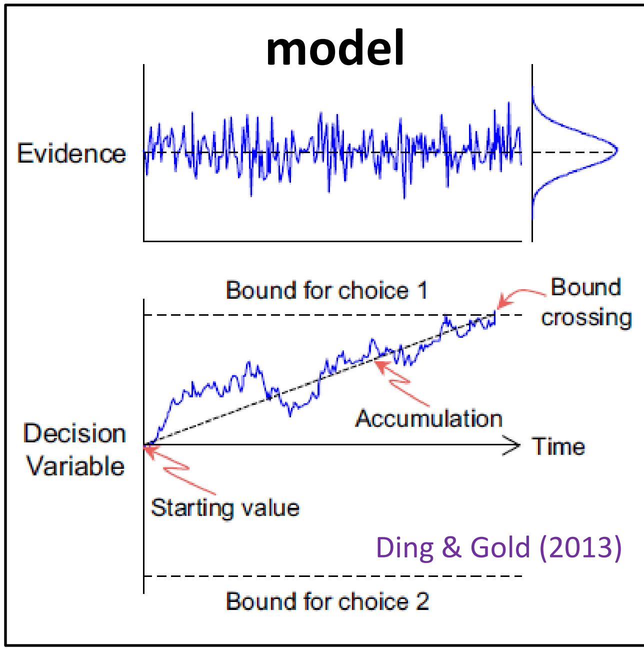
guide model

construction

Decision signals in monkey neurophysiology



Combining models and neural measures



apply

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construction

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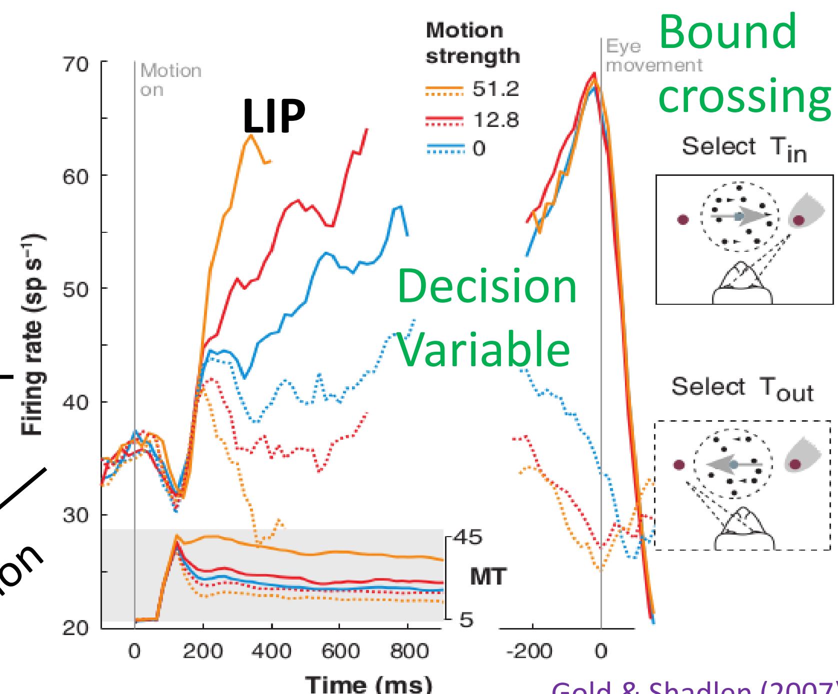
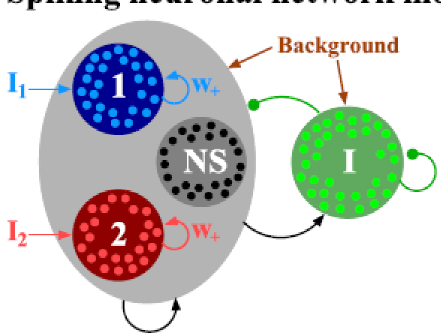
Decision signals in monkey neurophysiology



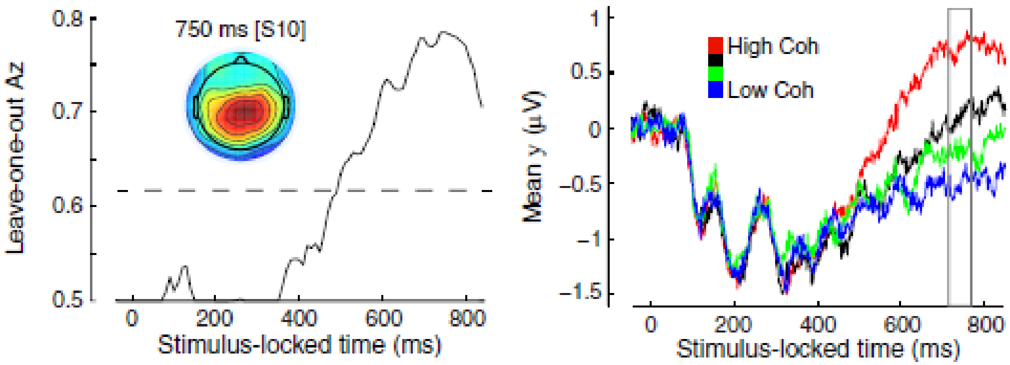
Gold & Shadlen (2007)

Spiking neuronal network model



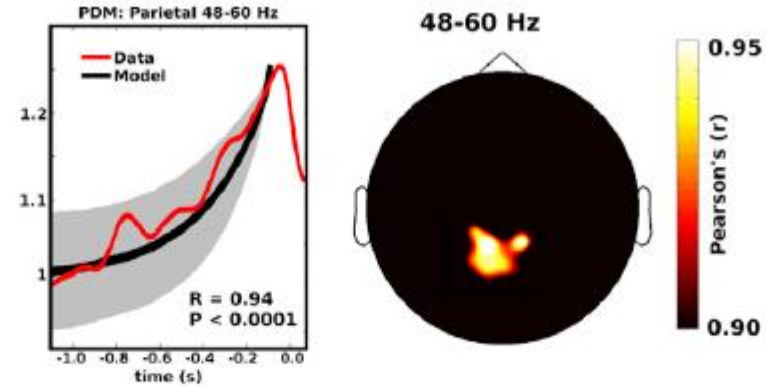
EEG studies of perceptual decision making

High vs low coherence discriminant



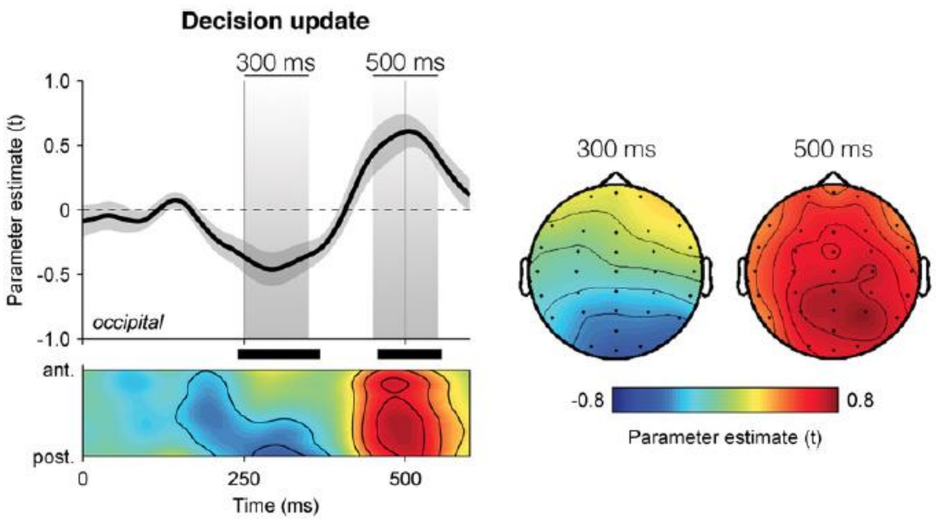
Philiastides et al (2014)

Gamma activity



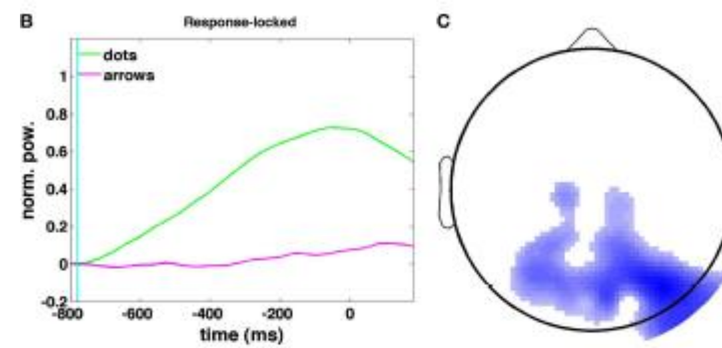
Polania et al (2014)

Regression against physical evidence changes



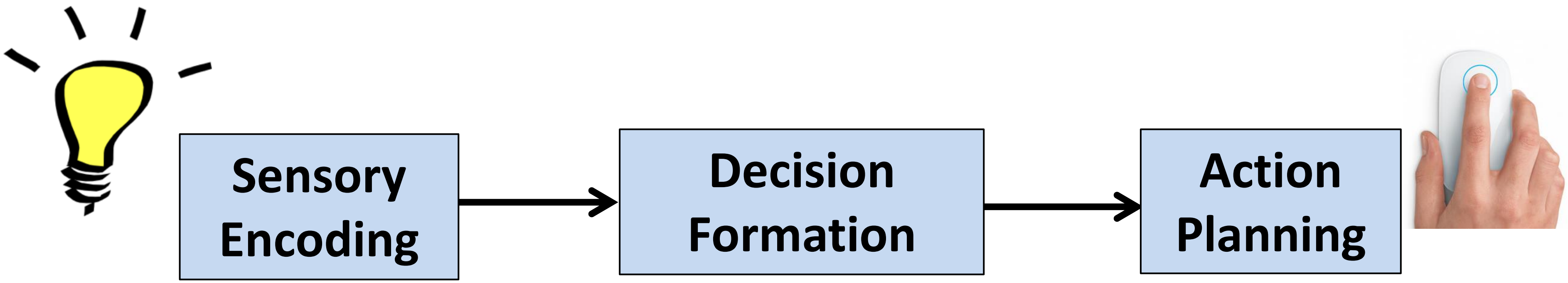
Wyart & Summerfield (2012)

Theta activity



Van Vugt et al (2012)

From Sensation to Action



Paradigm Design Goal:

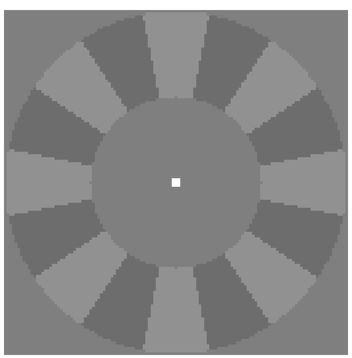
trace **each** information processing stage, in parallel and in isolation

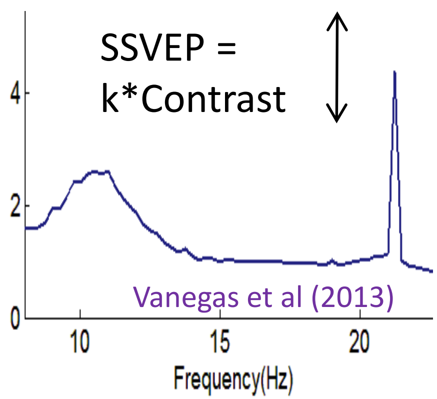
From Sensation to Action

Sensory Encoding → **Decision Formation** → **Action Planning**

Task: Detect gradual change in **contrast**

21 Hz flicker





Gradual change eliminates transient sensory response & signal overlap problem

From Sensation to Action

Sensory Encoding → **Decision Formation** → **Action Planning**

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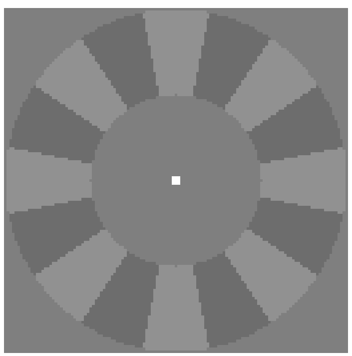
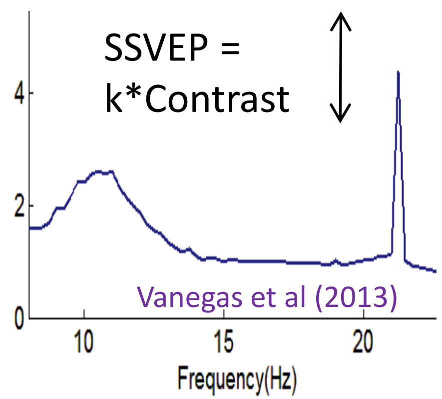
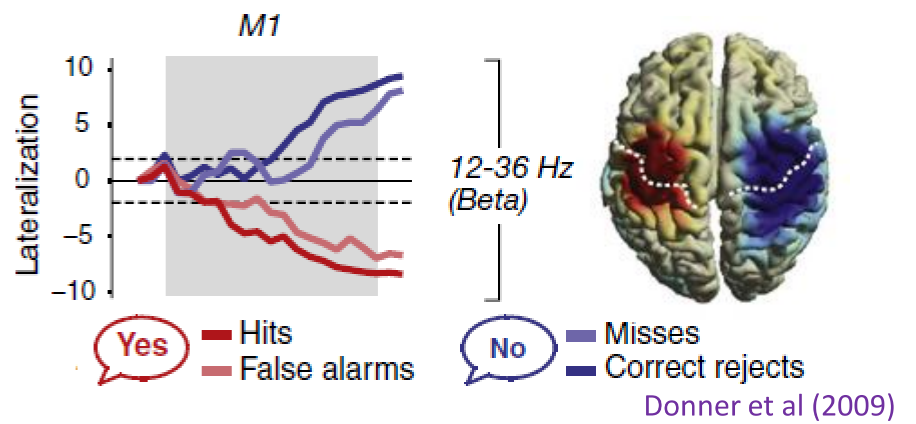
21 Hz flicker





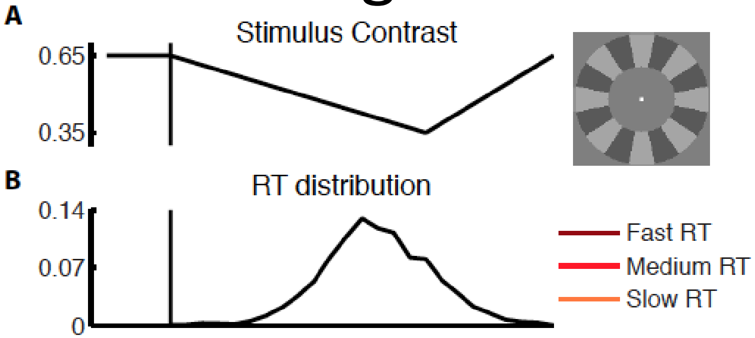
Gradual change eliminates transient sensory response & signal overlap problem

Respond by unilateral button press



Beta activity decreases with contralateral motor preparation

Decision Signals account for Reaction Time

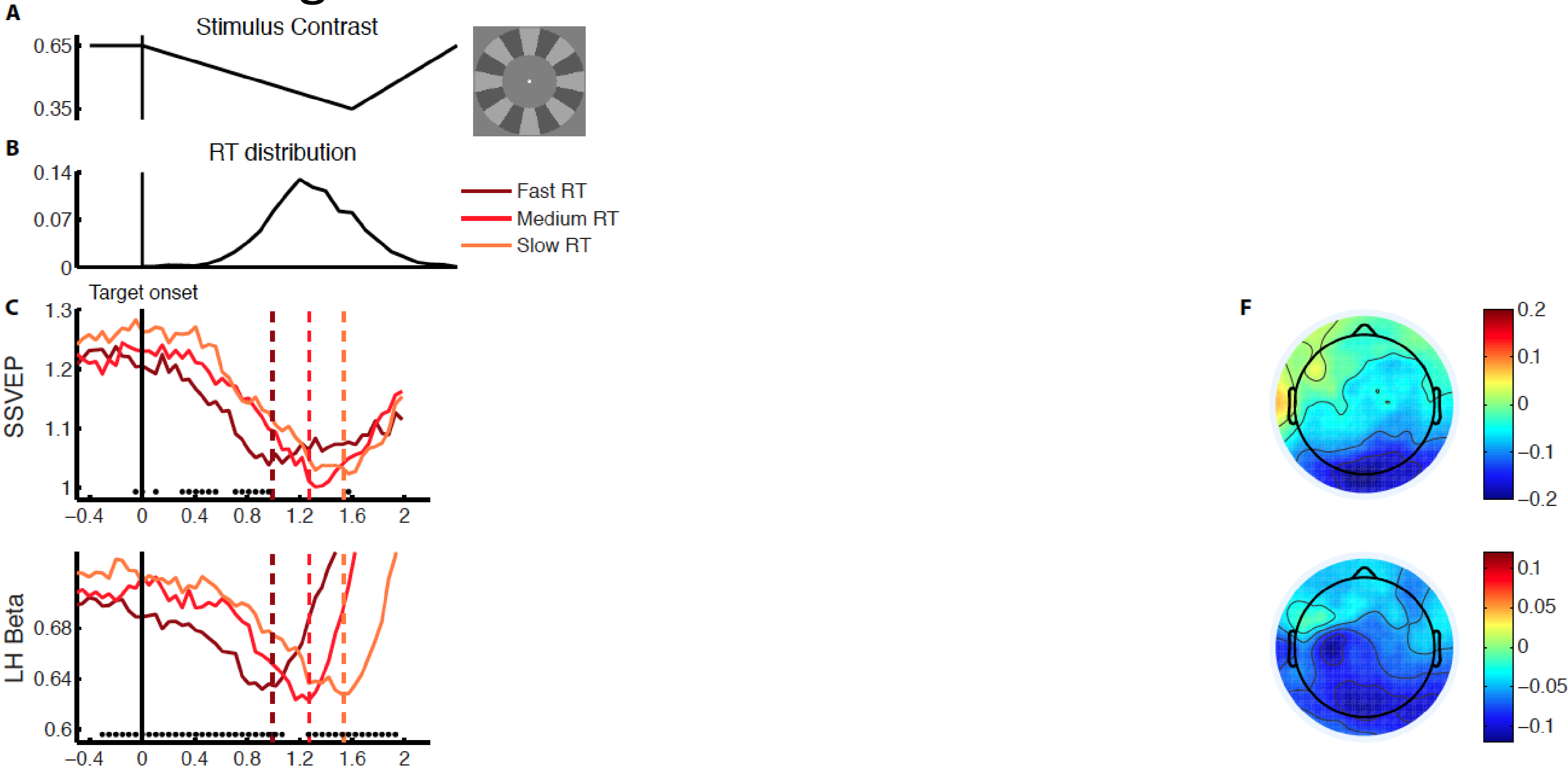


O'Connell, Dockree & Kelly (2012)

Decision Signals account for Reaction Time

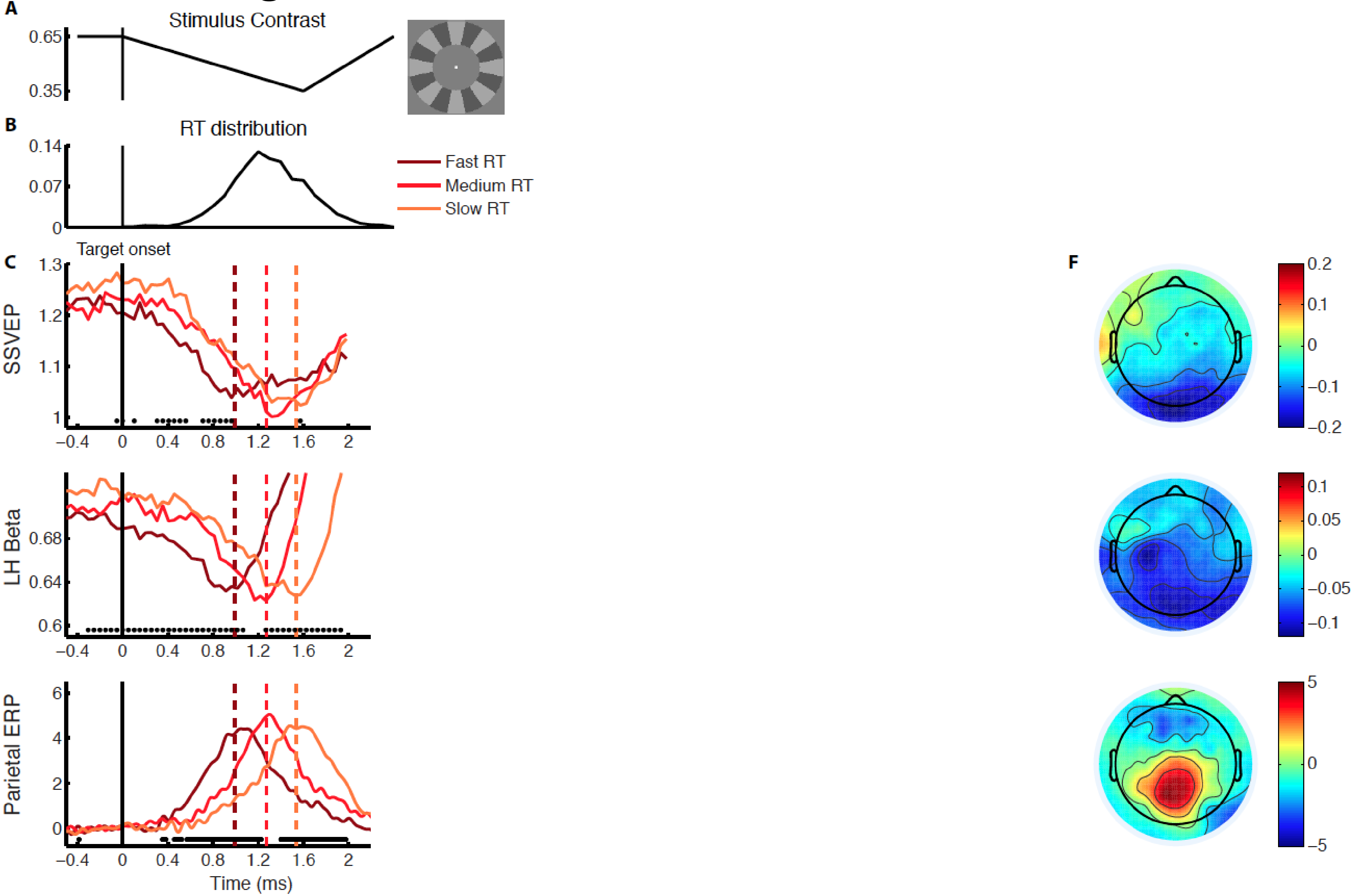
O'Connell, Dockree & Kelly (2012)

Decision Signals account for Reaction Time



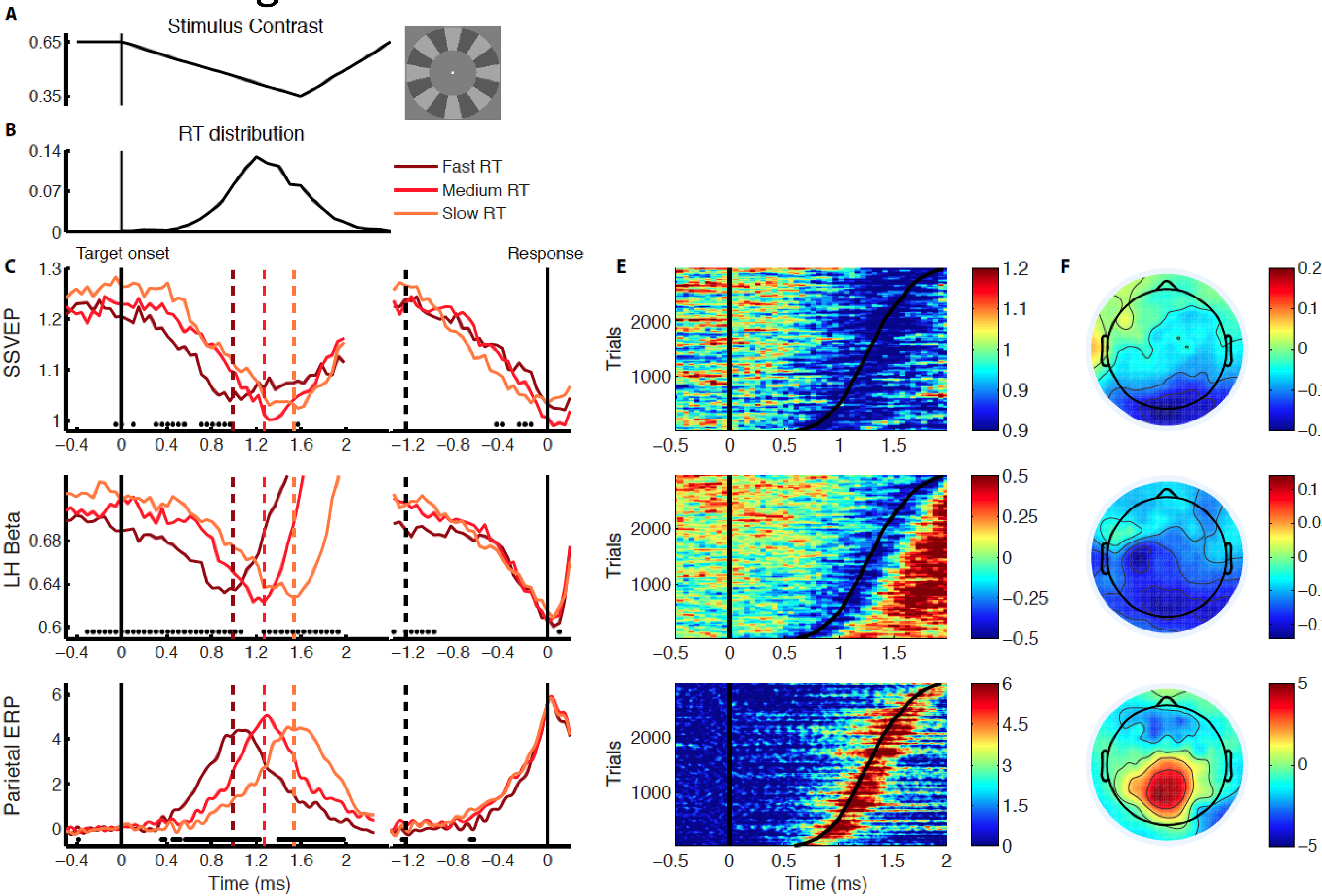
O'Connell, Dockree & Kelly (2012)

Decision Signals account for Reaction Time



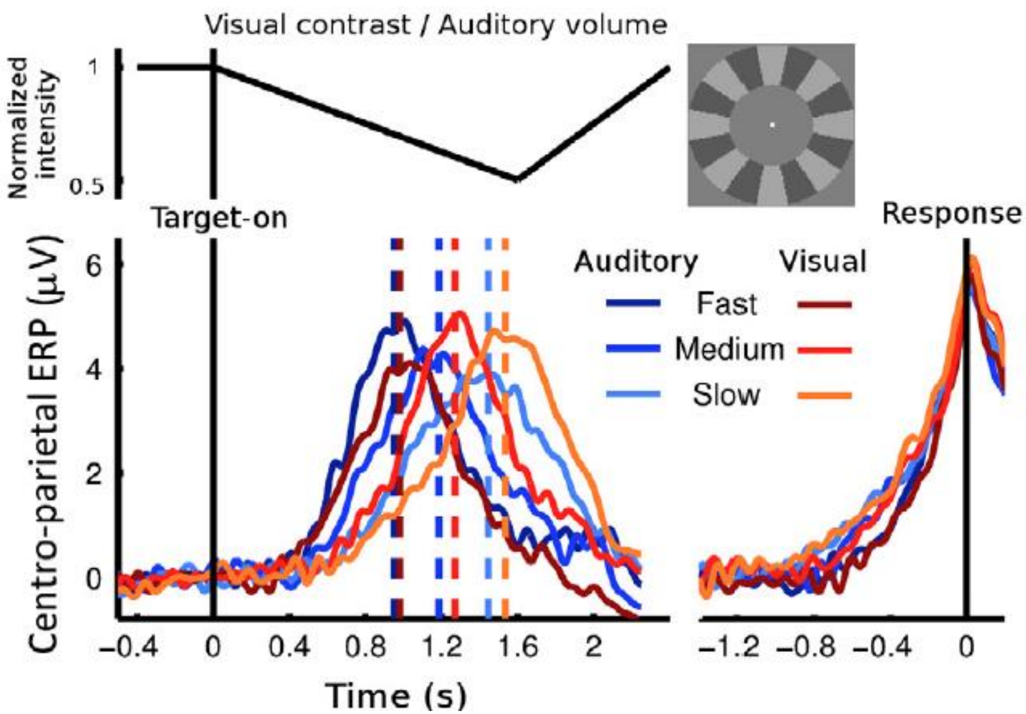
O'Connell, Dockree & Kelly (2012)

Decision Signals account for Reaction Time



O'Connell, Dockree & Kelly (2012)

CPP:
A supramodal, motor-independent, dynamic evidence accumulator



O'Connell, Dockree & Kelly (2012)

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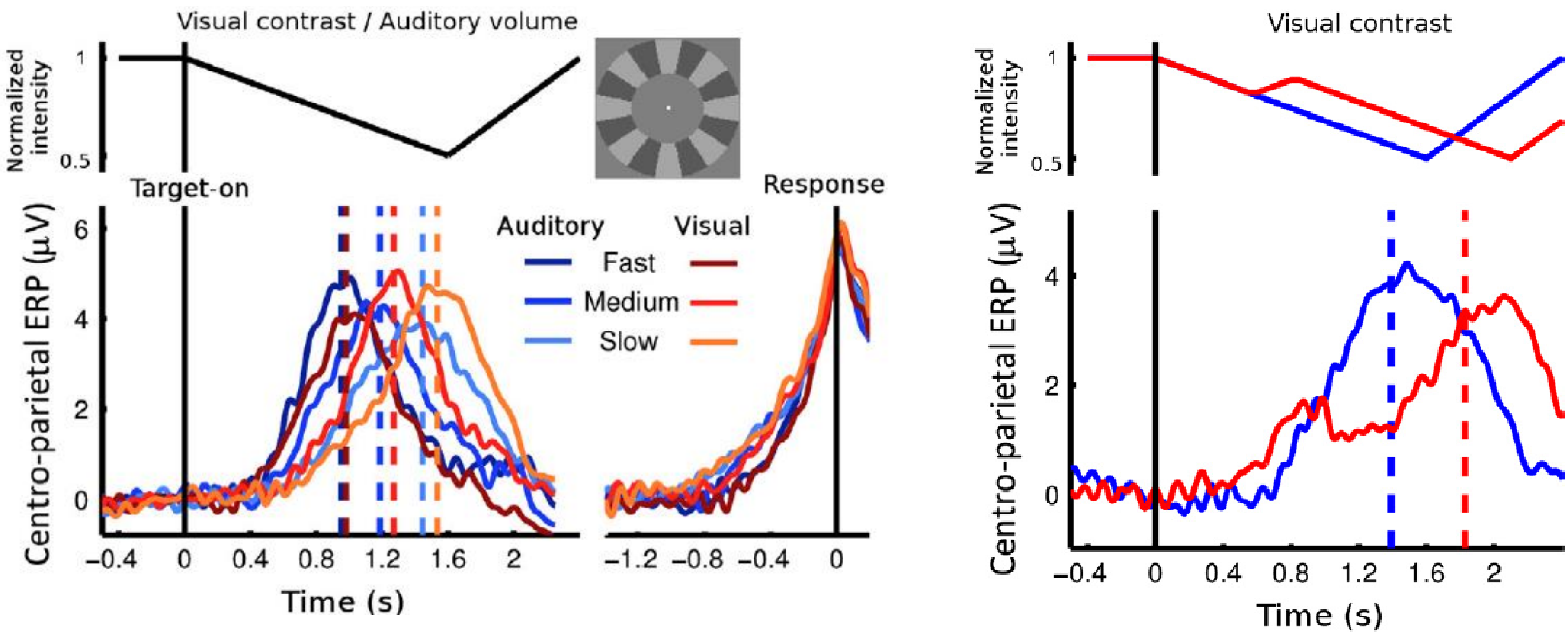
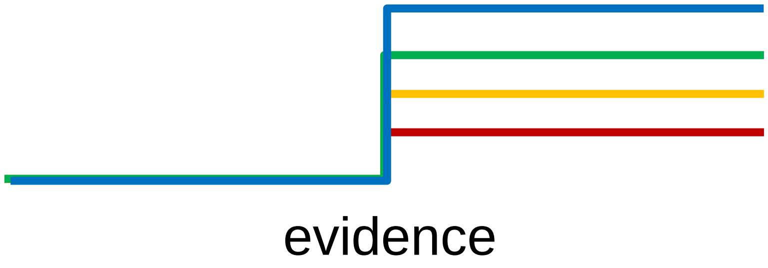
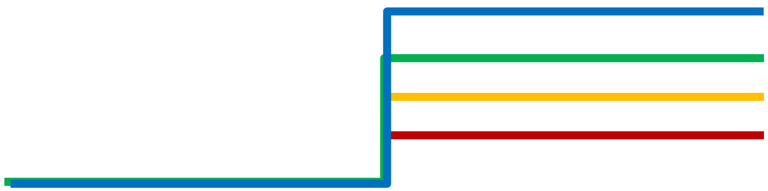


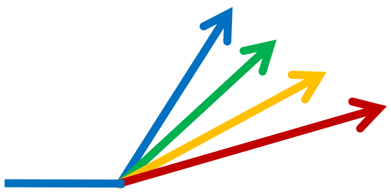
O'Connell, Dockree & Kelly (2012)

Evidence-dependent buildup?

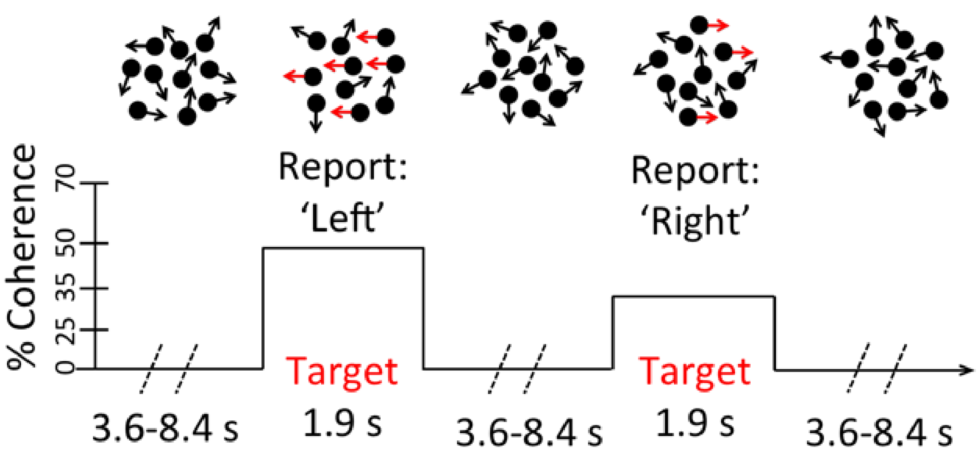


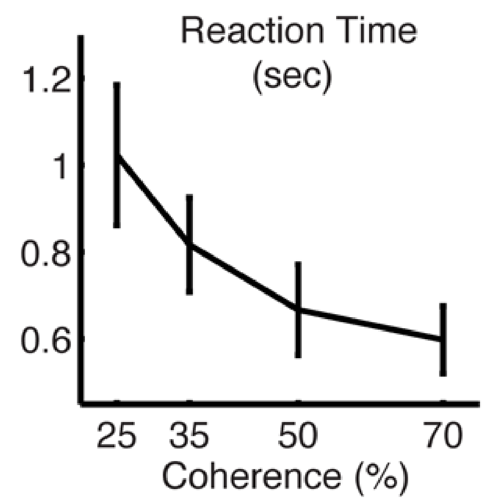
Evidence-dependent buildup?





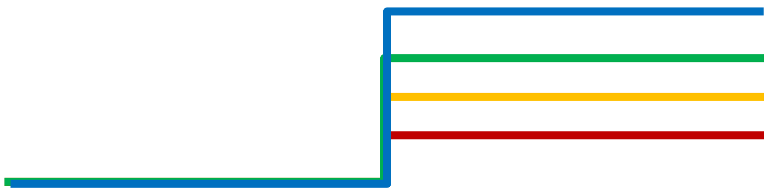
Continuous Dot-Motion Task



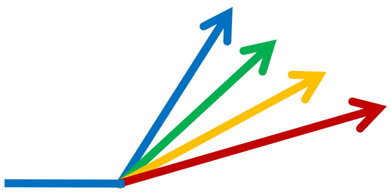


Kelly & O'Connell (2013)

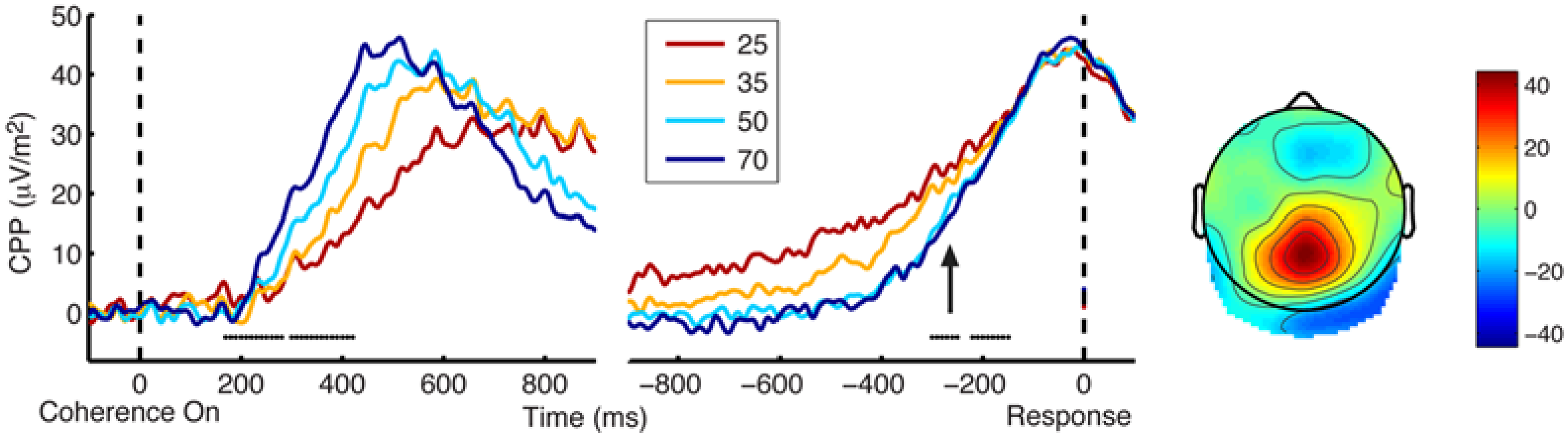
Evidence-dependent buildup?



evidence



Decision Variable

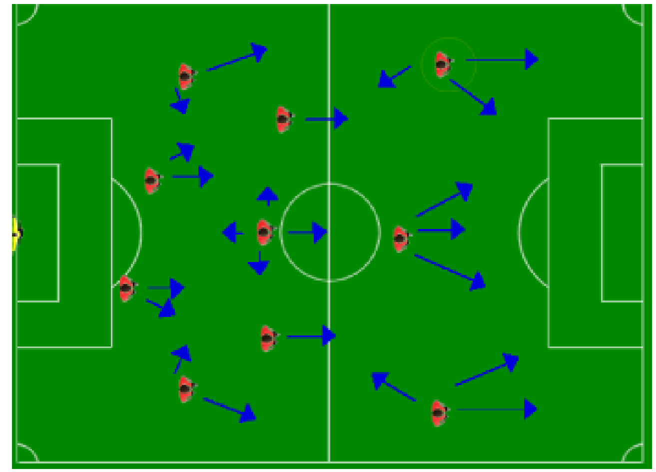


Kelly & O'Connell (2013)

Prior Information in Perceptual Decisions

Time pressure

Perceptual ambiguity



We can expedite decisions when we need to, usually at a cost to accuracy

We can bias our decisions in favour of more probable events

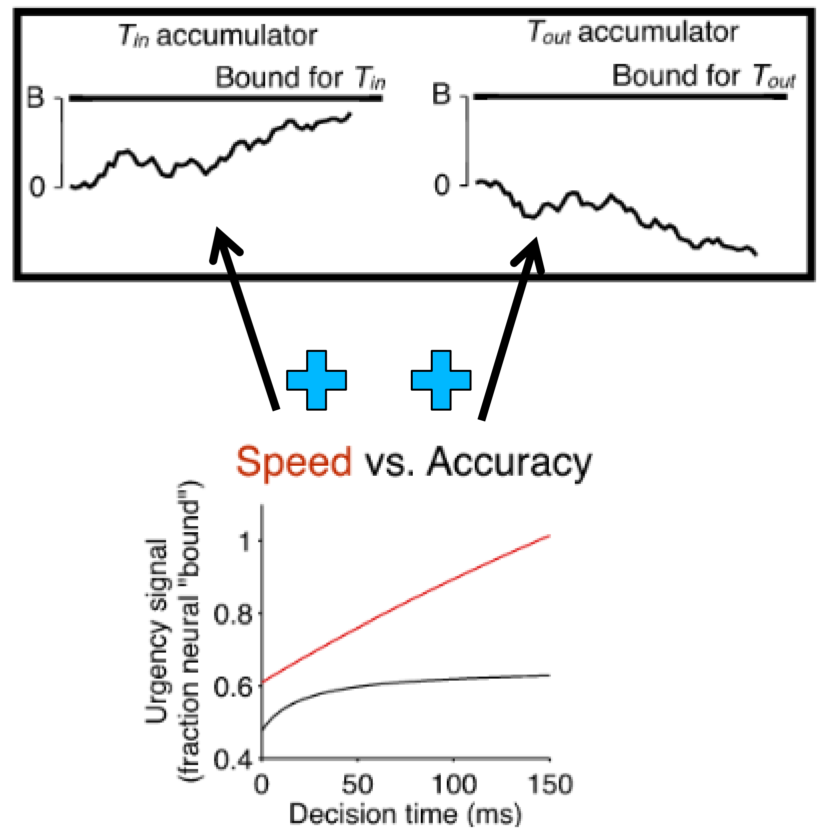
Prior Information in Perceptual Decisions

Standard models: Speed-accuracy tradeoff

Adjustment of constant bound

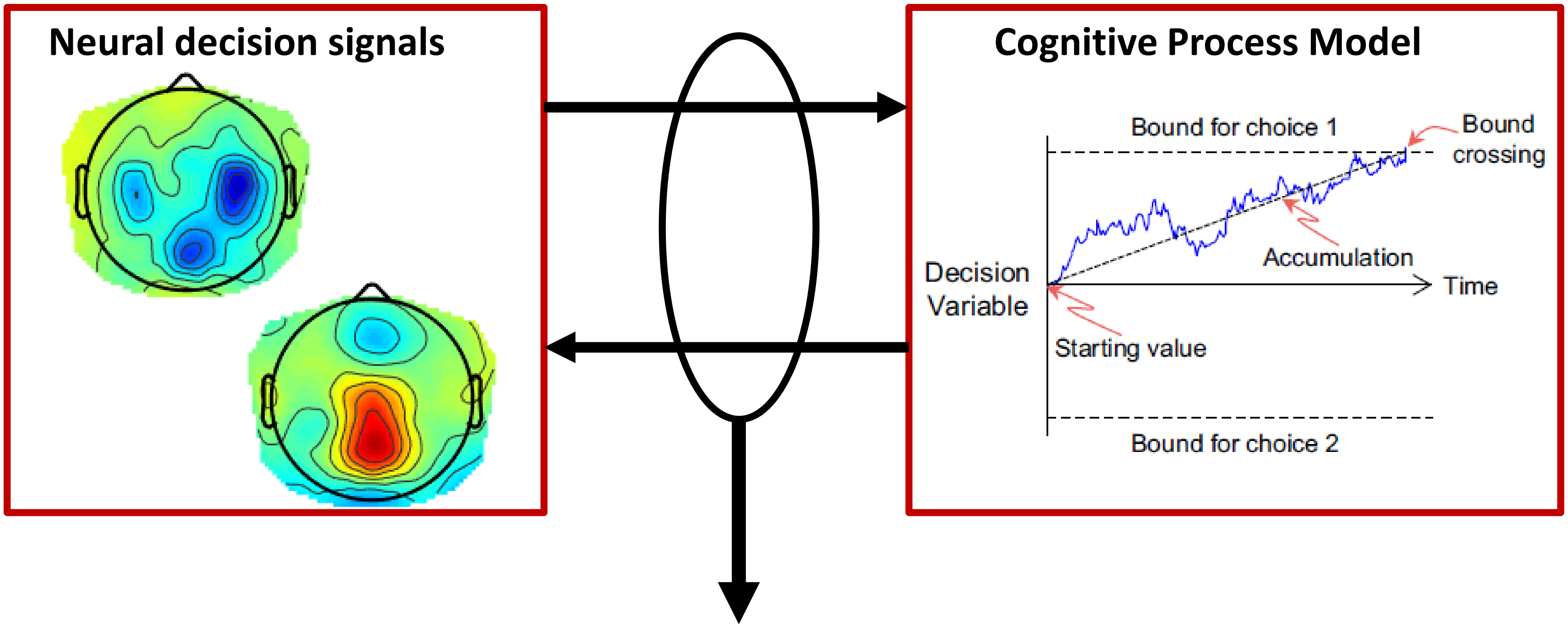
Bogacz et al (2010)

Evidence-independent "Urgency"



Hanks et al (2014)

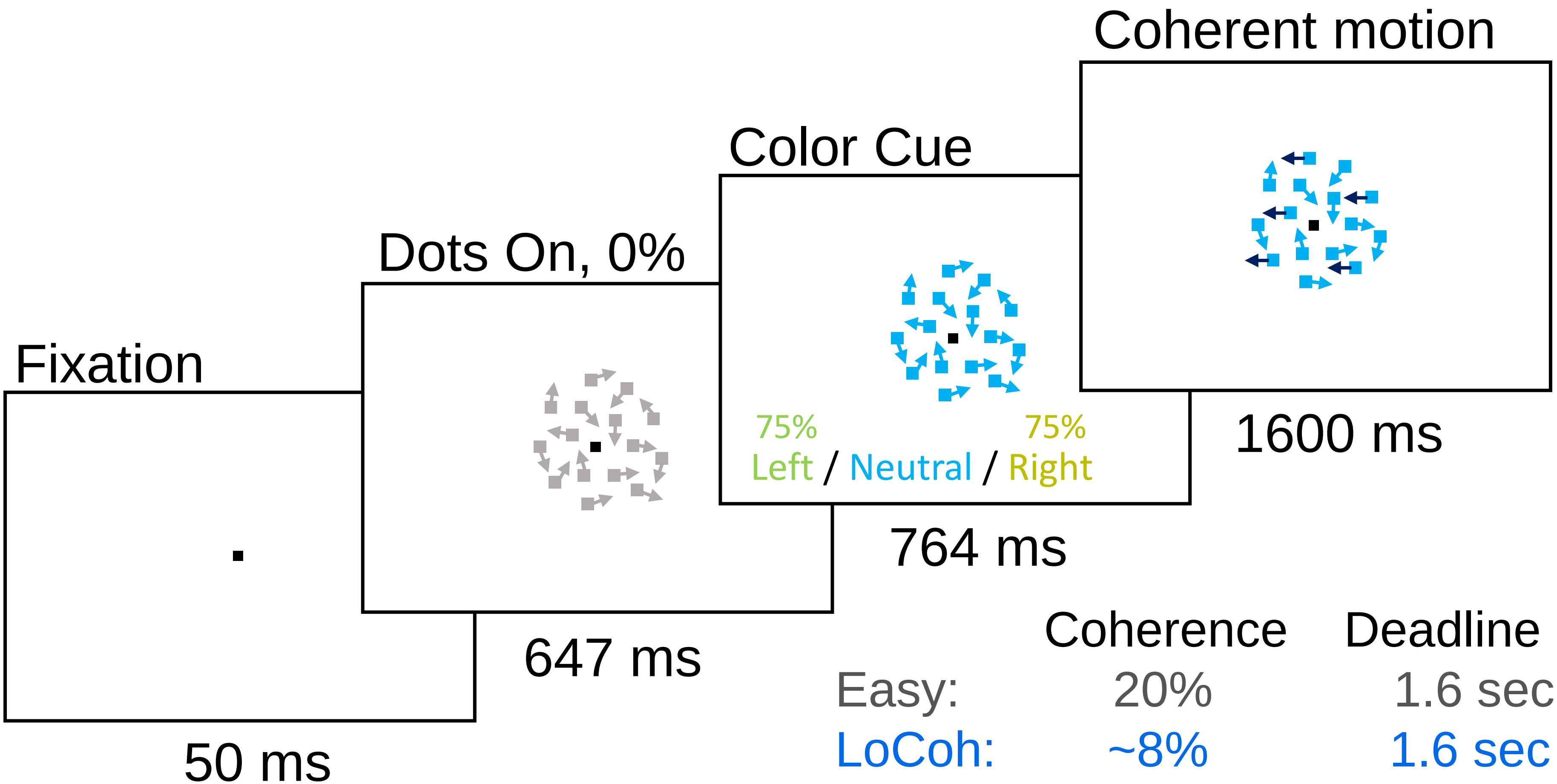
Joint neural-computational approach



Neurally-informed cognitive model

- Convergent evidence for mechanisms and adjustments
- Reflects neural implementation at broad systems level

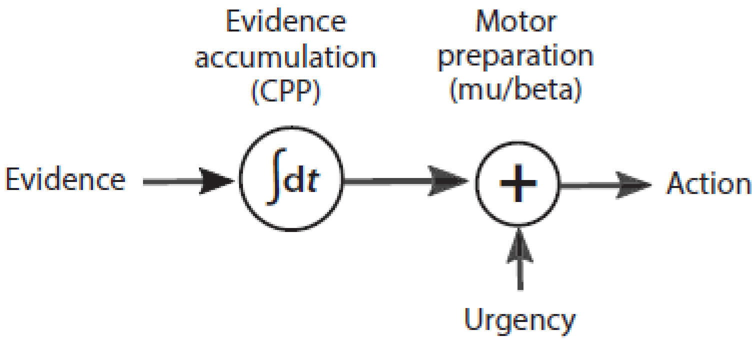
Prior-informed Motion task



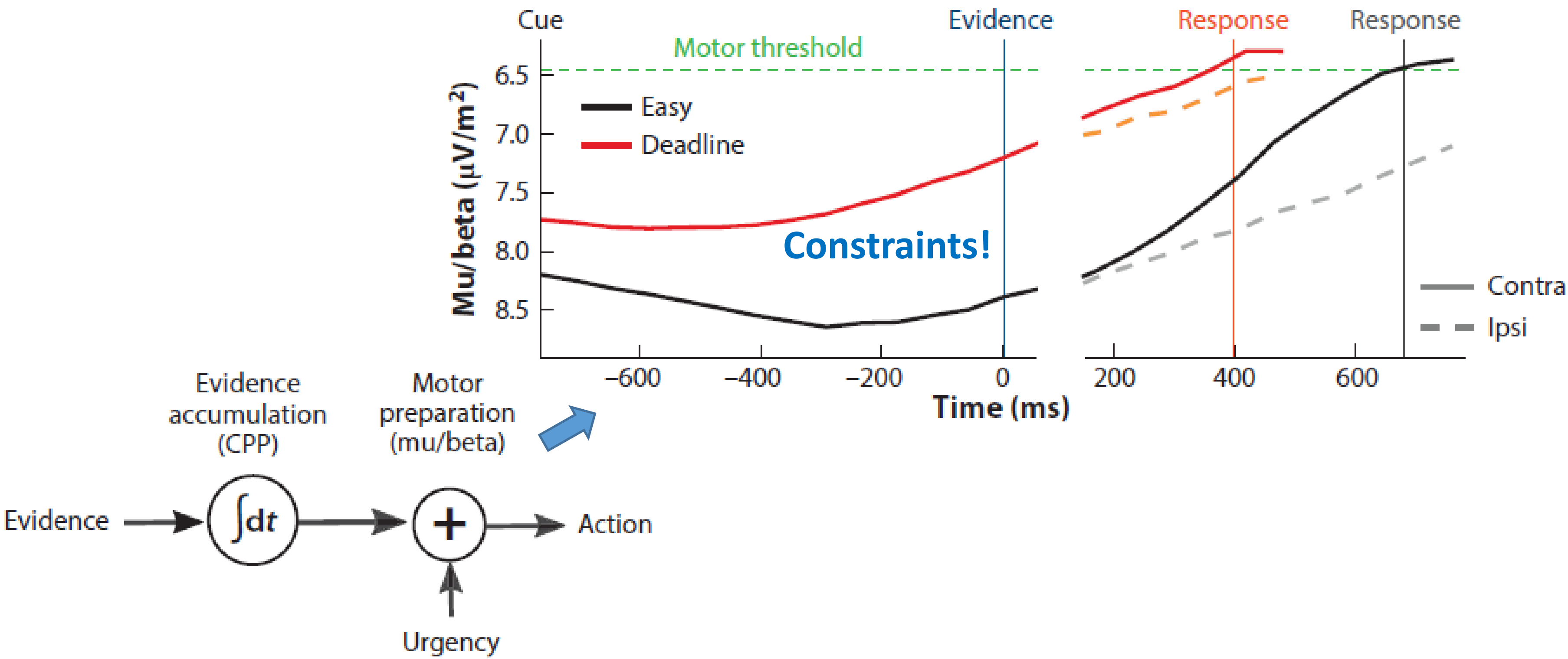
	Coherence	Deadline
Easy:	20%	1.6 sec
LoCoh:	~8%	1.6 sec
Deadline:	20%	~0.5 sec

Manipulated prior information WITHIN blocks
Manipulated temporal/perceptual demands ACROSS blocks
Subjects reported decisions by clicking button with left/right hand

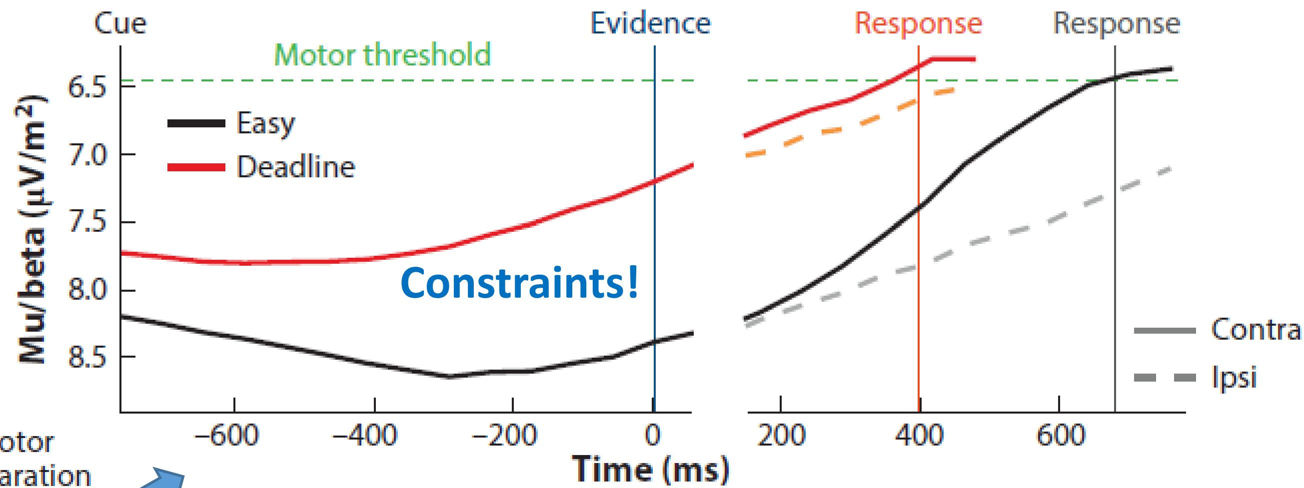
Neurally-informed (NI) model

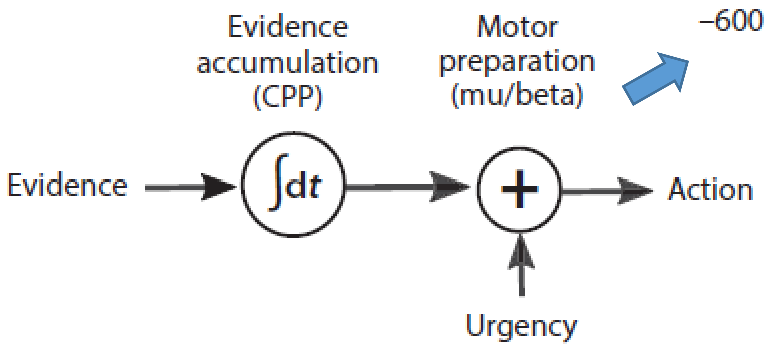


Neurally-informed (NI) model

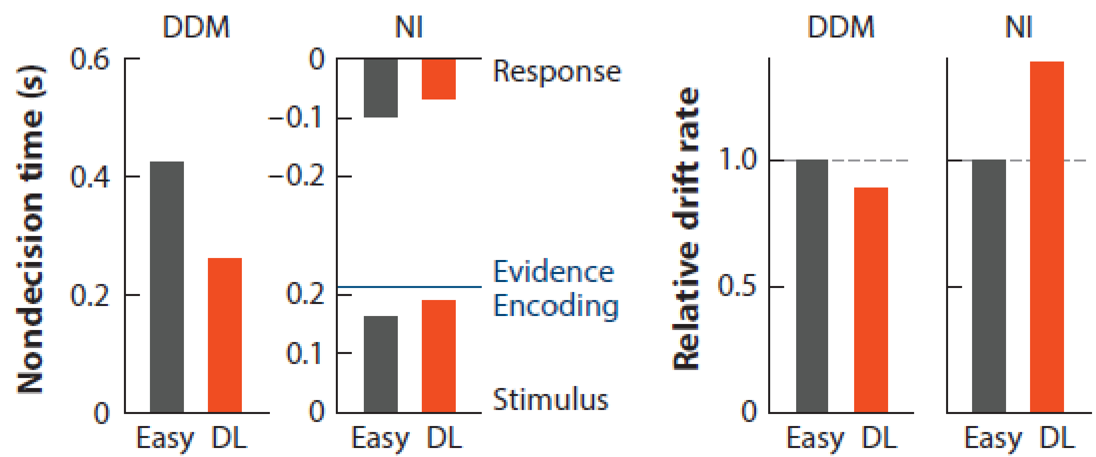


Neurally-informed (NI) model

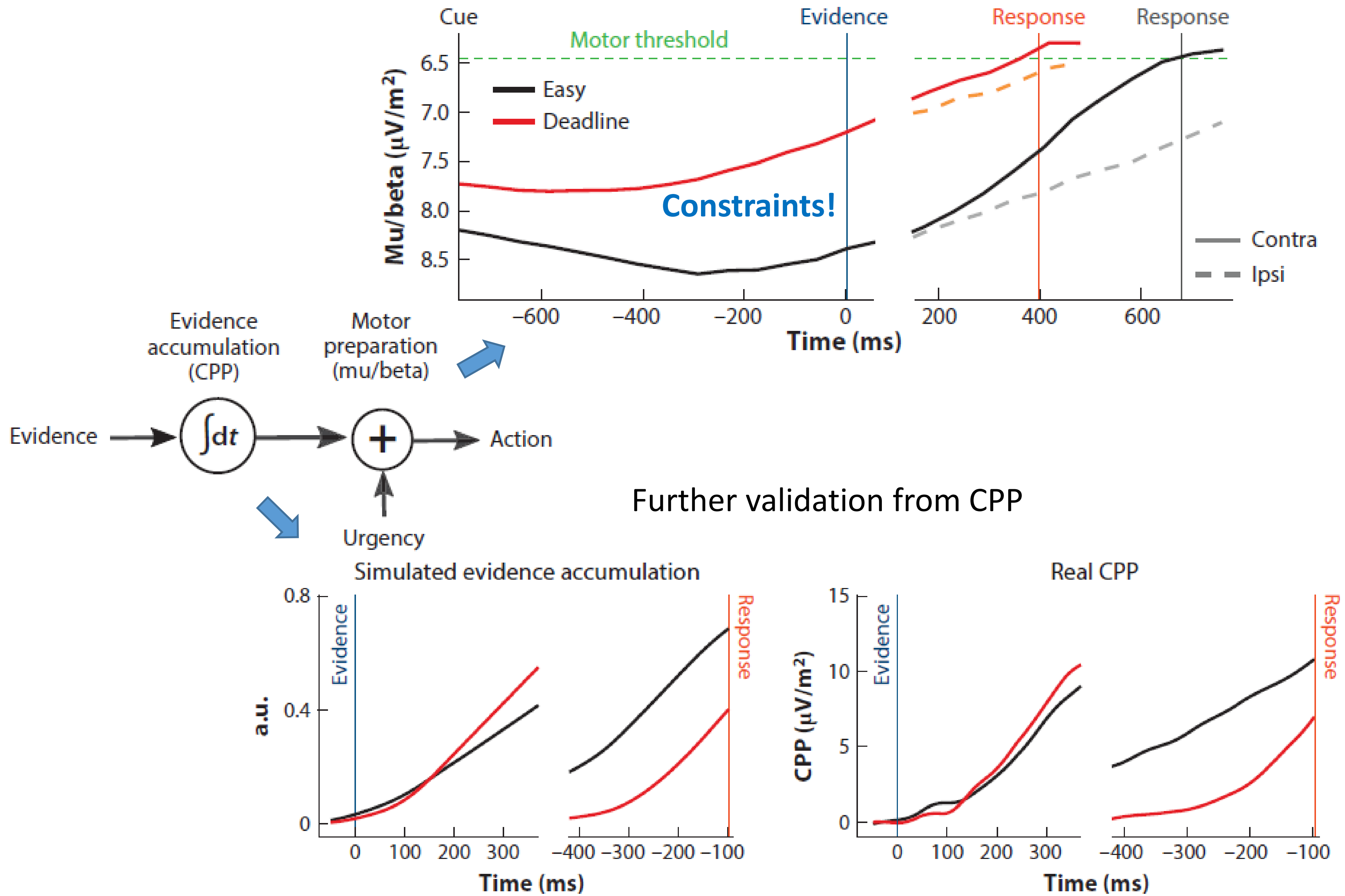




Very different predictions relative to DDM

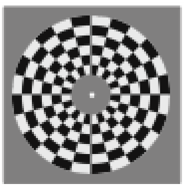


Neurally-informed (NI) model

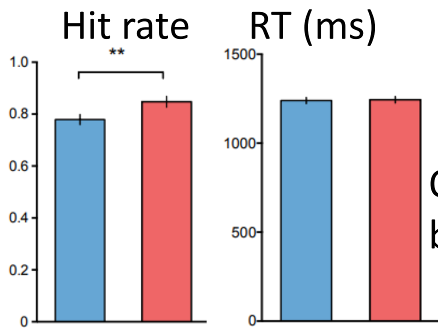


Applications to studies with clinical relevance

Reconciling age-related changes in behavioural and neural indices of human perceptual decision making

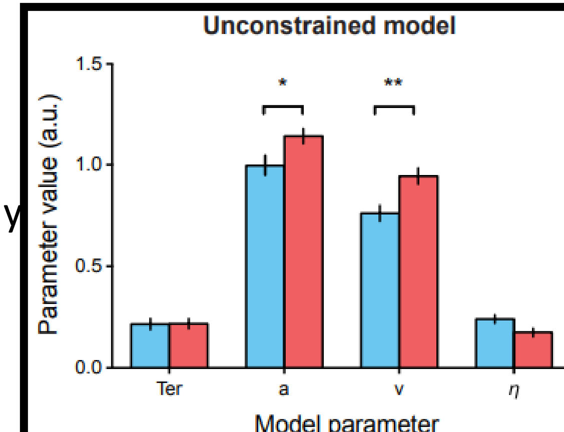


Contrast change detection



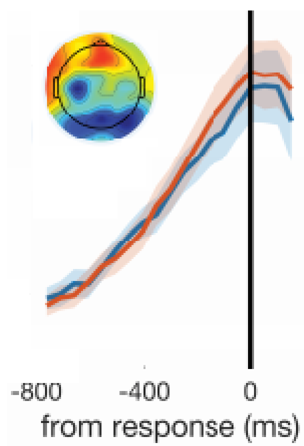
Young
Old

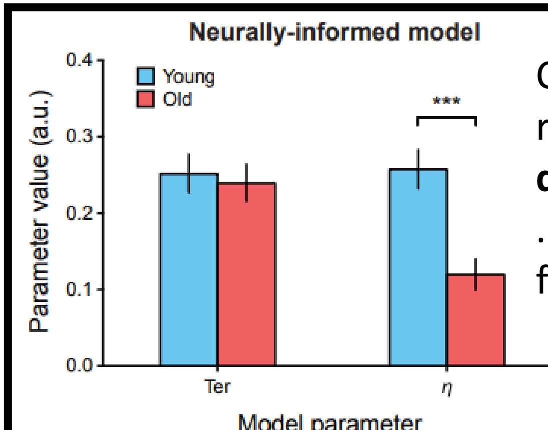
Older slightly better



Standard DDM says older people have **higher bound** and **higher drift rate**

But neural decision signals indicate there is no difference in either bound or drift rate!





Constrained model reveals difference in **drift rate variability** … and Alpha-band fluctuations concur!

McGovern et al, *Nature Human Behaviour* (2018)

Overview

- Intro to **Psychophysics**
- Signal detection theory
- Applying SDT to understand the neural basis of perceptual **detection**
- Perceptual **discrimination** and its sensory neural correlates
- Perceptual **decision making**: neurally-informed modelling
- **Attention**: Perceptual and neural effects
- Behavioural paradigms for other cognitive functions, e.g. memory and learning

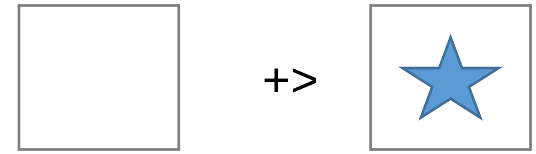
Attention

- Improvement of perceptual processing and action selection by prioritising based on prior knowledge or salience, or by being more alert

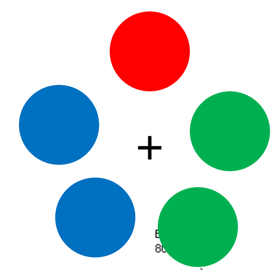
Attention Paradigms

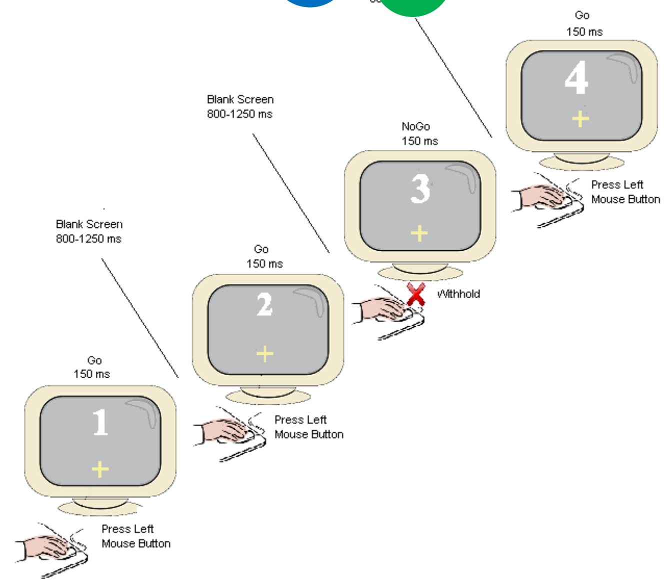
- **Selective attention** – preferential processing of certain sensory information deemed to be relevant or important. The info is “relevant” either because it’s associated with your current goals (**Endogenous** attention) or because it’s physically salient, e.g., loud or bright, or sudden (**exogenous** attention). Selection can be:
    - **SPATIAL**
    - **FEATURE-BASED**
- **Vigilant attention** - the ability to maintain a mindful goal-directed focus in contexts whose repetitive, nonarousing qualities provide little external stimulation.

Spatial cueing



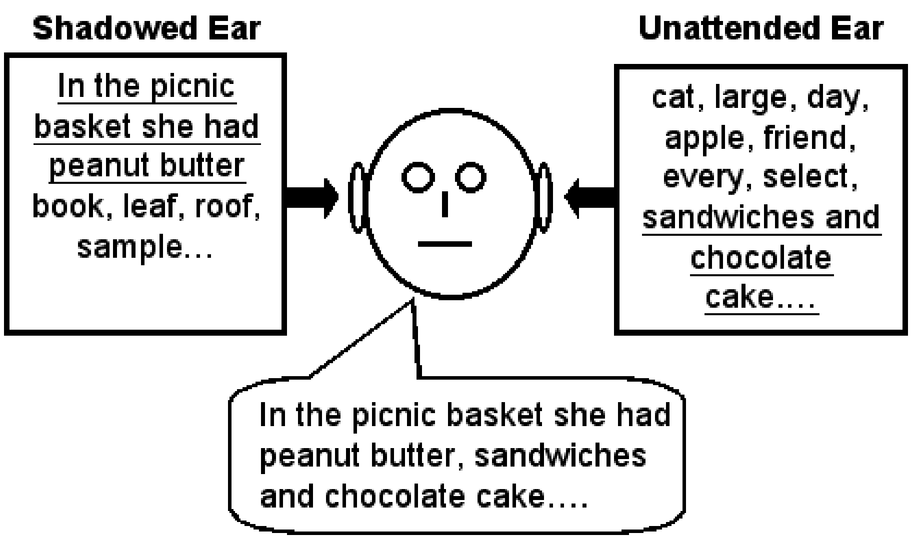
Visual search





The Locus of Selection – early or late?

e.g. Treisman (1960):



Cocktail Party

- Unattended information can be hugely attenuated but not gated out completely.
- So are the sensory representations themselves modulated?

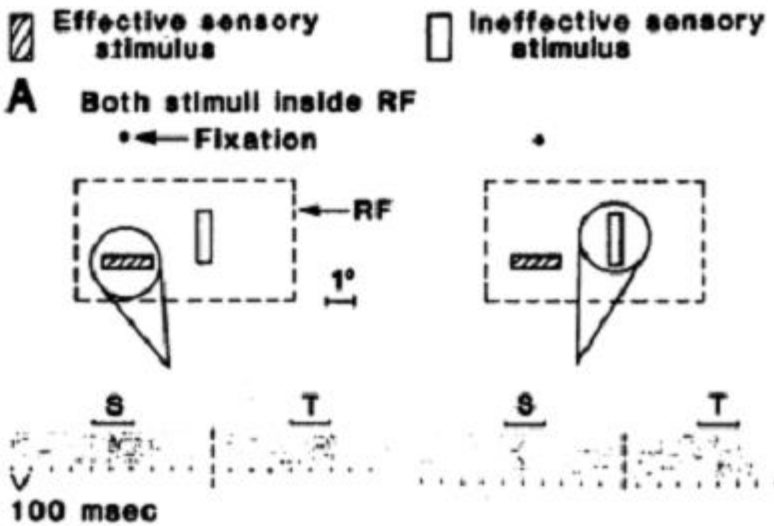
Attentional Modulation of Sensory Neural Responses

Intracranial single-unit

Selective Attention Gates Visual Processing in the Extrastriate Cortex

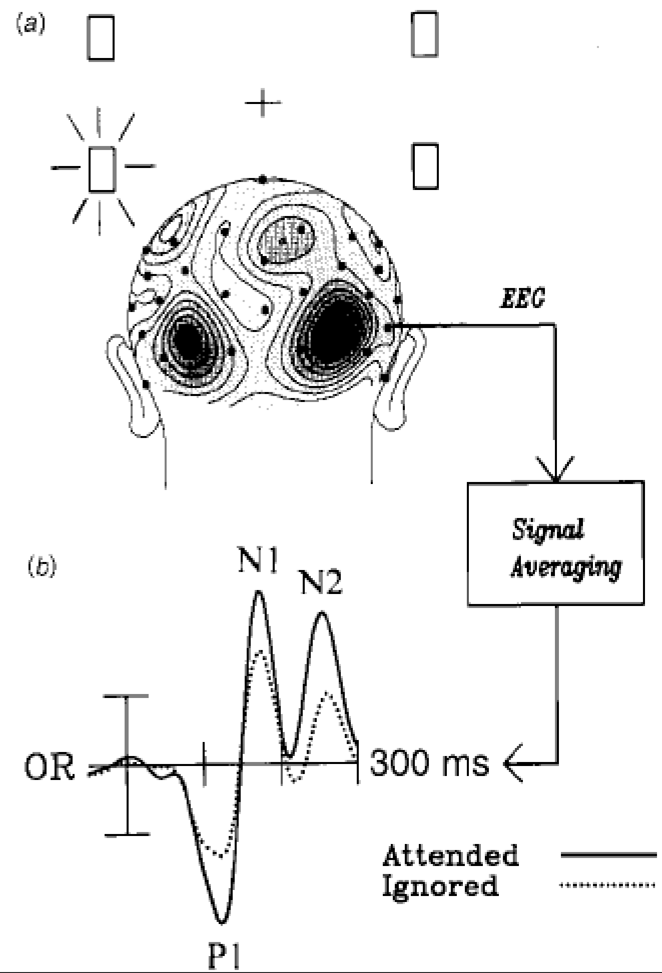
JEFFREY MORAN
ROBERT DESIMONE

(1985)



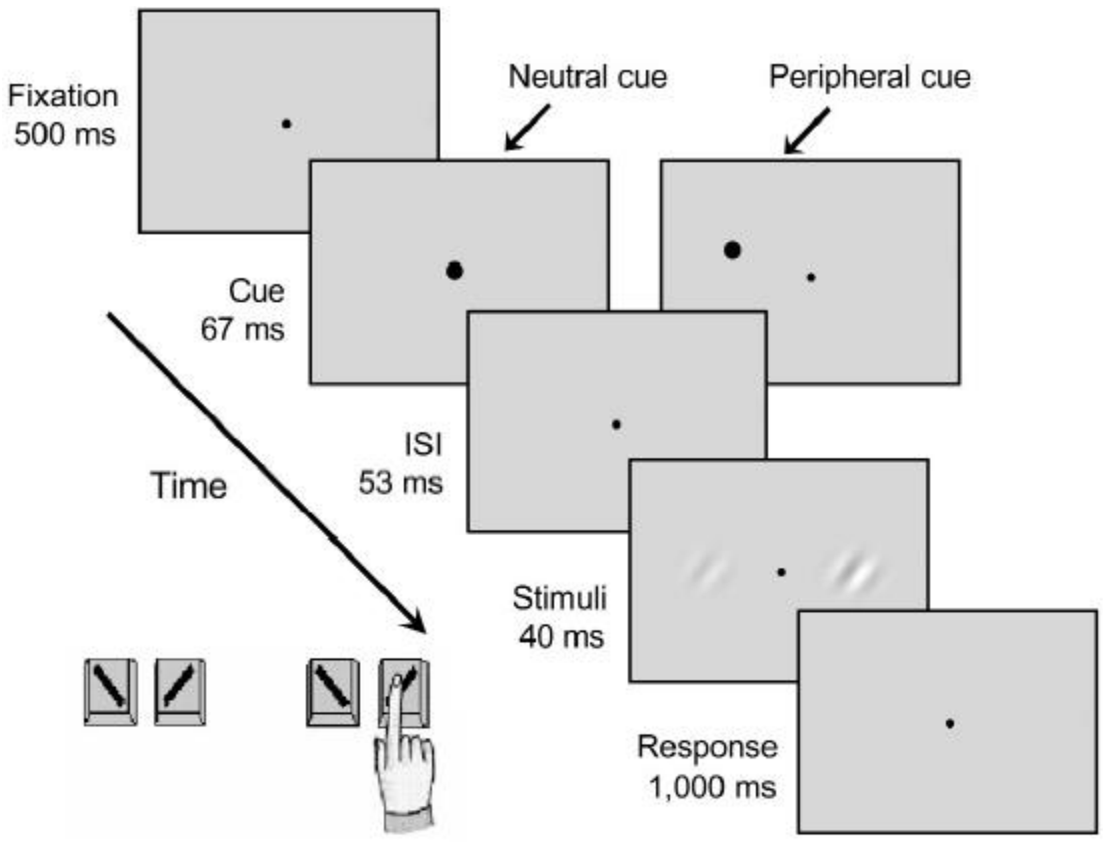
Scalp event-related potential (ERP)

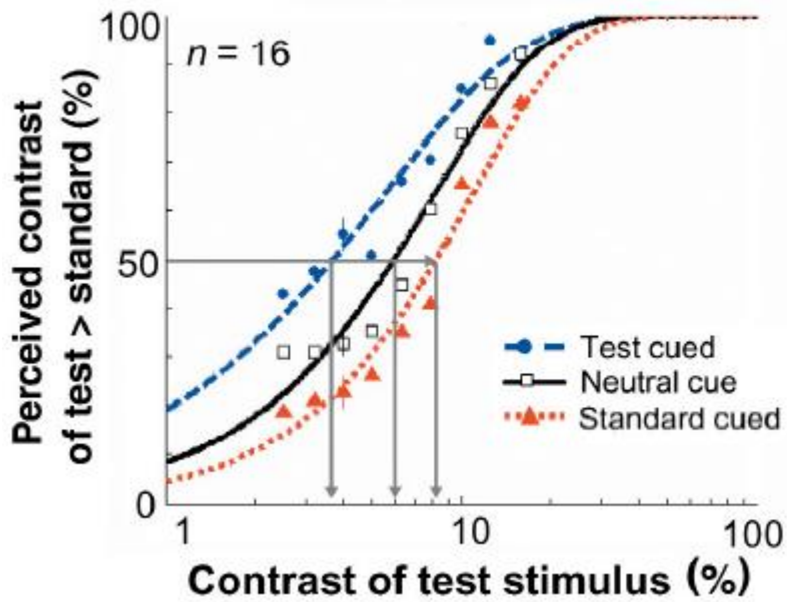
Mangun et al (1993)



Attention alters appearance

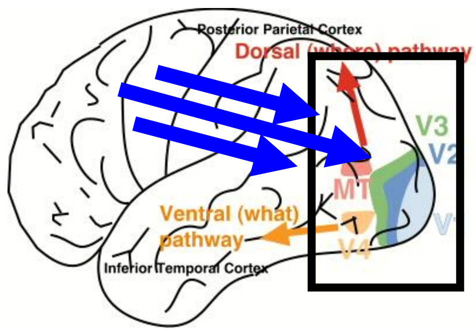
- Exogenous ("attention-grabbing") spatial attention cues caused a shift in perceptual choices consistent with seeing the cued grating as more intense





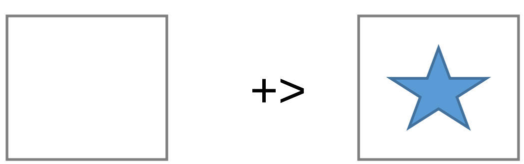
Carrasco et al (2004)

How does top-down attention operate on sensory areas?

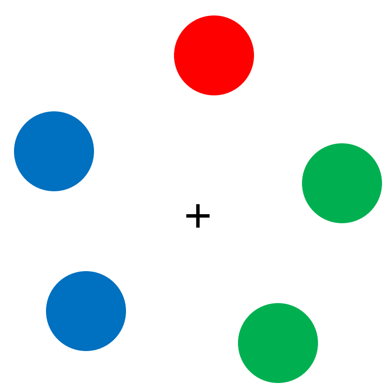


It depends on the task…

Spatial cueing



Visual search

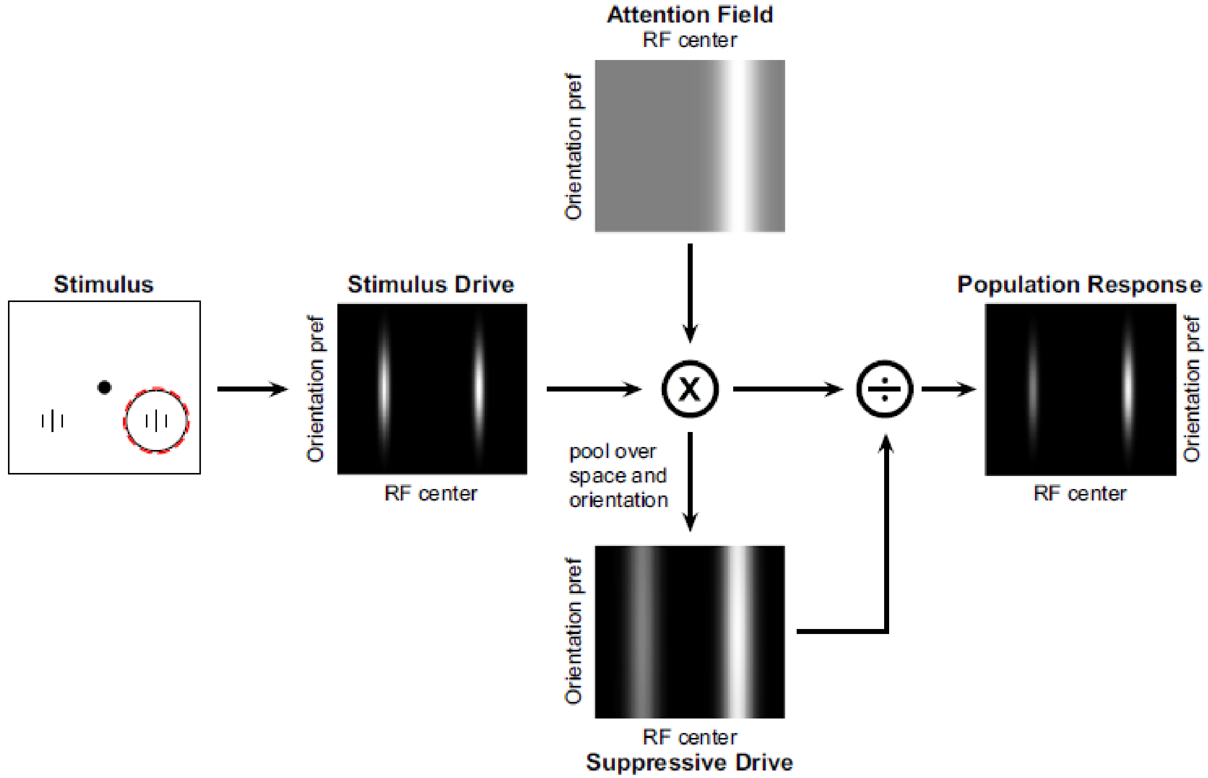


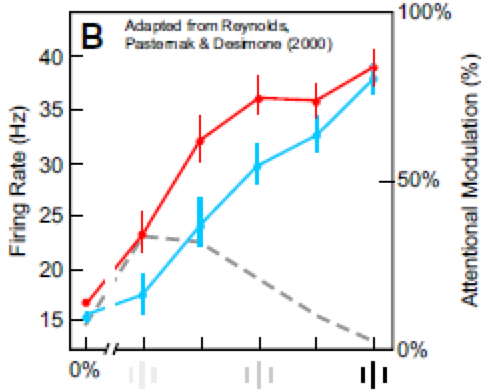
Computational models to the rescue

Example: Contrast Gain Vs Response Gain?

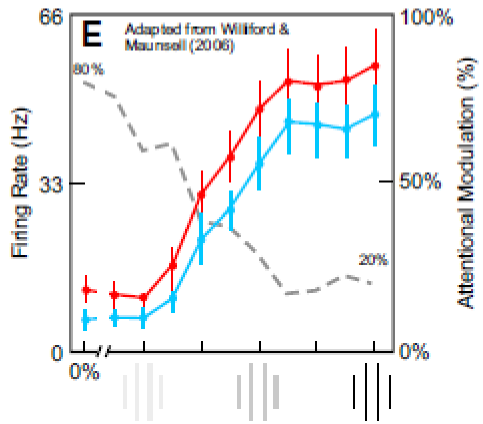
The Normalization Model

Reynolds & Heeger (2009)





Reynolds et al (2000)



Williford & Maunsell (2006)

Computational models to the rescue
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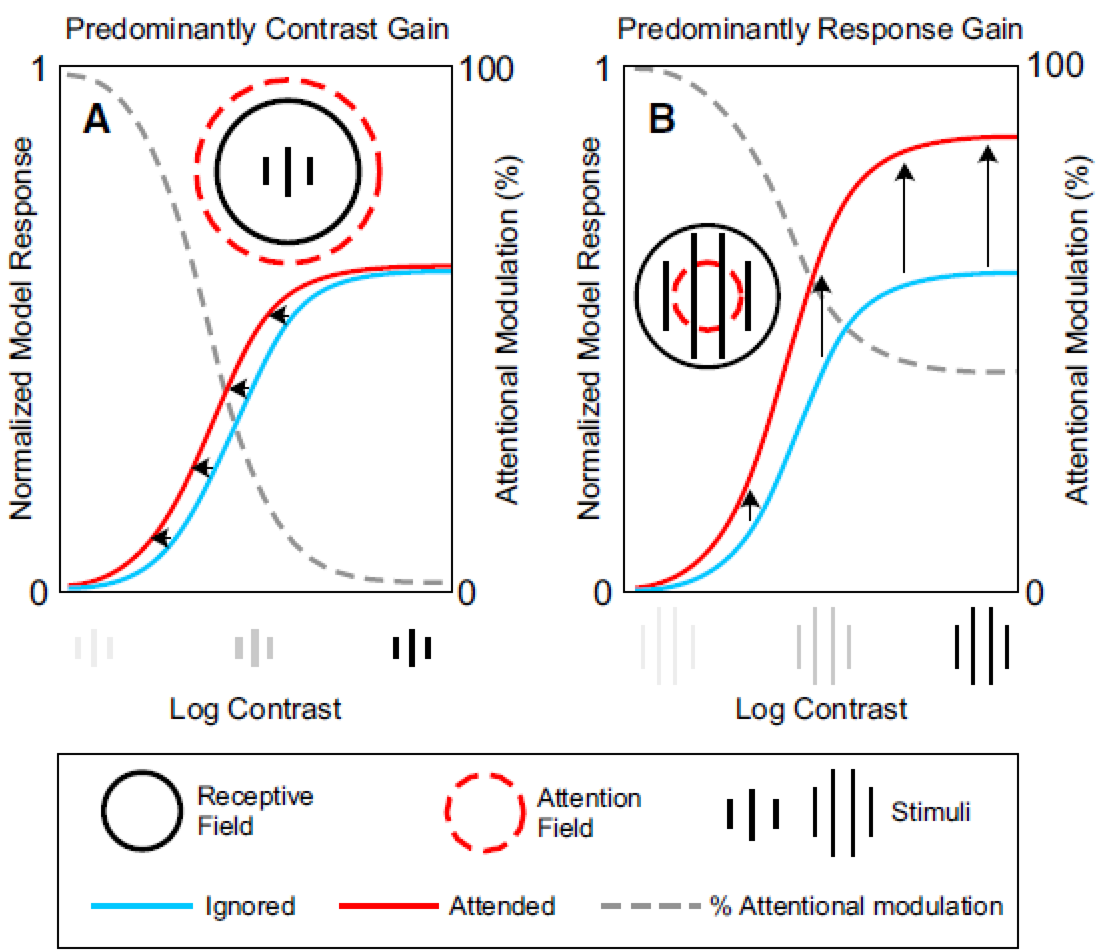
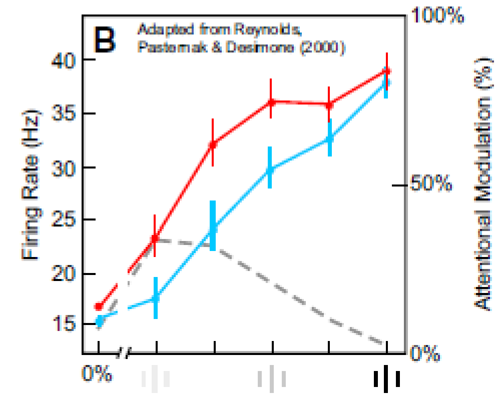
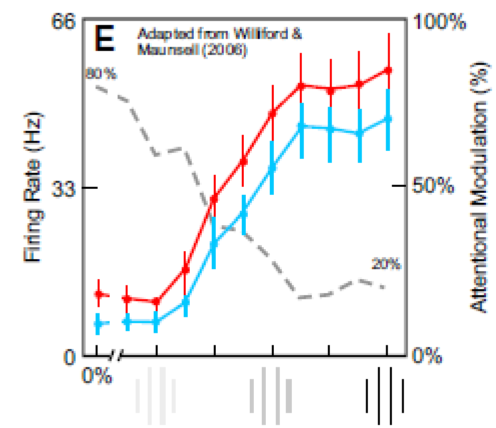


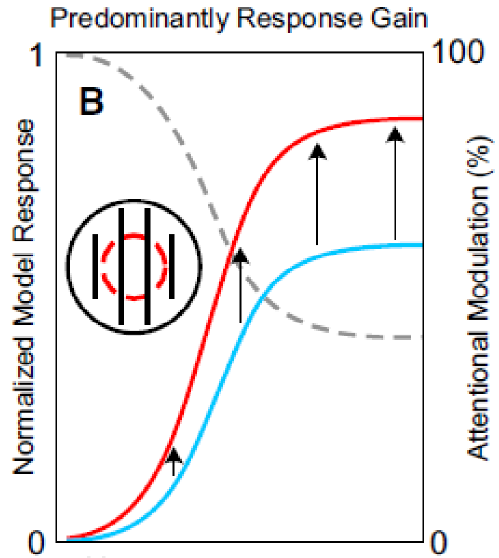


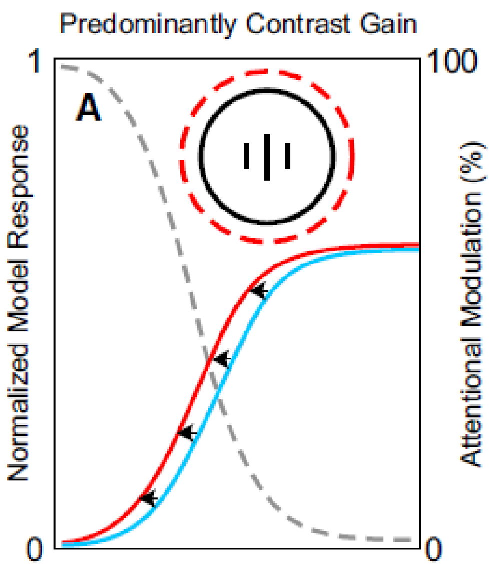
Reynolds et al (2000)



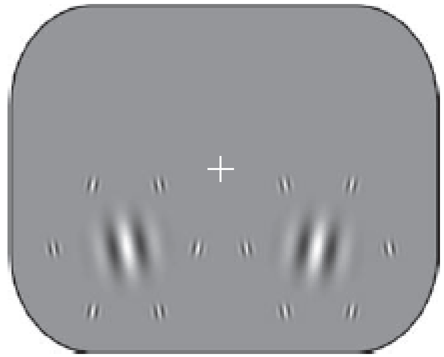
Williford & Maunsell (2006)

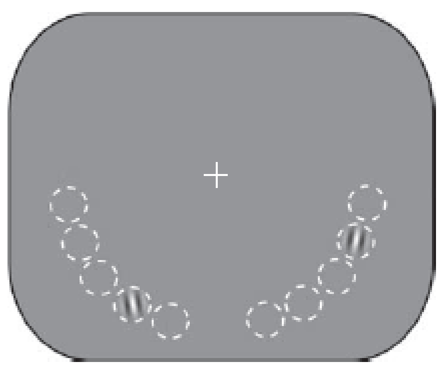
Computational models to the rescue
Example: Contrast Gain Vs Response Gain?

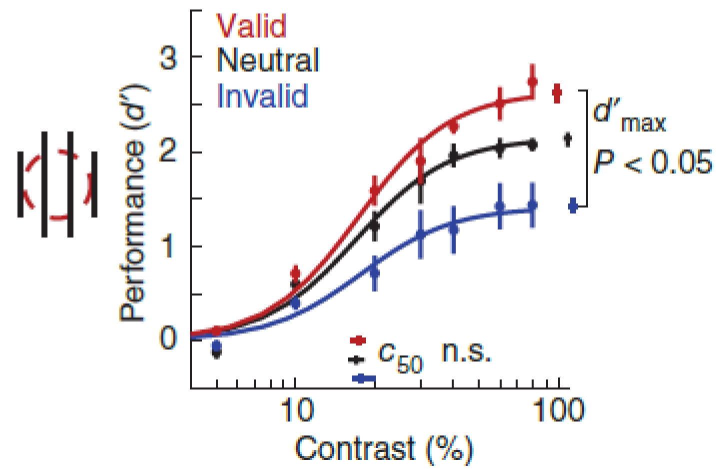


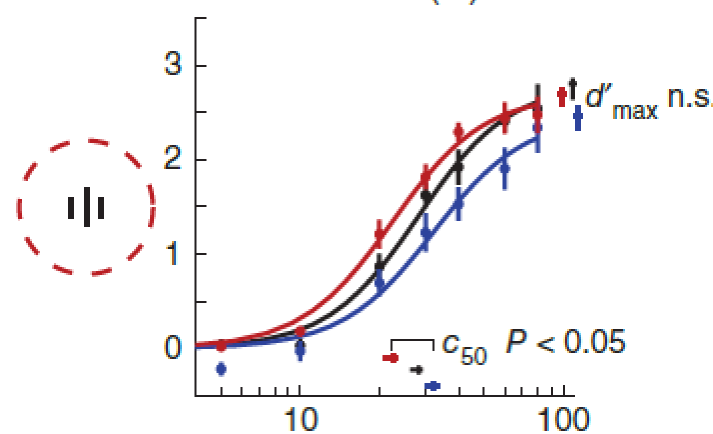


Testing through psychophysics









Herrmann et al (2010)

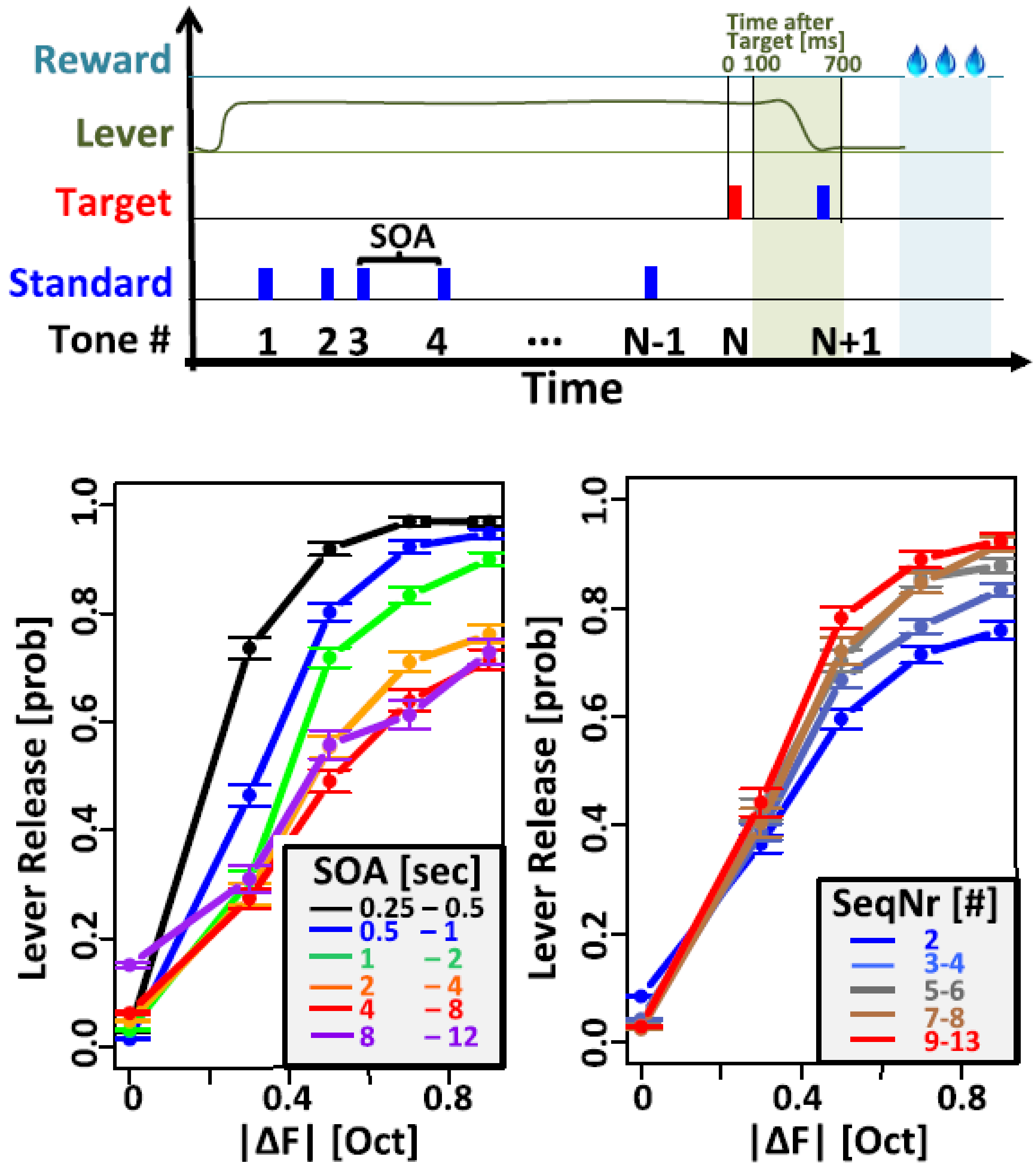
Overview

- Intro to **Psychophysics**
- Signal detection theory
- Applying SDT to understand the neural basis of perceptual **detection**
- Perceptual **discrimination** and its sensory neural correlates
- Perceptual **decision making**: neurally-informed modelling
- **Attention**: Perceptual and neural effects
- Behavioural paradigms for other cognitive functions, e.g. memory and learning

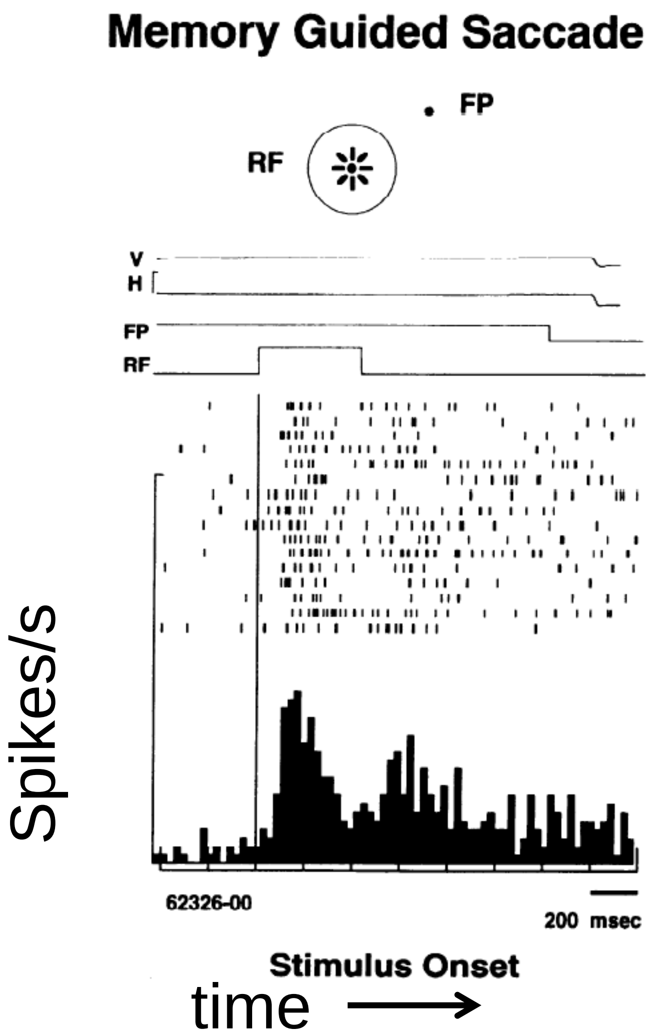
Measuring Memory

- Short-term memory
  - Sensory / iconic / echoic
- Working memory
  - Maintenance "3, 6, 1, 8, 7, 3, 5…"
  - Manipulation "5, 3, 7, 8, 1, 6, 3…"
- Long-term memory

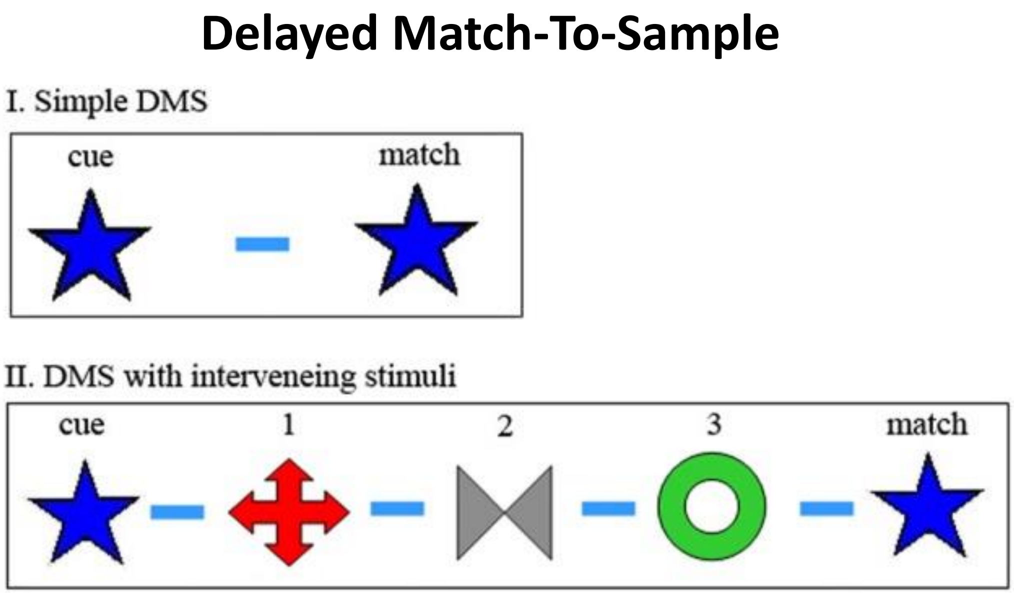
Echoic memory



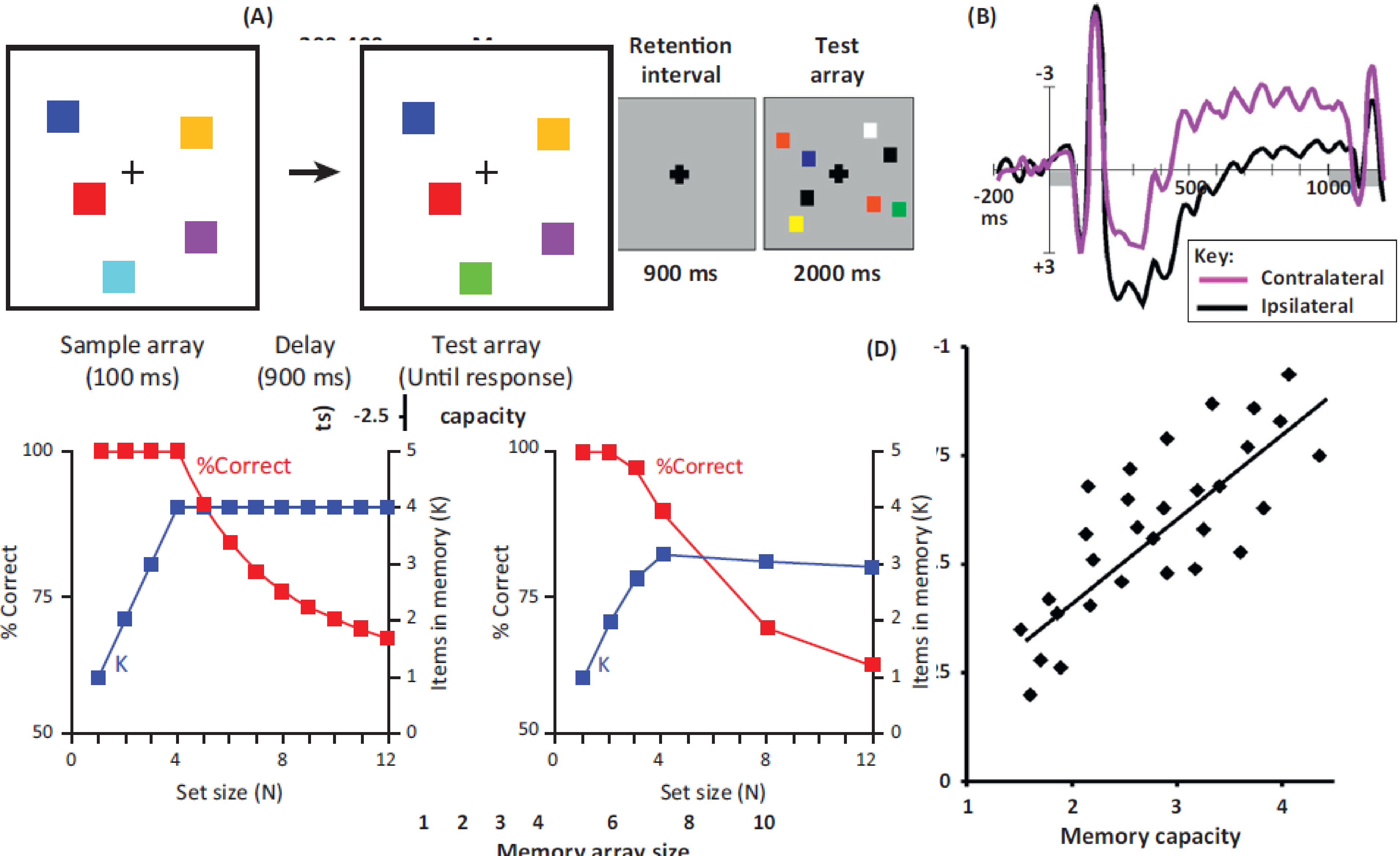
Working memory Tasks



Colby et al (1996)



Working memory



Typical memorisation Paradigm

"Difference due to memory" ("Dm")

"encoding phase"

child

guitar

beetroot

desk

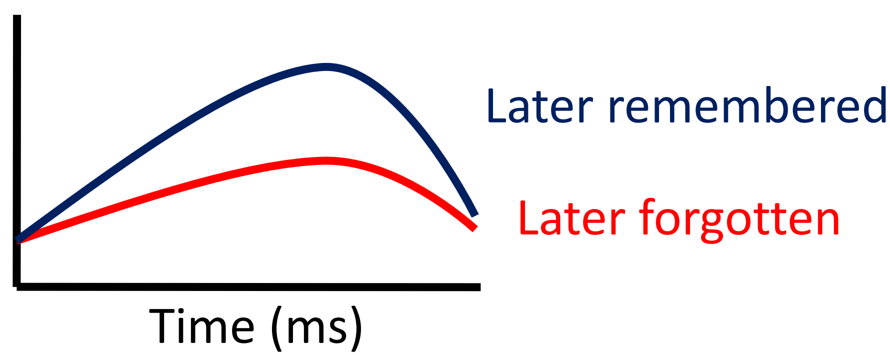
Trial series

. . .

Later recall

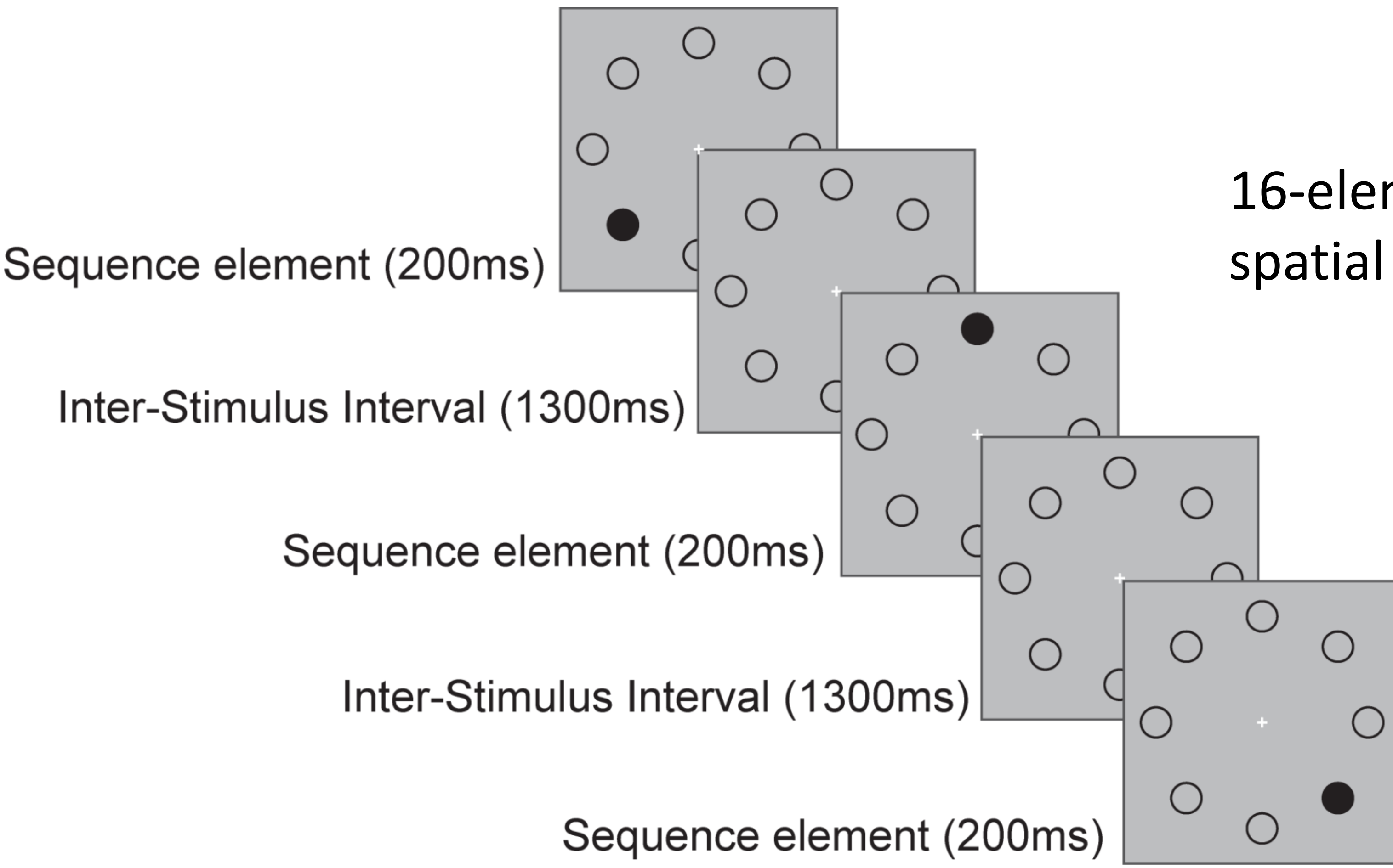
guitar

Have you seen this word?



Explicit Sequence Learning Task

Pre-block recall test



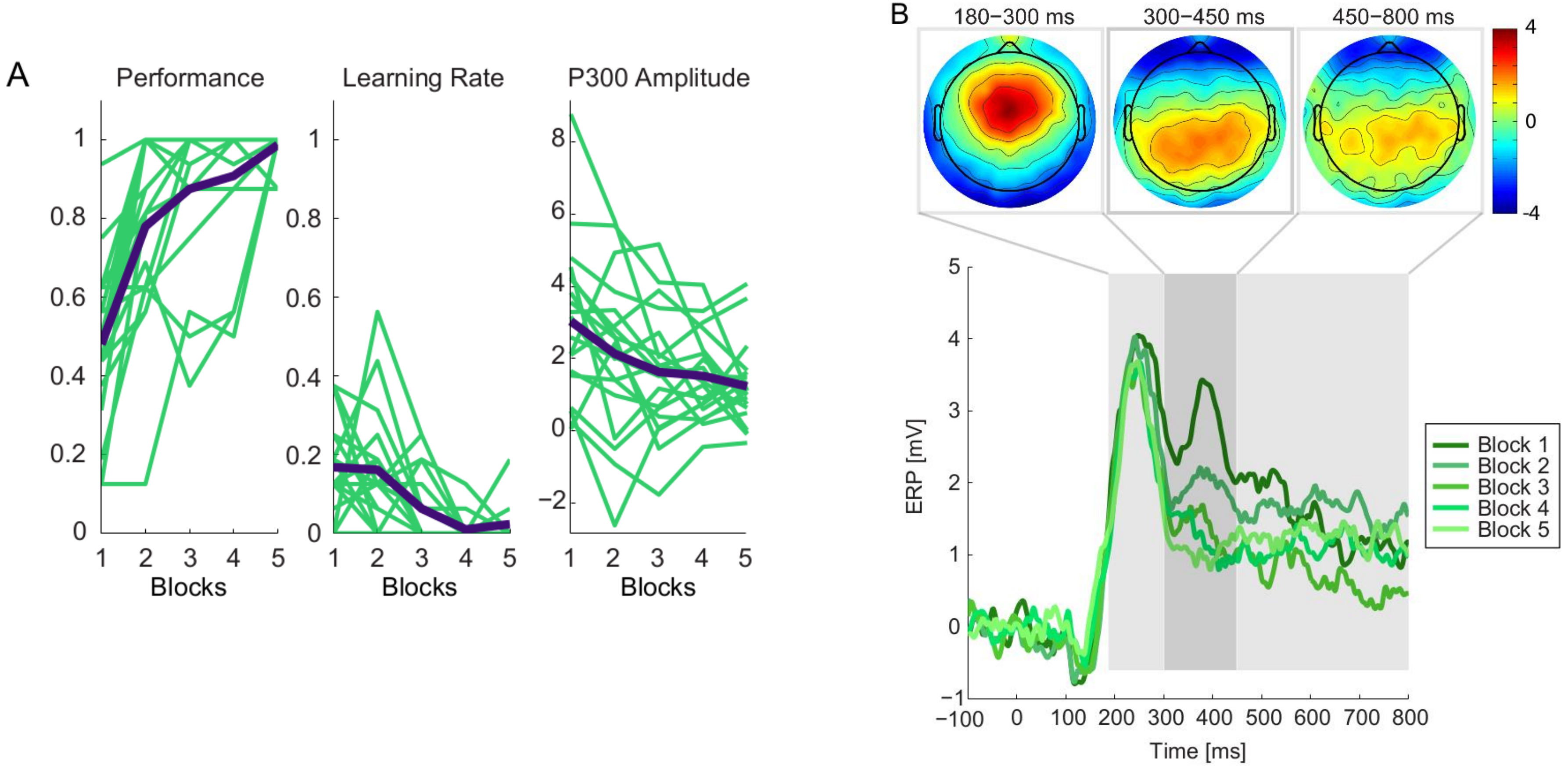
16-element spatial sequence

Post-block recall test

Steinemann et al (2016)

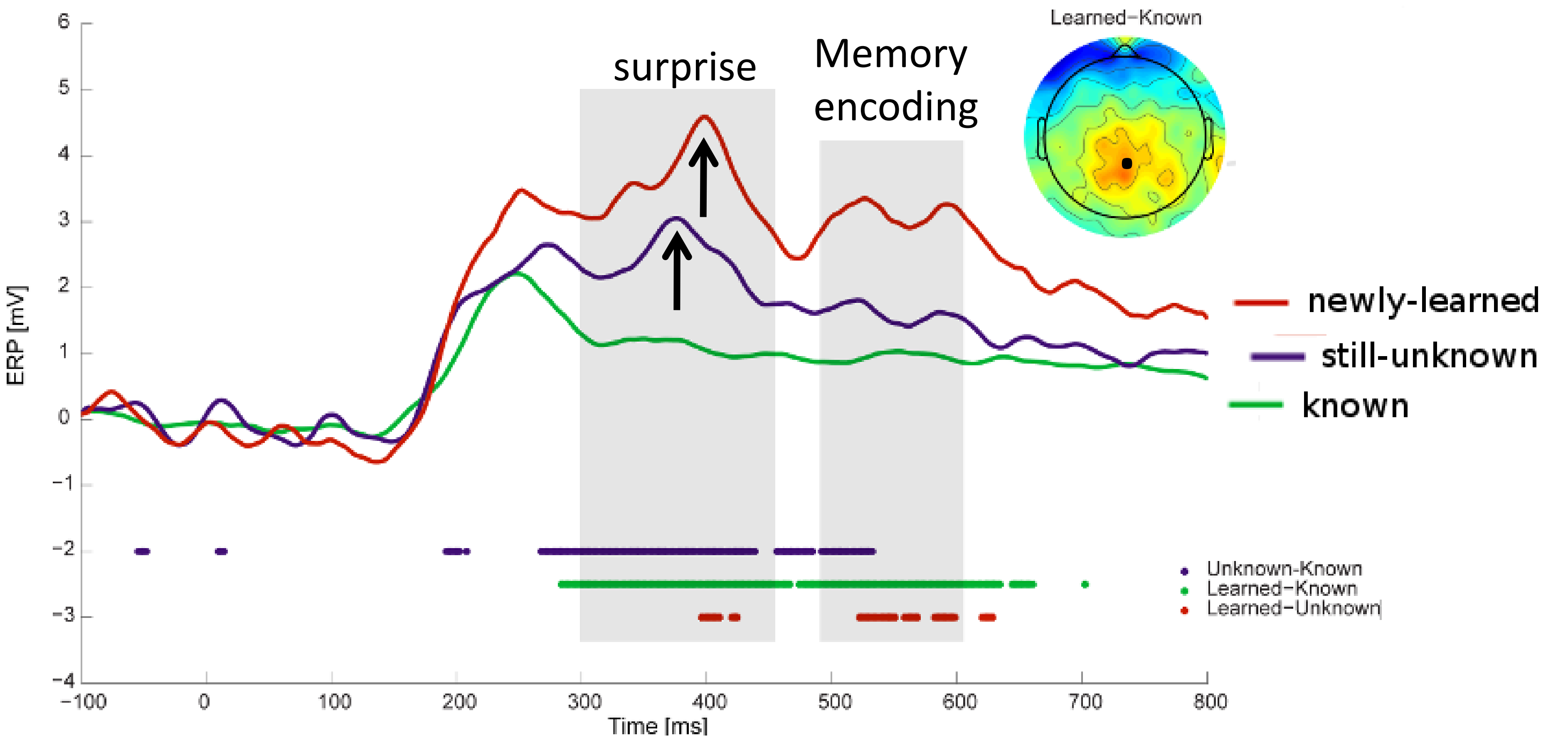
Explicit Sequence Learning Task

- "P300" component scales with "surprise" (prior uncertainty)
- Better learned sequence elements are less surprising



Steinemann et al (2016)

Explicit Sequence Learning Task



Steinemann et al (2016)

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sfi Science Foundation Ireland

NIH National Institute of Mental Health