

# LESSON 6

## Perceptual uncertainty, part 1

Perceptual uncertainty, part 2 (lesson 7)

Perceptual uncertainty, part 3 (lesson 8)

### Perceptual Uncertainty

- What is it?
- How can the brain overcome uncertainty?
- Can instances of perceptual uncertainty help us understand something?
- What sorts of confusion occur when the brain simply cannot overcome uncertainty?

But first... reminder of our overall approach to examining perceptual coding.

# deciphering perception by correlations

- Behistun Inscription, large rock relief on a cliff at Mount Behistun in the Kermanshah Province
- Darius the Great (522–486 BC)
- inscription includes three versions of the same text, written in three different cuneiform script languages: Old Persian, Elamite, and Babylonian.
- arduous efforts to understand Old Persian paved the way to deciphering the Elamite and Babylonian

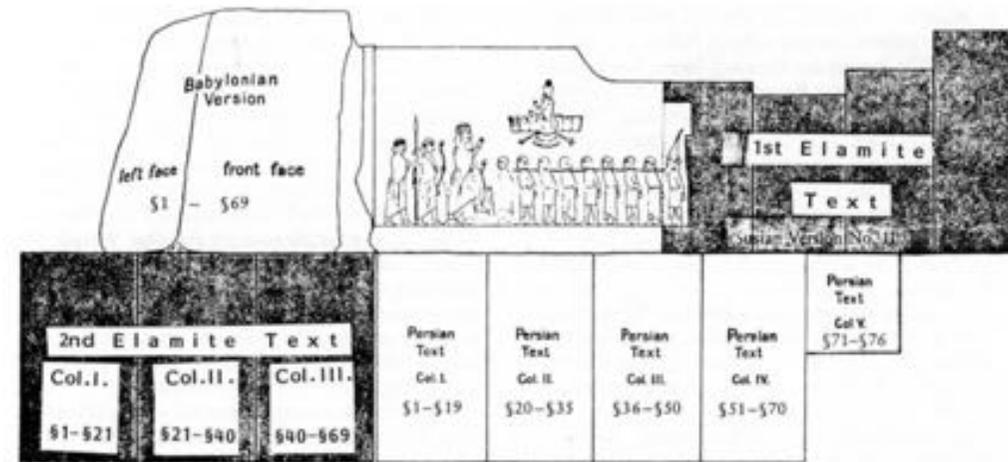
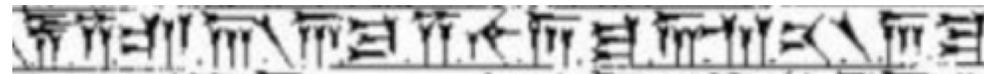


Figure 21. The positions of the Old Persian, Elamite, and Babylonian versions of the major trilingual inscription DB on the rock at Bisotún. Source: King and Thompson, pl. VI; corrected by Borger, fig. 2; adapted by R. Schmitt

old Persian (known)



Elamite (unknown)

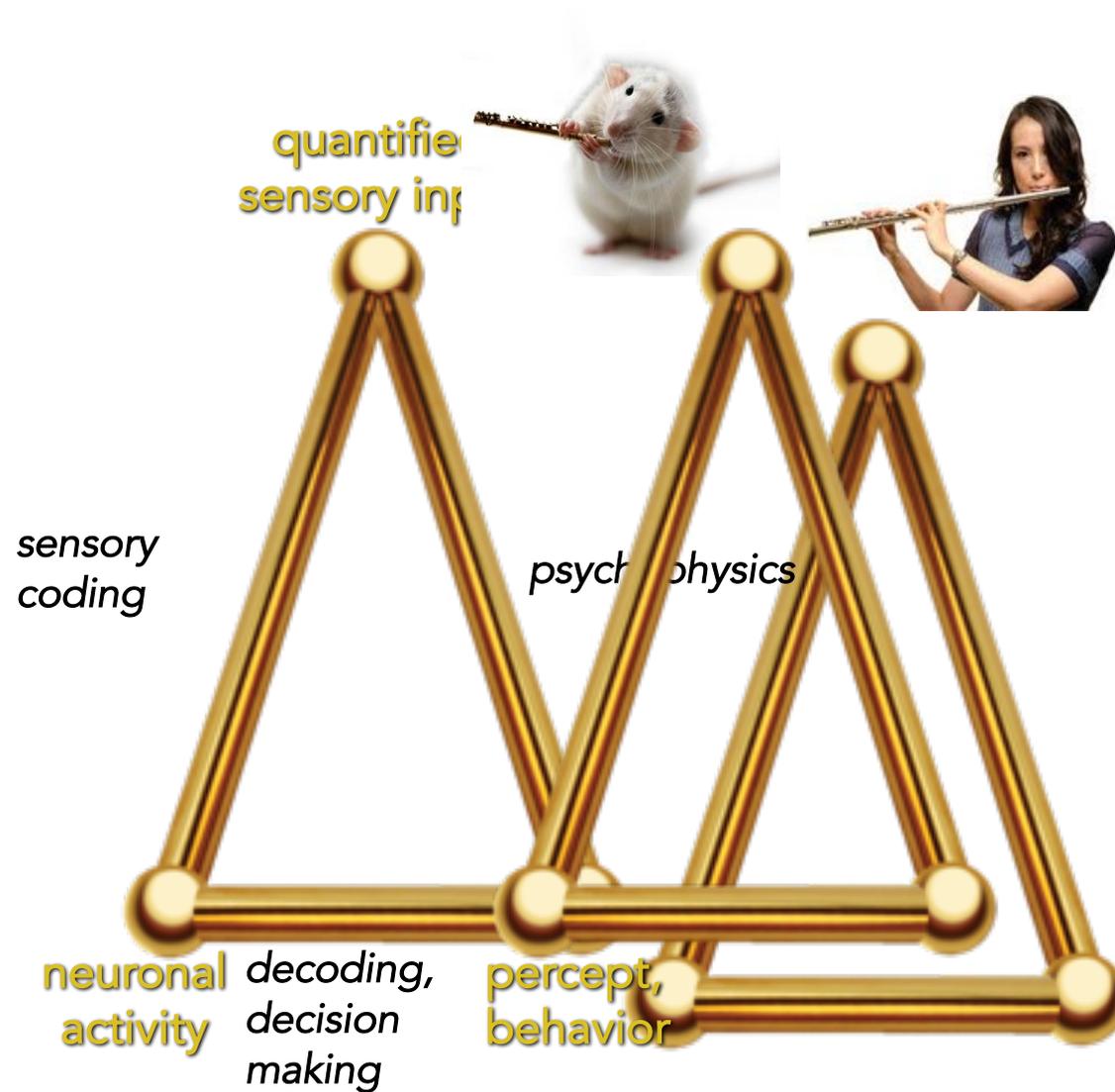


Babylonian (unknown)



# Experimental variables

*Strategies, approaches*



- *healthy, relaxed rat is a more intelligent rat*



## perceptual uncertainty

*inability of the brain's perceptual (subjective) readout to have exact knowledge about sensory events, even though the physical features or parameters of that event are, in some way encoded.*

- *incoming signal is somewhat ambiguous*
- *divergence/convergence of sensory channels*
- *bias*
- *recent or distant history*
- *other causes*

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- we live in a noisy and ambiguous world...



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PRIMER

## Perceptual uncertainty

Mathew E. Diamond \*

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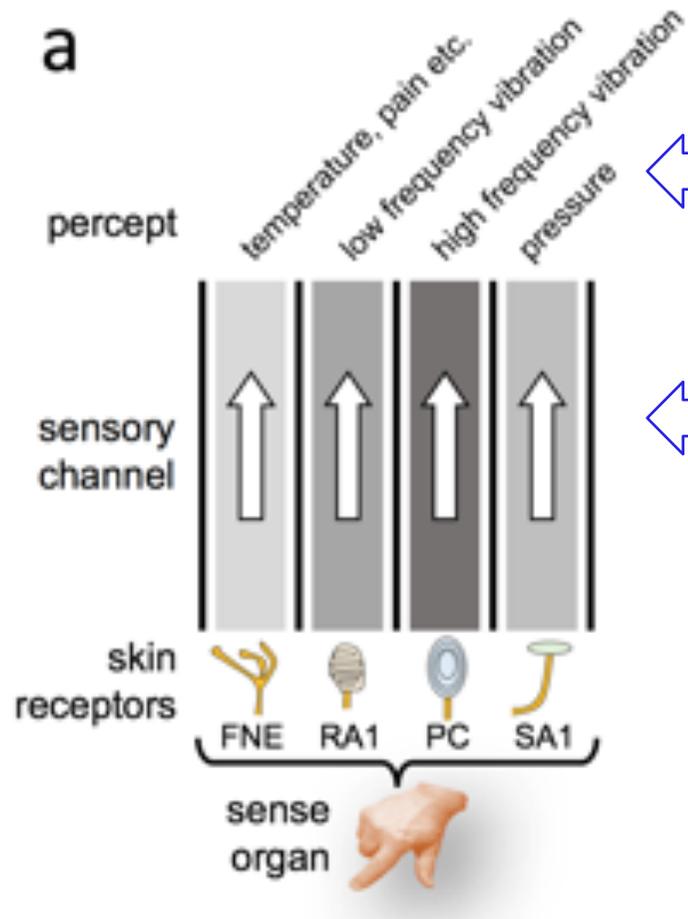
**Citation:** Diamond ME (2019) Perceptual uncertainty. PLoS Biol 17(8): e3000430. <https://doi.org/10.1371/journal.pbio.3000430>

**Published:** August 27, 2019

### Abstract

The number of the distinct tactile percepts exceeds the number of receptor types in the skin, signifying that perception cannot be explained by a one-to-one mapping from a single receptor channel to a corresponding percept. The abundance of touch experiences results from multiplexing (the coexistence of multiple codes within a single channel, increasing the available information content of that channel) and from the mixture of receptor channels by divergence and convergence. When a neuronal representation emerges through the combination of receptor channels, perceptual uncertainty can occur—a perceptual judgment is affected by a stimulus feature that would be, ideally, excluded from the task. Though uncertainty seems at first glance to reflect nonoptimality in sensory processing, it is actually a consequence of efficient coding mechanisms that exploit prior knowledge about objects that are touched. Studies that analyze how perceptual judgments are “fooled” by variations in sensory input can reveal the neuronal mechanisms underlying the tactile experience.

a



← elementary percepts

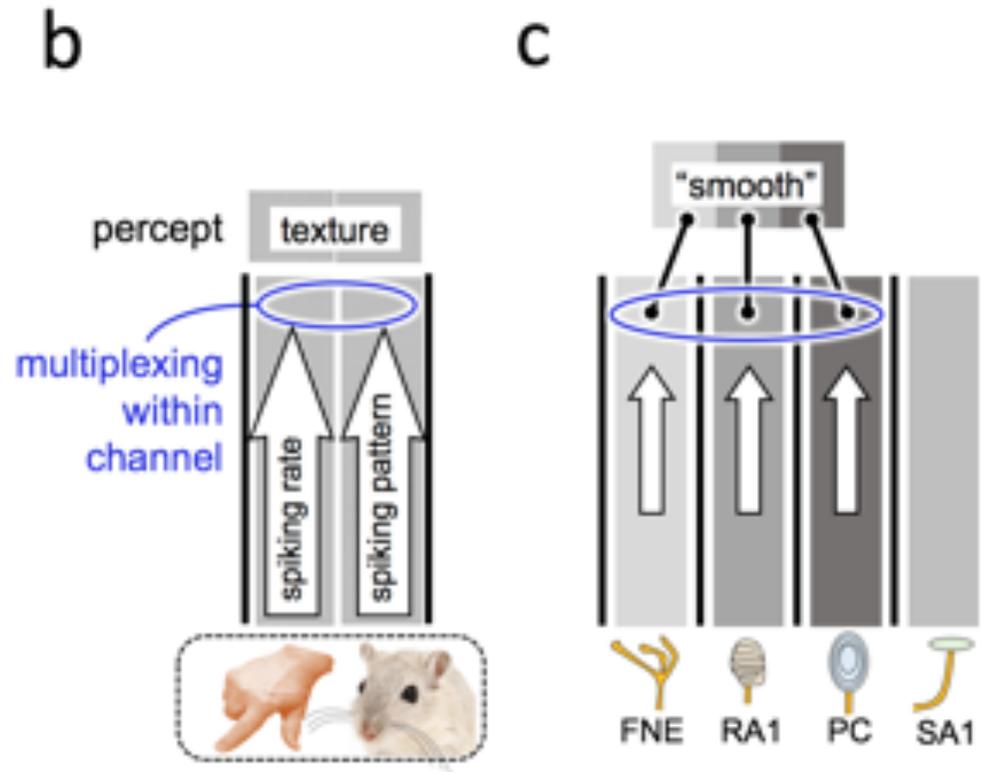
← elementary channels

Yet somehow fingertip skin percepts include:

- surface microstructure (from rough to smooth)
- temperature (from warming to cooling)
- compliance (from soft to stiff)
- pointedness (from sharp to blunt)
- pressure (from light to strong)
- vibration frequency (from low to high)
- adhesiveness (from sticky to slippery)
- moistness (from dry to wet)
- much more (textures)

Whereas some of these dimensions can be mapped to receptor types (e.g., FNE expressing transient receptor potential (TRP) channels for thermal change), most of them cannot.

How?



receptor channel convergence and divergence is a brilliant mechanism for expanding the richness of the perceptual code, but it is not without some cost.

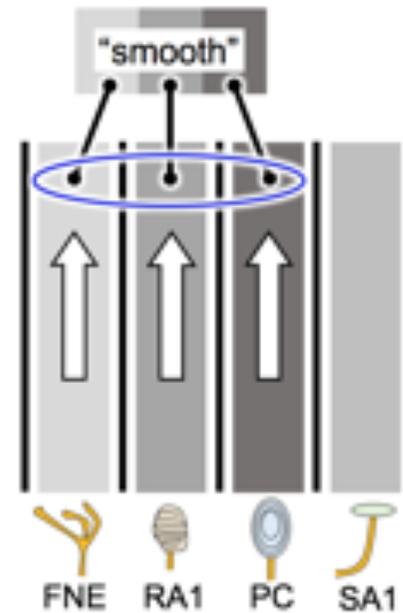
## Perceptual uncertainty

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C

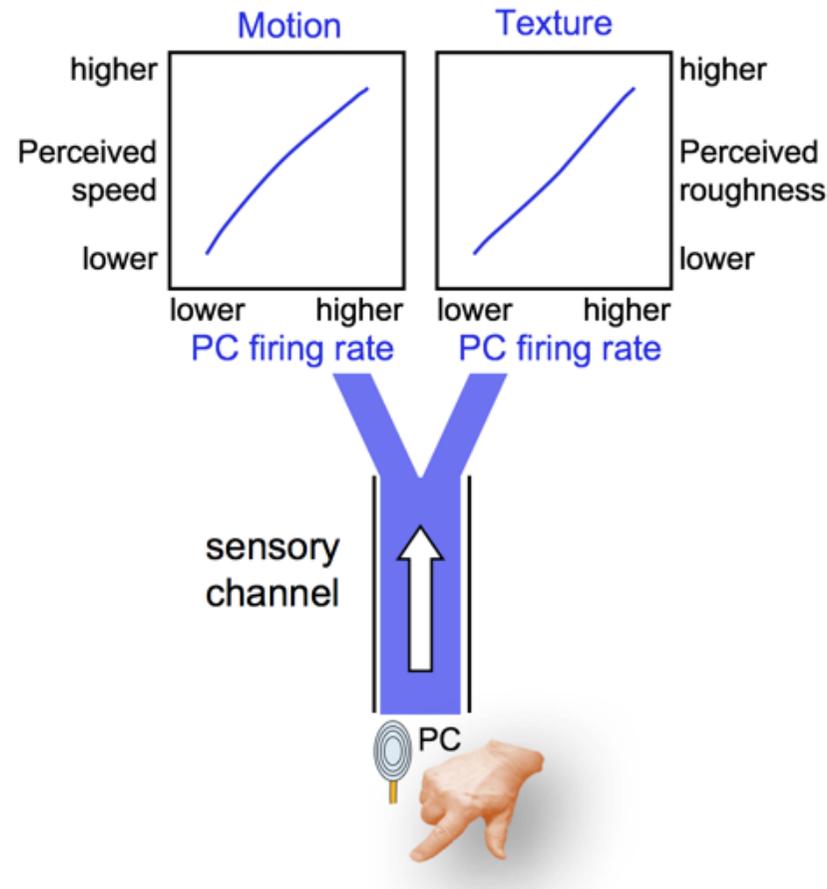


Using prior knowledge in a Bayesian manner can boost a percept but can also cause confusion.

The case of smooth & cool

Recall: perceptual uncertainty is the inability of the brain's perceptual (subjective) readout to have exact knowledge about sensory events, even though the physical features or parameters of that event are, in some way encoded.

The screenshot shows the top of a PLOS Biology article page. At the top left is the PLOS logo with 'BIOLOGY' and 'FIFTEENTH ANNIVERSARY' below it. To the right are links for 'BROWSE', 'PUBLISH', and 'ABOUT'. Below the logo, it says 'OPEN ACCESS' and 'PEER-REVIEWED' with a 'RESEARCH ARTICLE' label. The main title is 'Feeling fooled: Texture contaminates the neural code for tactile speed'. Below the title are the authors: 'Benoit P. Delhayes, Molly K. O'Donnell, Justin D. Lieber, Kristine R. McLellan, Silman J. Bensmaia' and the publication date: 'Published: August 27, 2019' with a DOI link. At the bottom of the article header is a navigation bar with tabs for 'Article', 'Authors', 'Metrics', 'Comments', and 'Media Coverage', with 'Comments' highlighted in green.



The PLOS Biology logo is at the top. Below it, the text reads 'PRIMER' and 'Perceptual uncertainty'. The author's name is 'Mathew E. Diamond' with a green checkmark icon. Below that is the affiliation: 'Cognitive Neuroscience, International School for Advanced Studies, Trieste, Italy' and the email address '\* diamond@sissa.it'.

## Perceptual Uncertainty

- What is it?
- How can the brain overcome uncertainty?
- Can instances of perceptual uncertainty help us understand something?
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## perceptual uncertainty

*inability of the brain's perceptual (subjective) readout to have exact knowledge about sensory events, even though the physical features or parameters of that event are, in some way encoded.*

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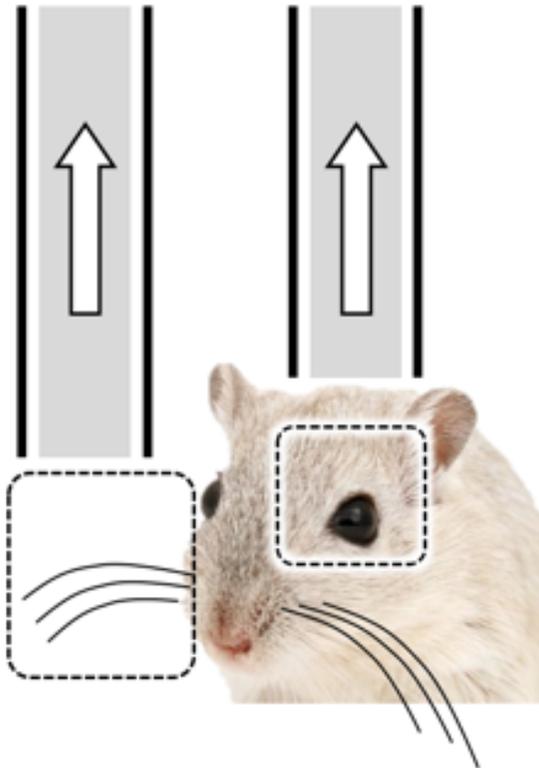
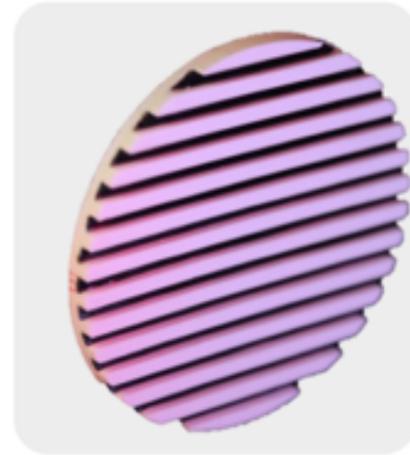
PRIMER

## Perceptual uncertainty

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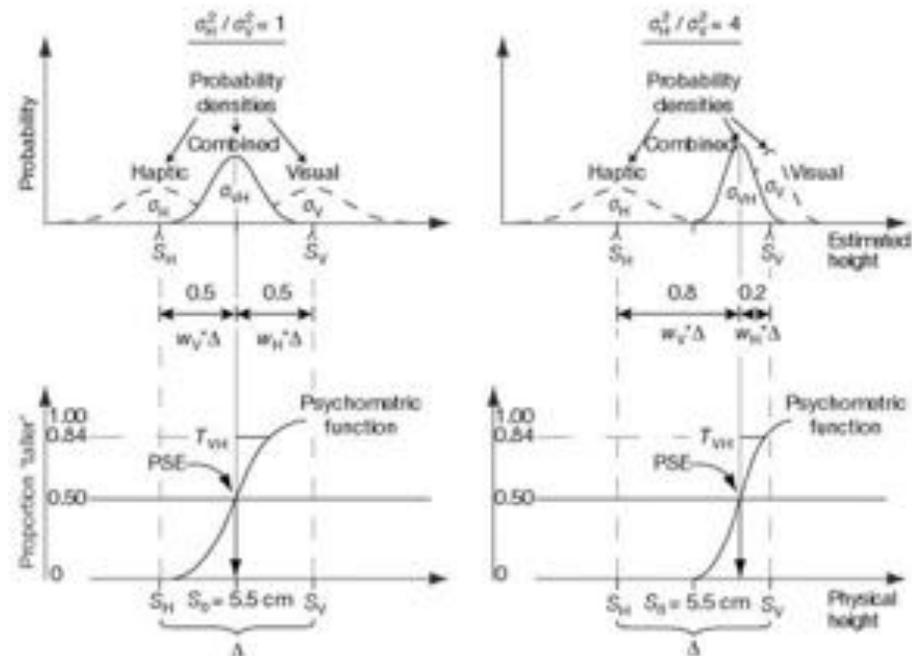
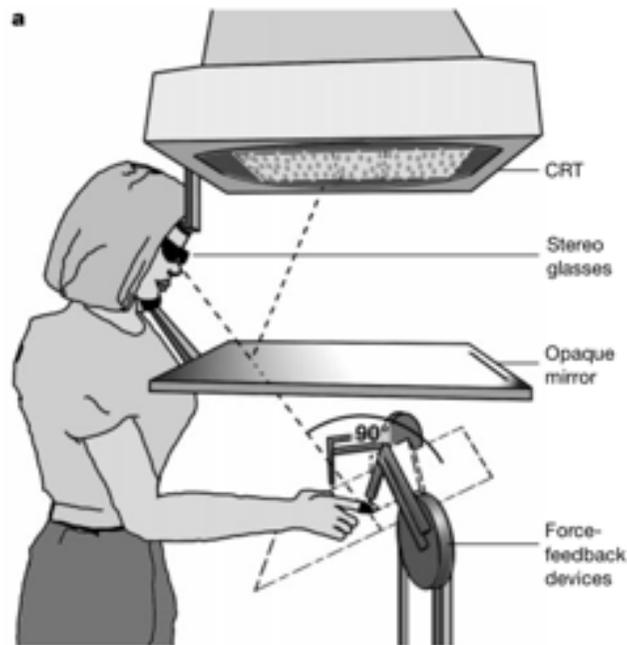
# Humans integrate visual and haptic information in a statistically optimal fashion

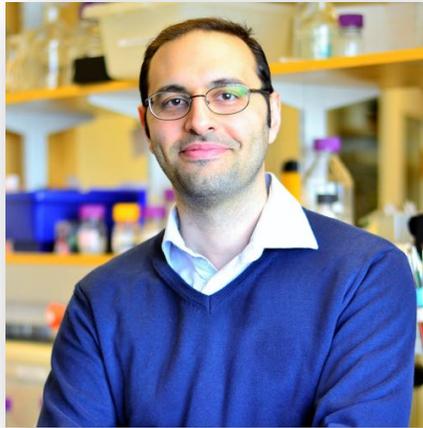
Marc O. Ernst\* & Martin S. Banks (2002)

Vision Science Program/School of Optometry, University of California, Berkeley  
94720-2020, USA

1. A simple formulation for optimal convergence
2. Discovery of near-optimality (linear summation) for vision-touch in humans

## letters to nature





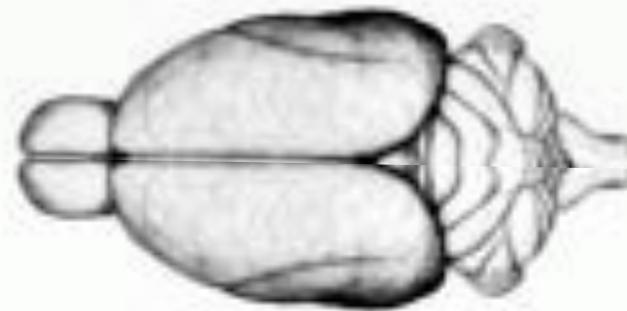
Nader Nikbakht  
SISSA Neuroscience thesis prize



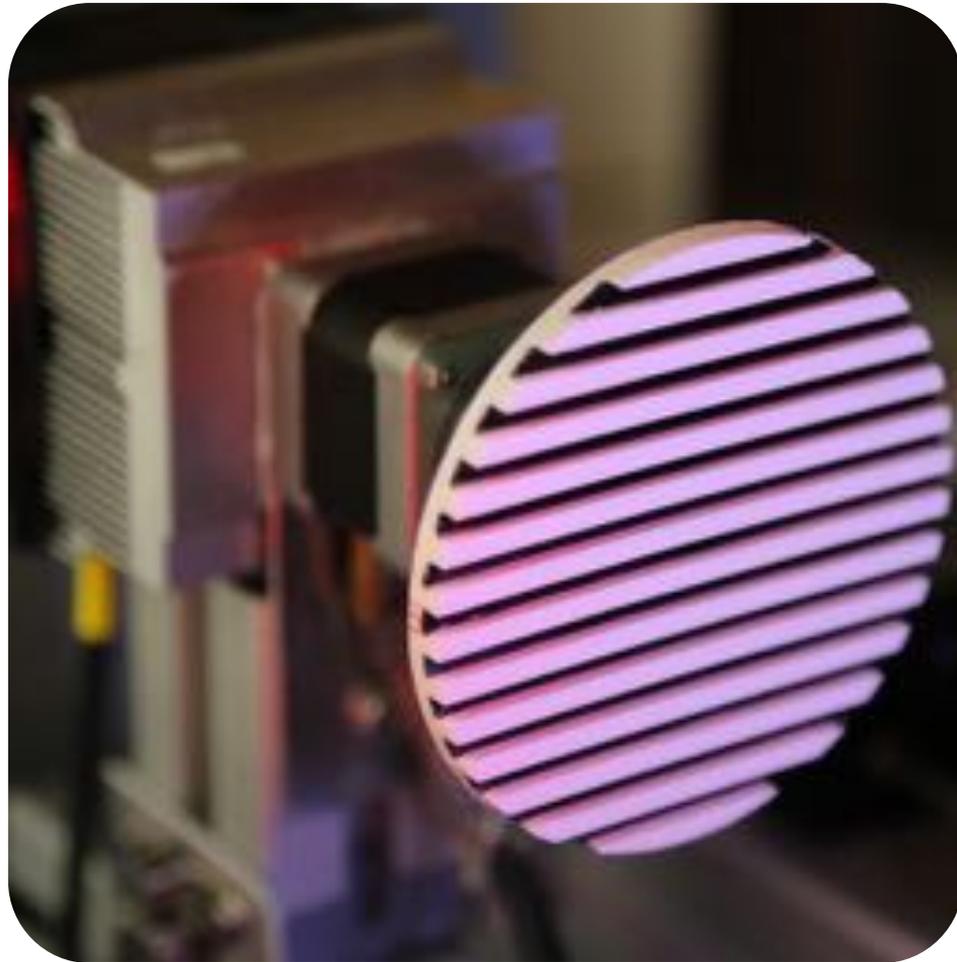
MIT  
Cambridge, MA

Nikbakht, N., et al.(2018). Supralinear and Supramodal Integration of Visual and Tactile Signals in Rats: Psychophysics and Neuronal Mechanisms. *Neuron*, 97(3), 626-639.

*where and how do modalities get combined?*



a real thing

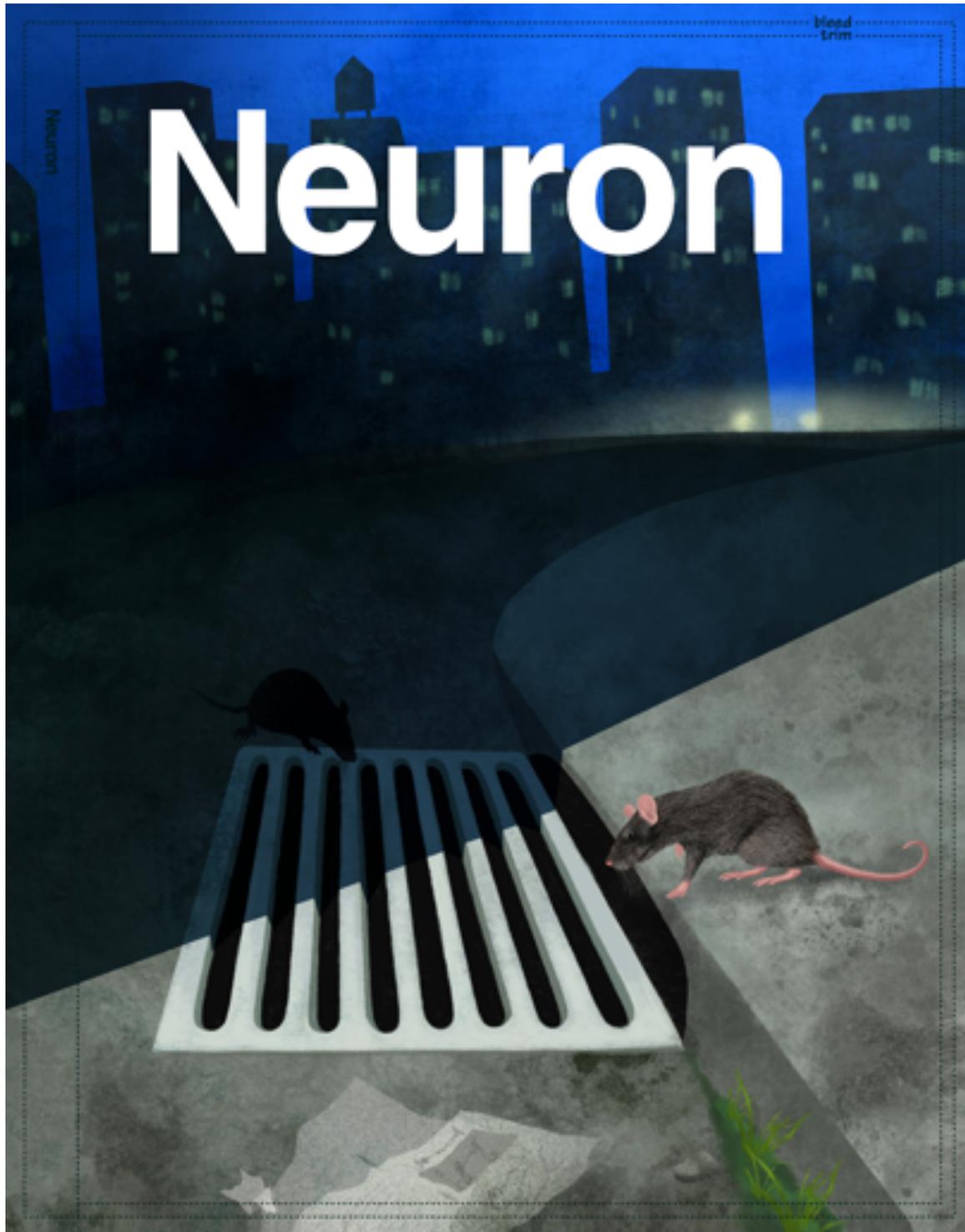




Neuron

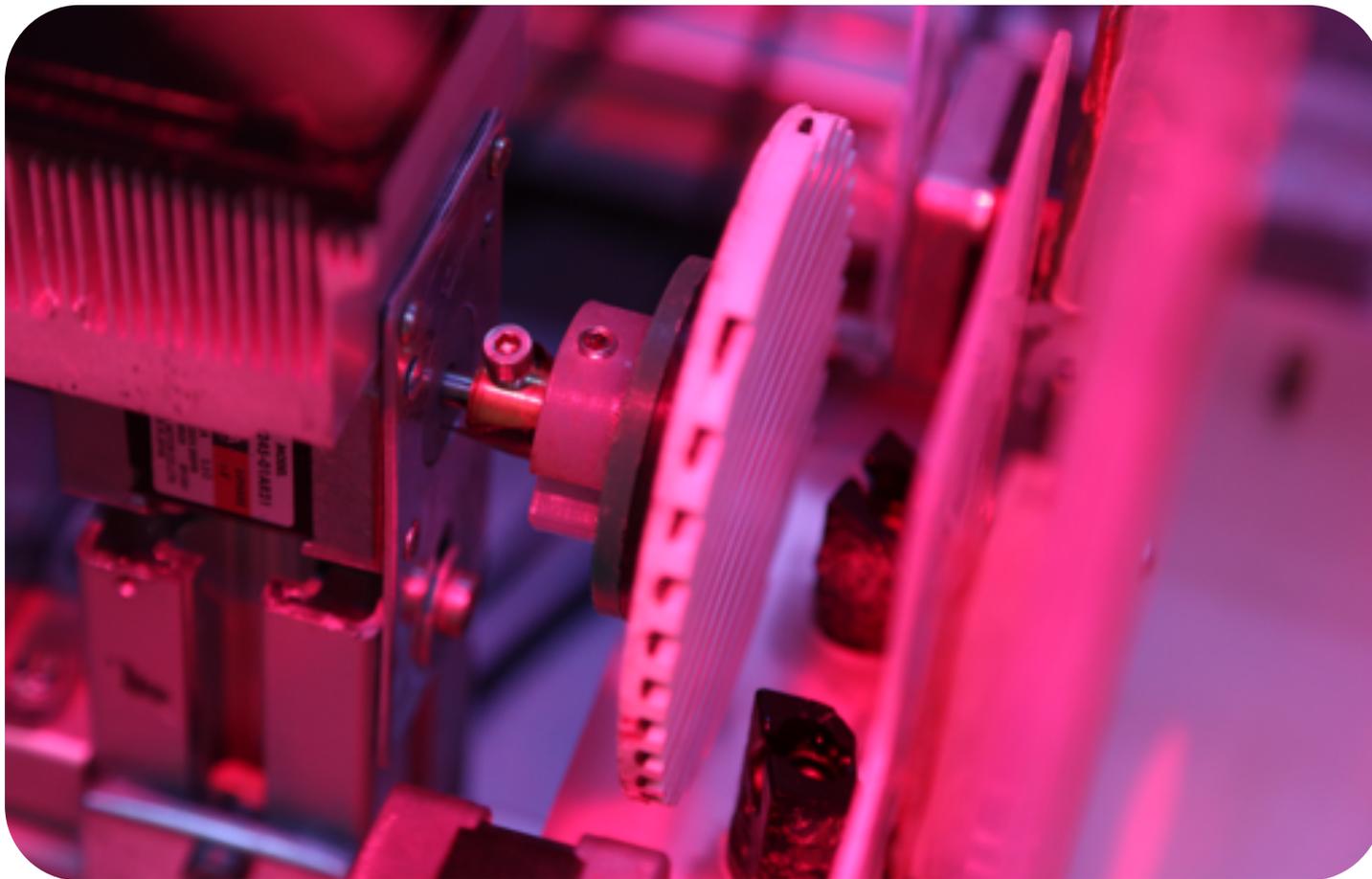
Head  
Trim

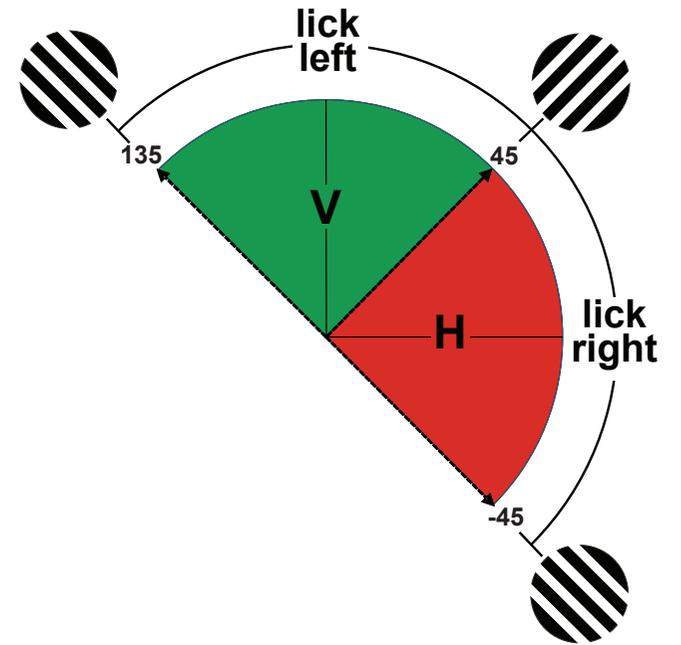
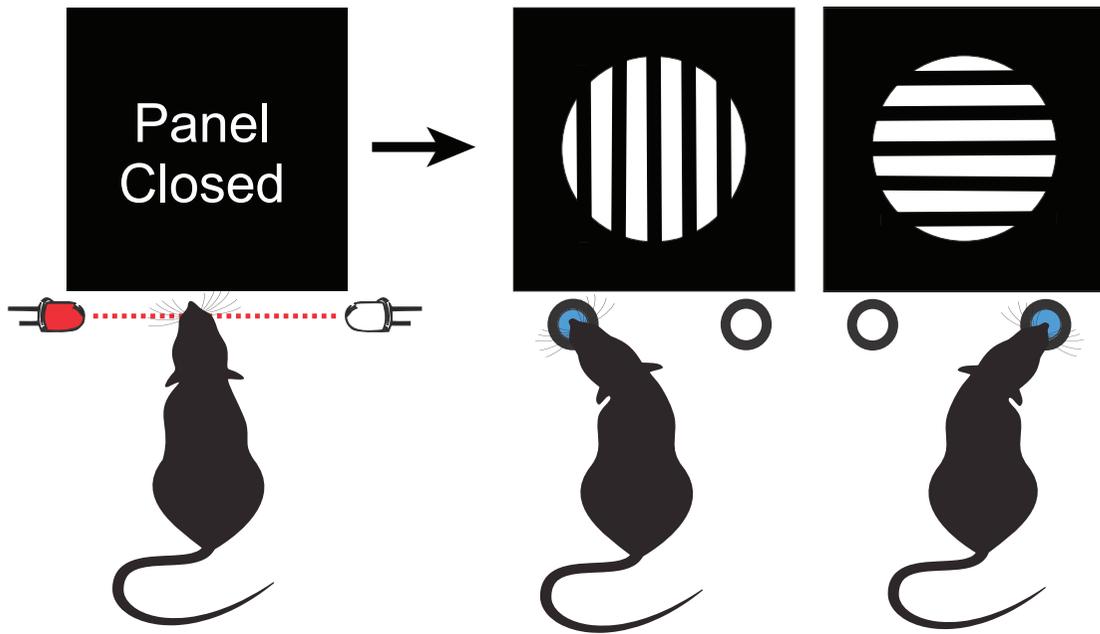
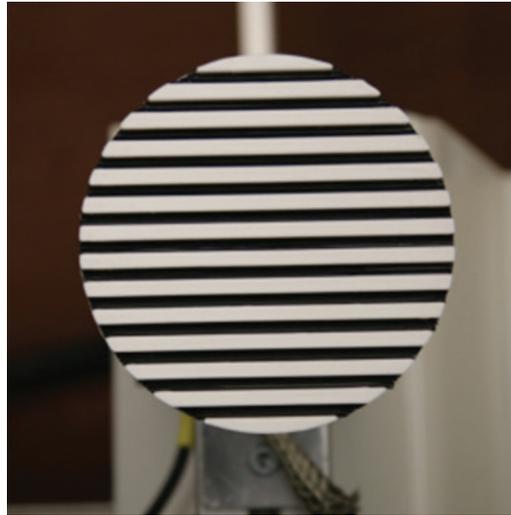
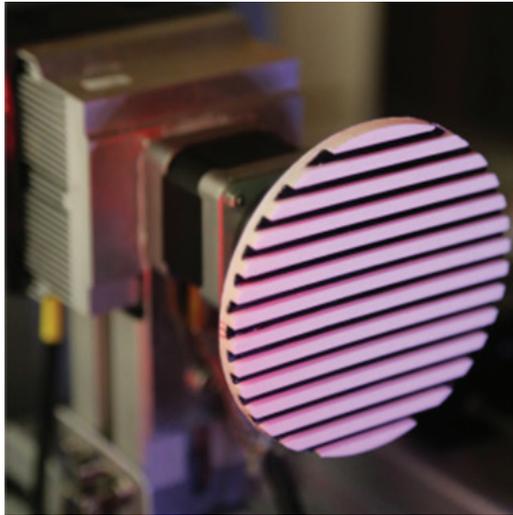
# Neuron



# Behavior

# Neurons





illumination is **infrared** only !!!

90 degrees  
LEFT is correct



Tactile condition

LEFT lick port



RIGHT lick port



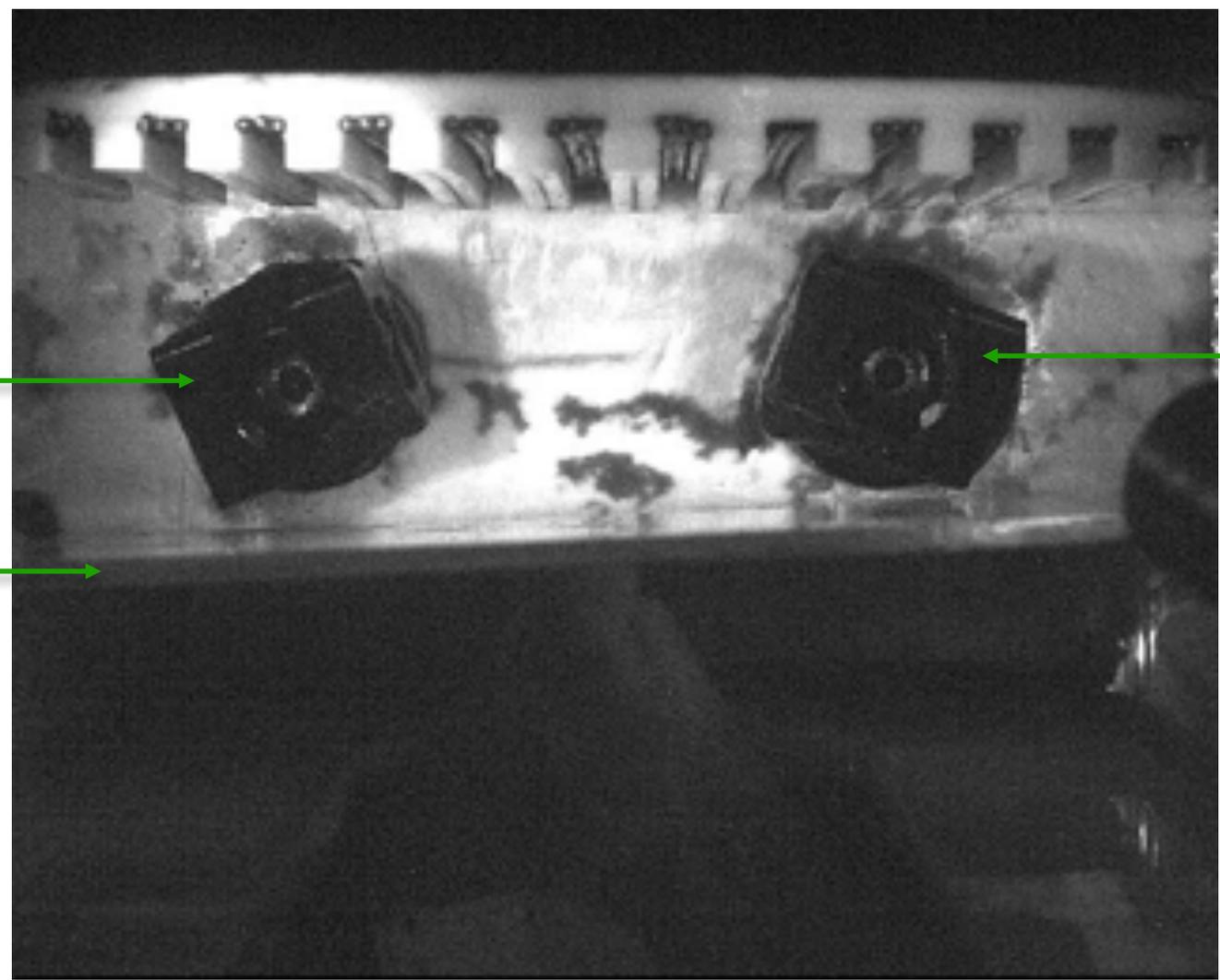
Infra-red light source



Opaque gate



head-poke sensor

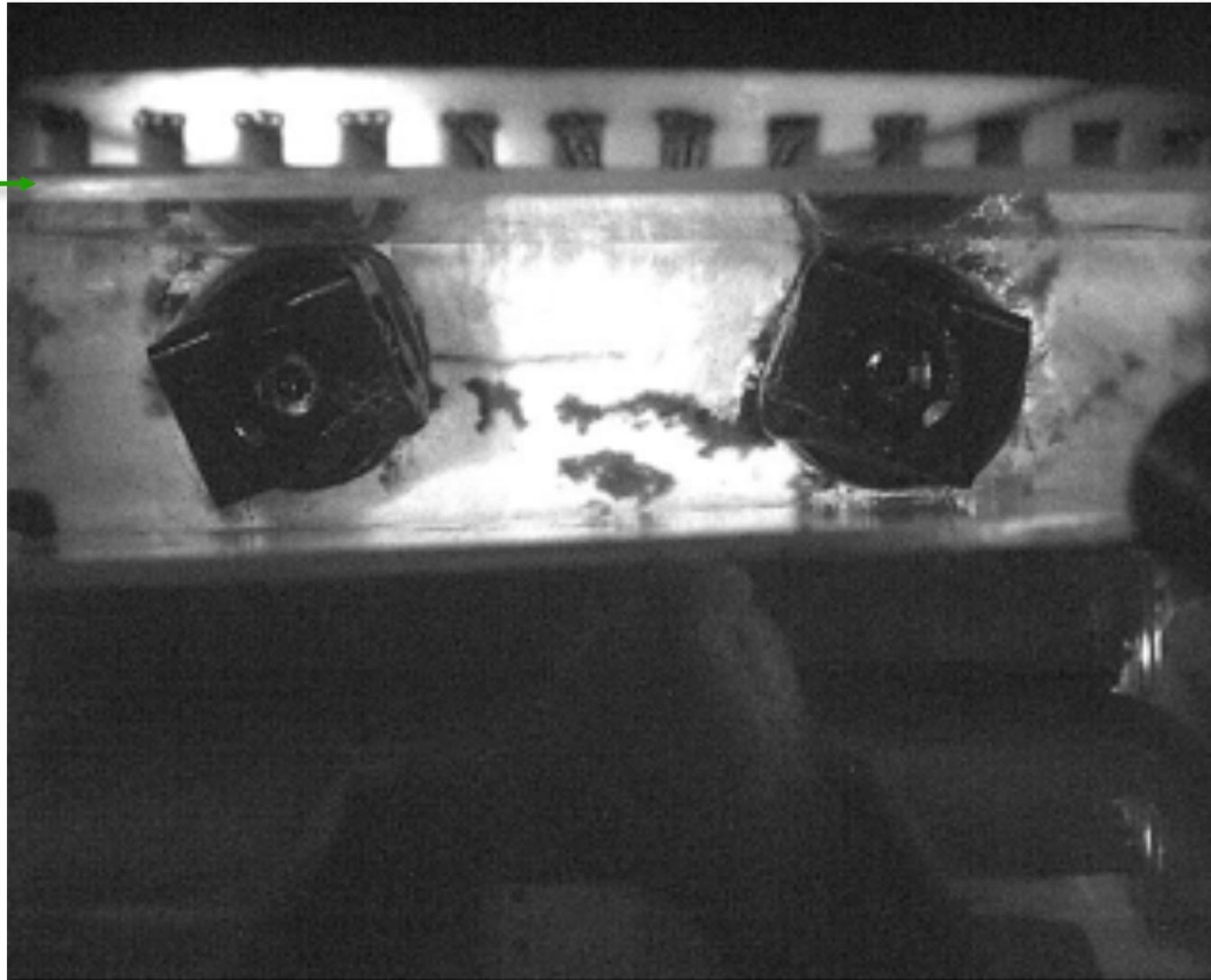


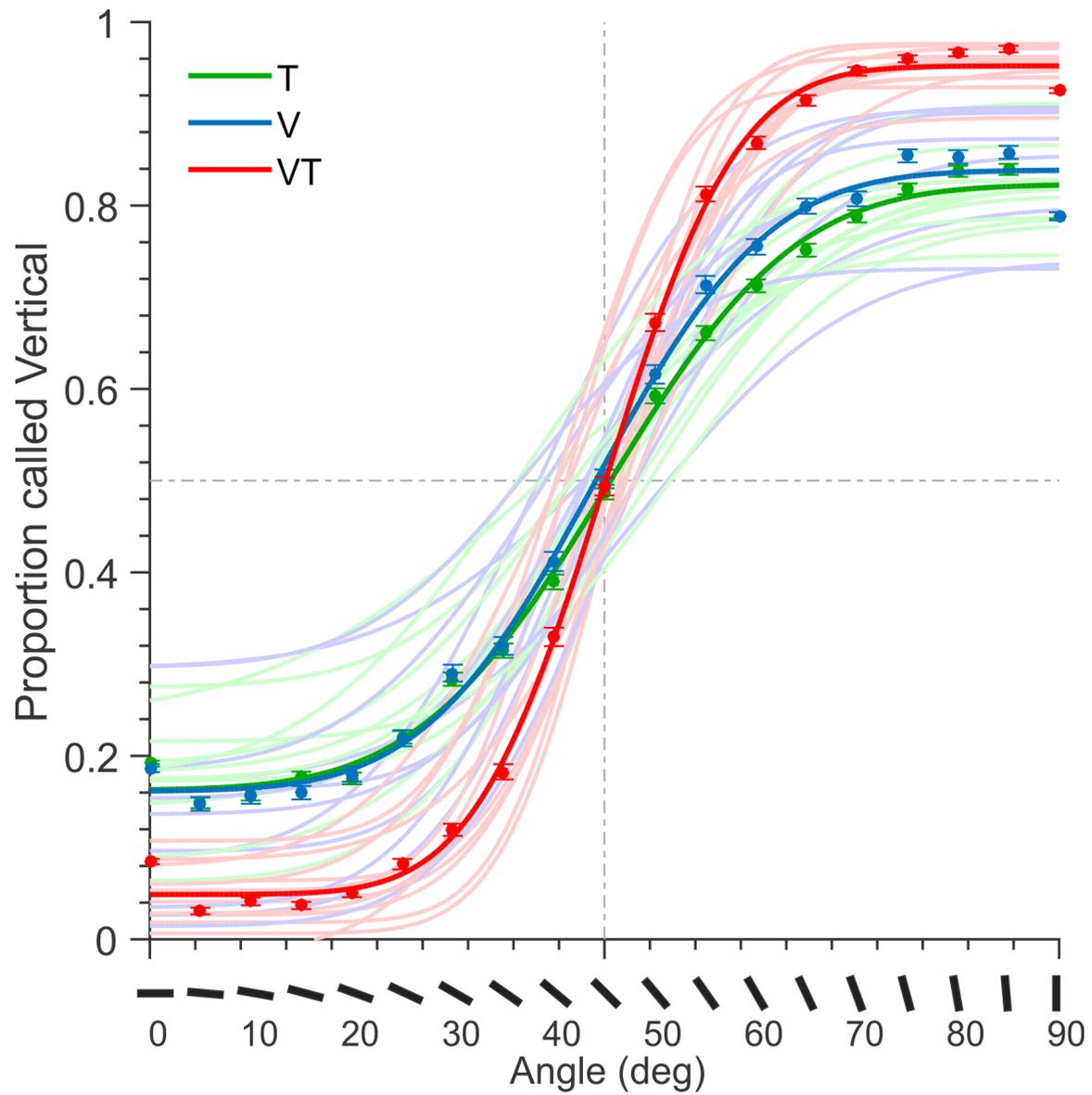
90 degrees  
LEFT is correct

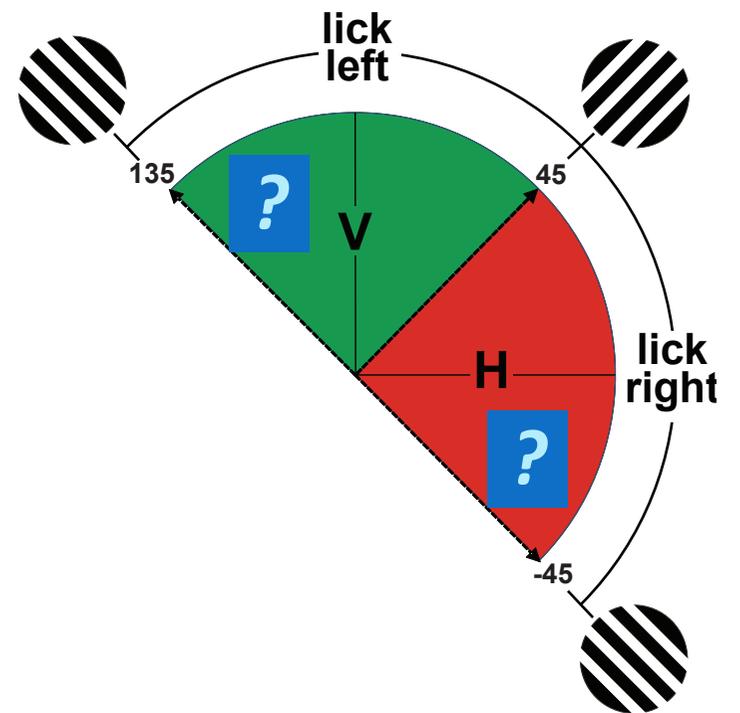
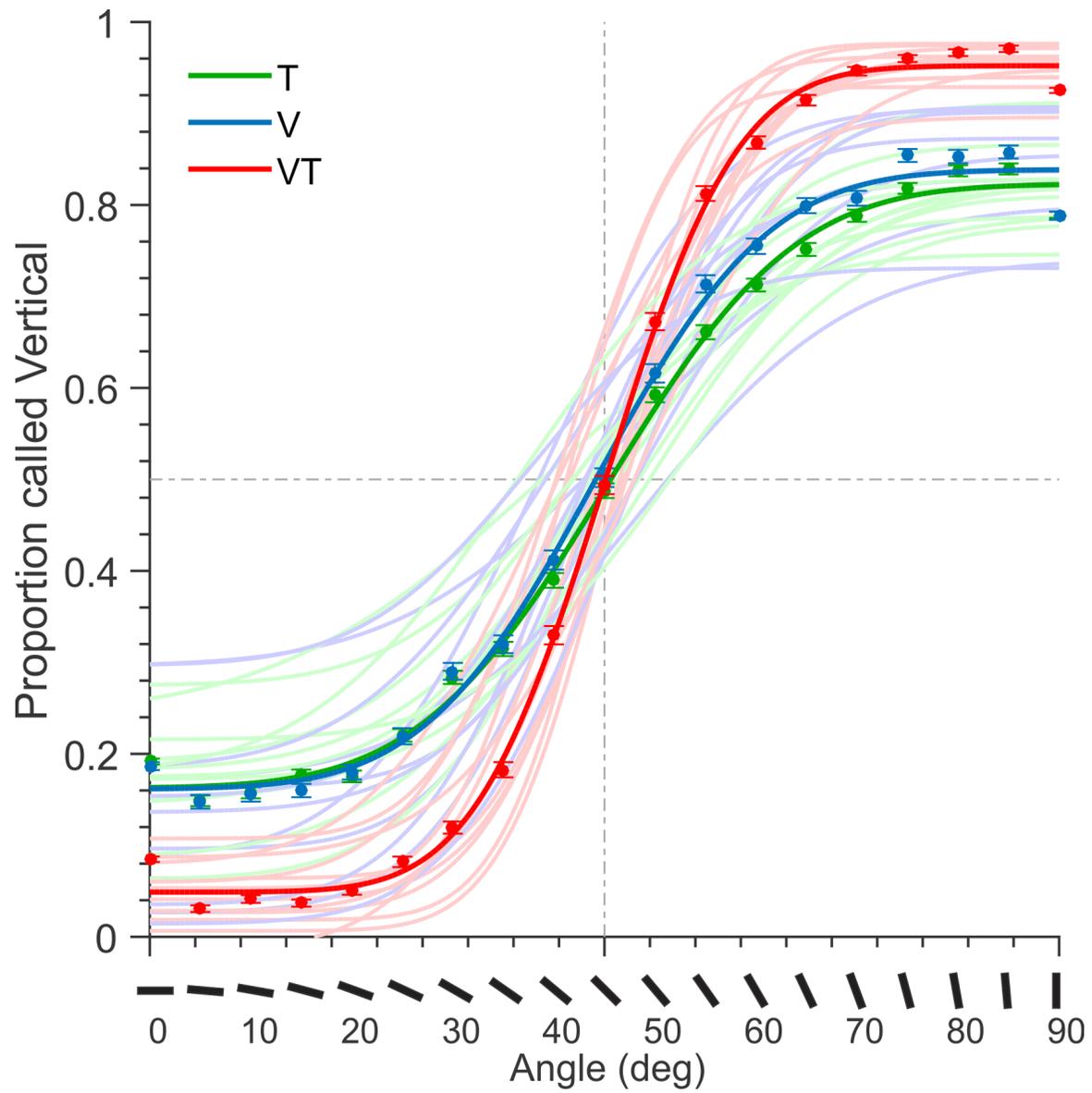


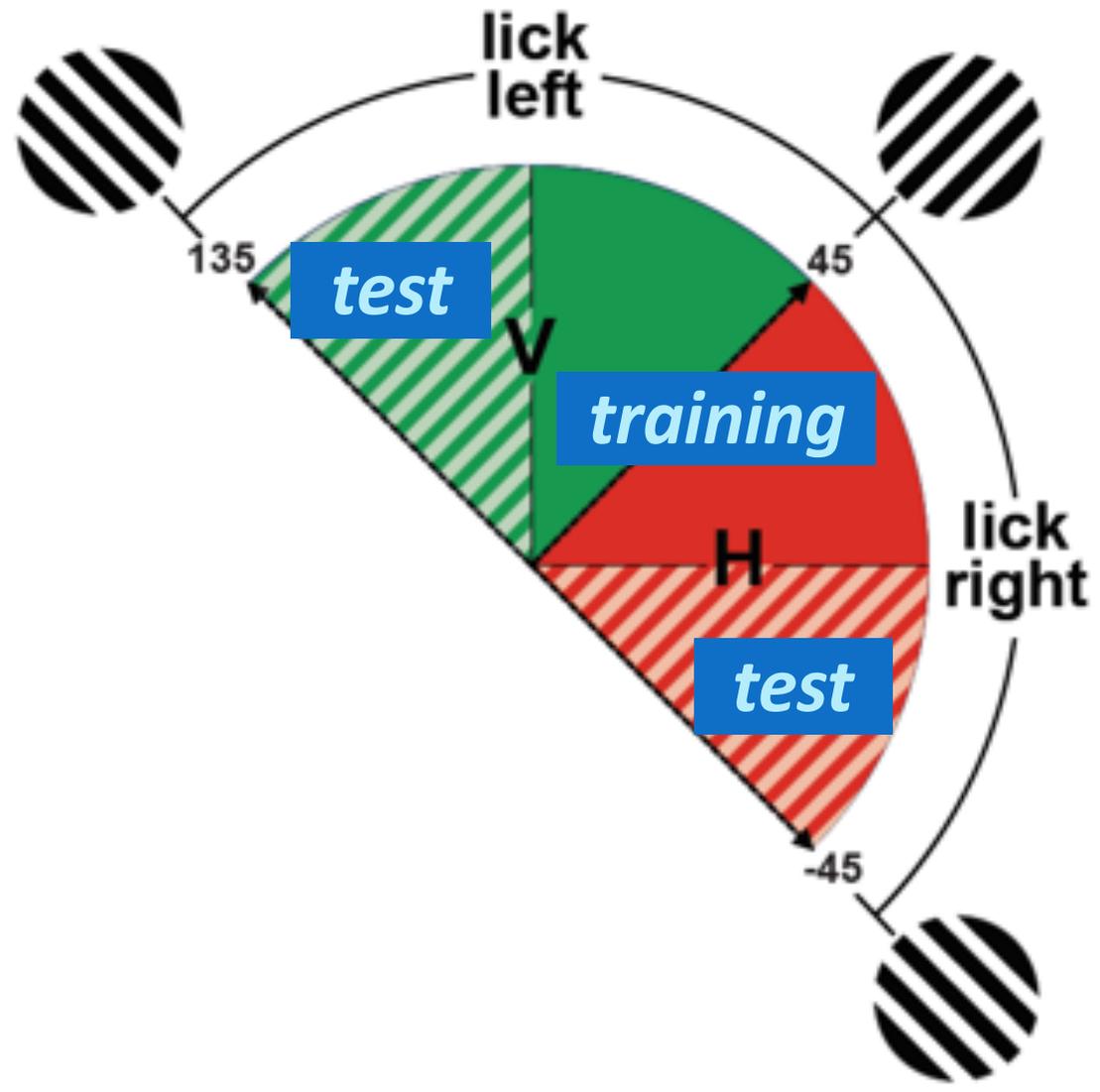
Visual condition

Transparent  
screen

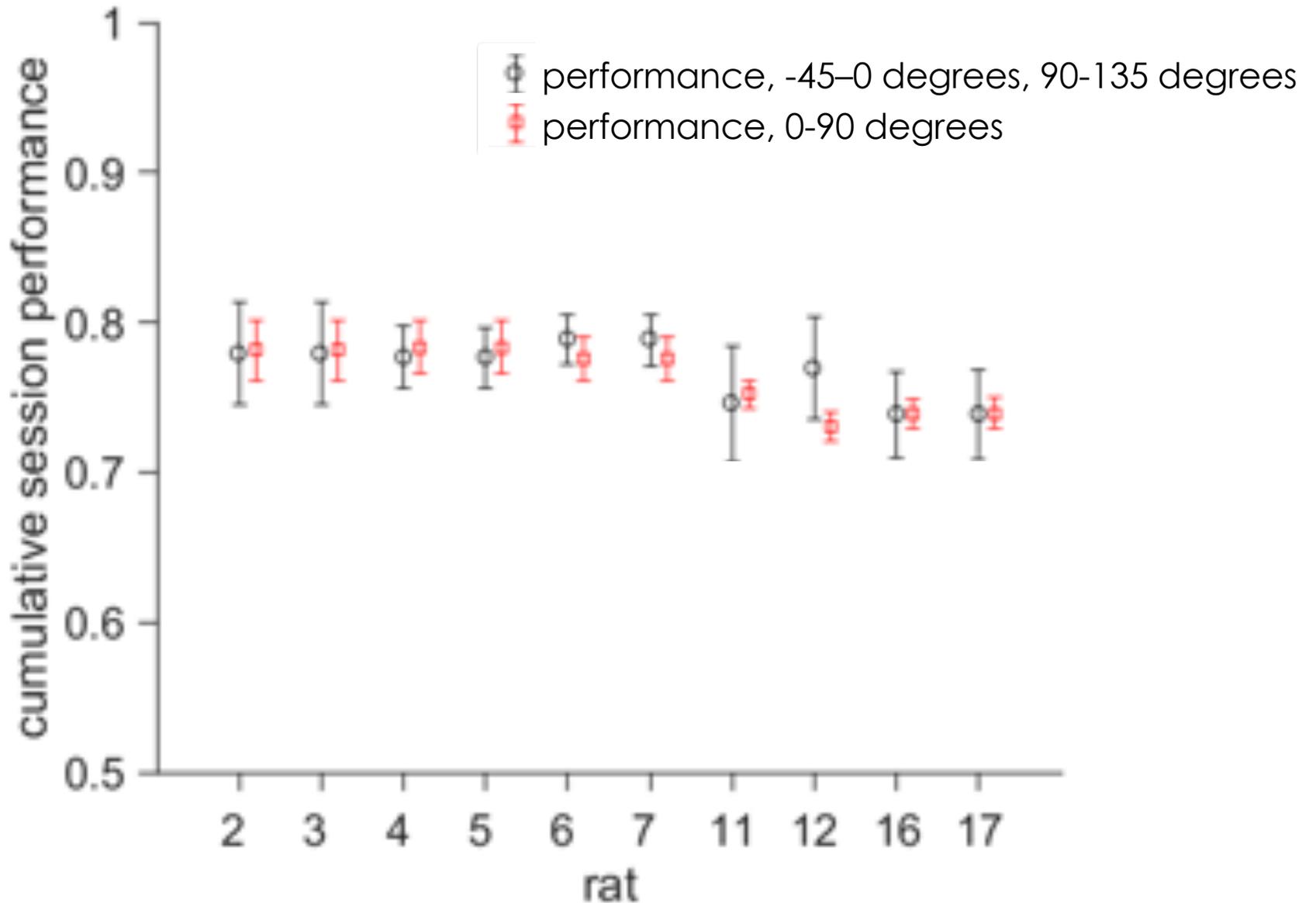








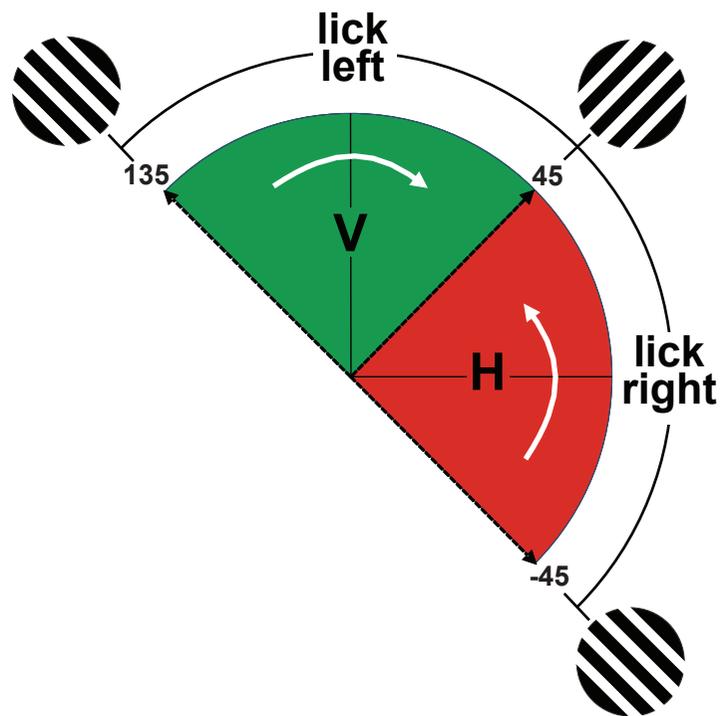
after training at 0-90 degrees,  
first test session at new angles



PIRE Workshop/Summer School 2017  
June, 18-19 2017  
Hotel La Costa Golf & Resort in Pals, Girona

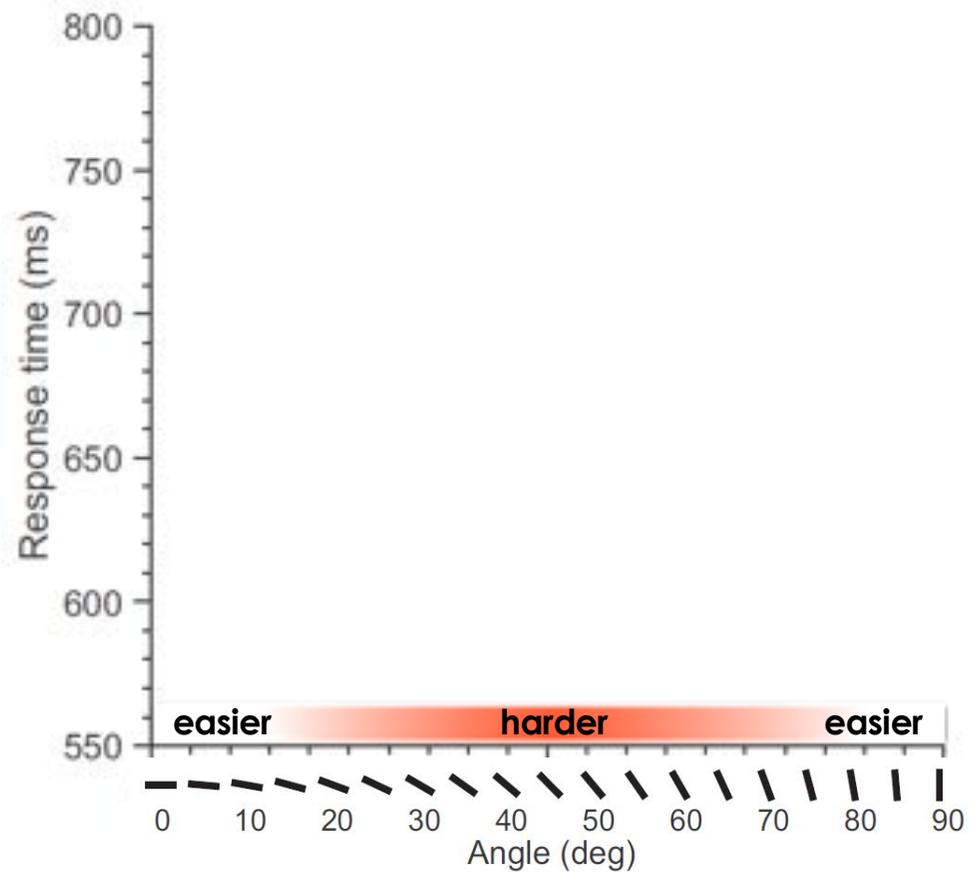
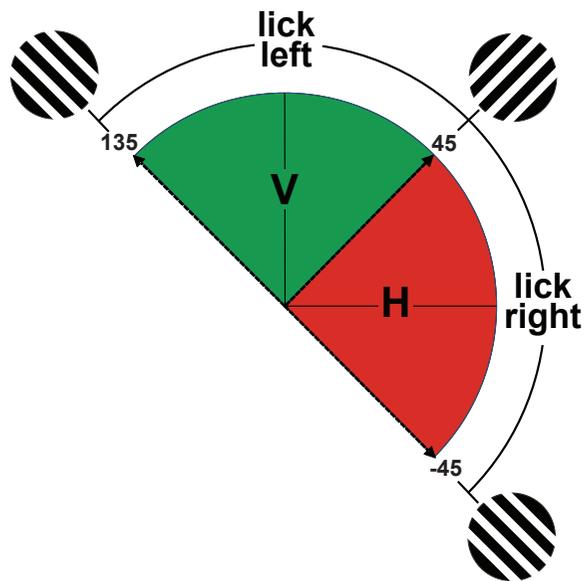
The ability to map sensory inputs to meaningful semantic labels, i.e., to recognize objects, is foundational to cognition, and the human brain excels at object recognition tasks along ventral processing pathways and across sensory domains. Examples include perceiving spoken speech, reading written words, even recognizing tactile Braille patterns.

*the rats, unwittingly, mapped the stimuli never before encountered to semantic labels of "vertical" and "horizontal"*

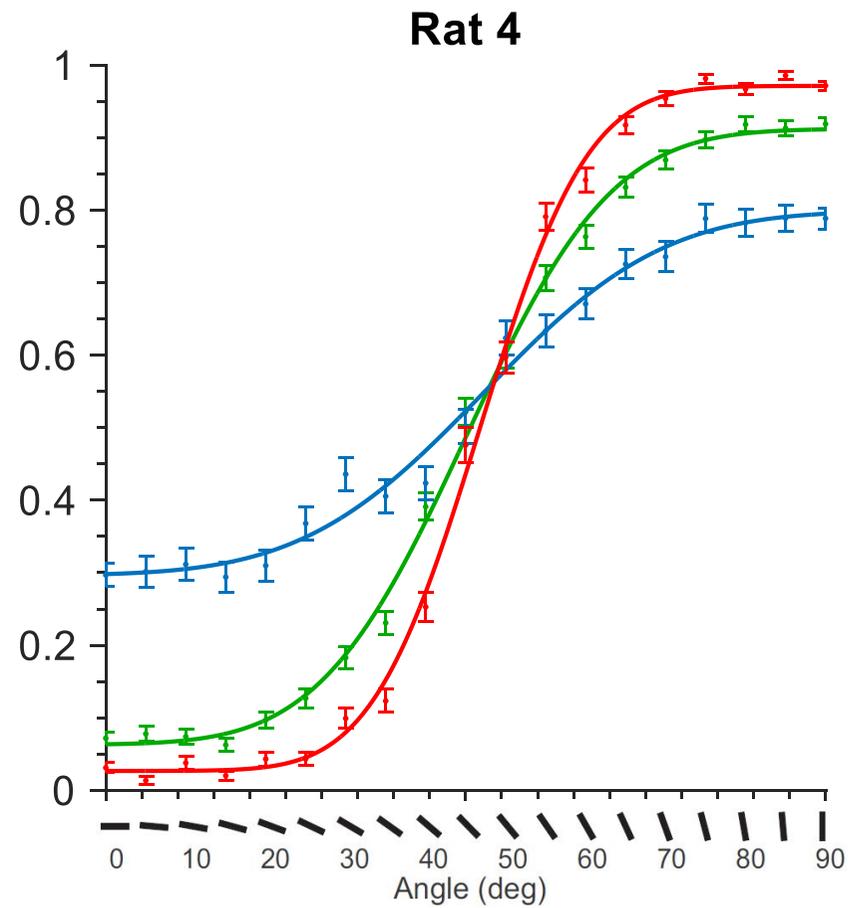
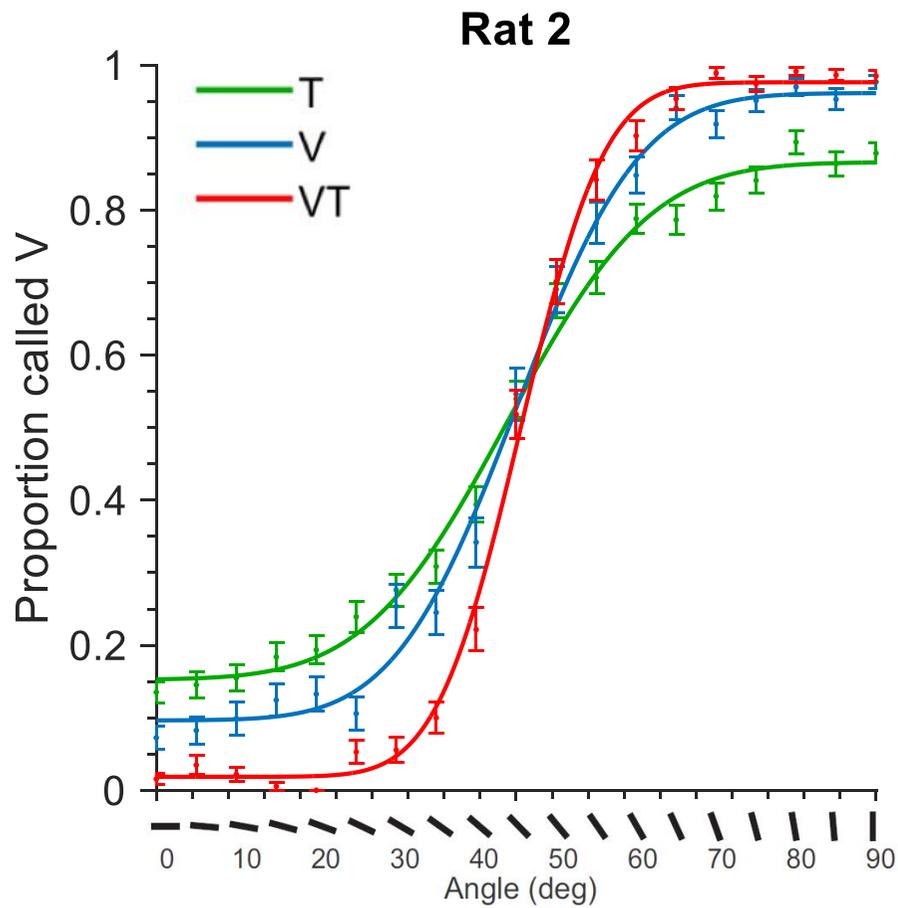


response times correlate with task difficulty

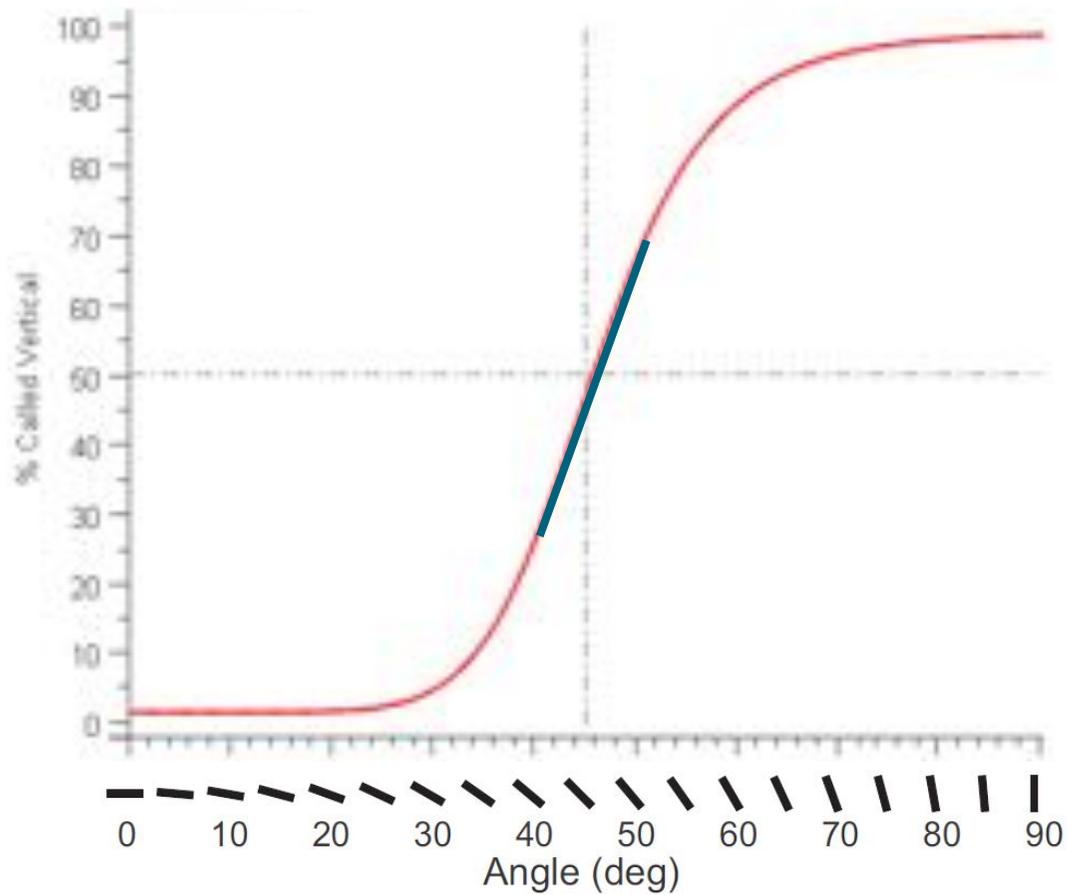
➔ *they do not “give up” on difficult trials, but try even harder*

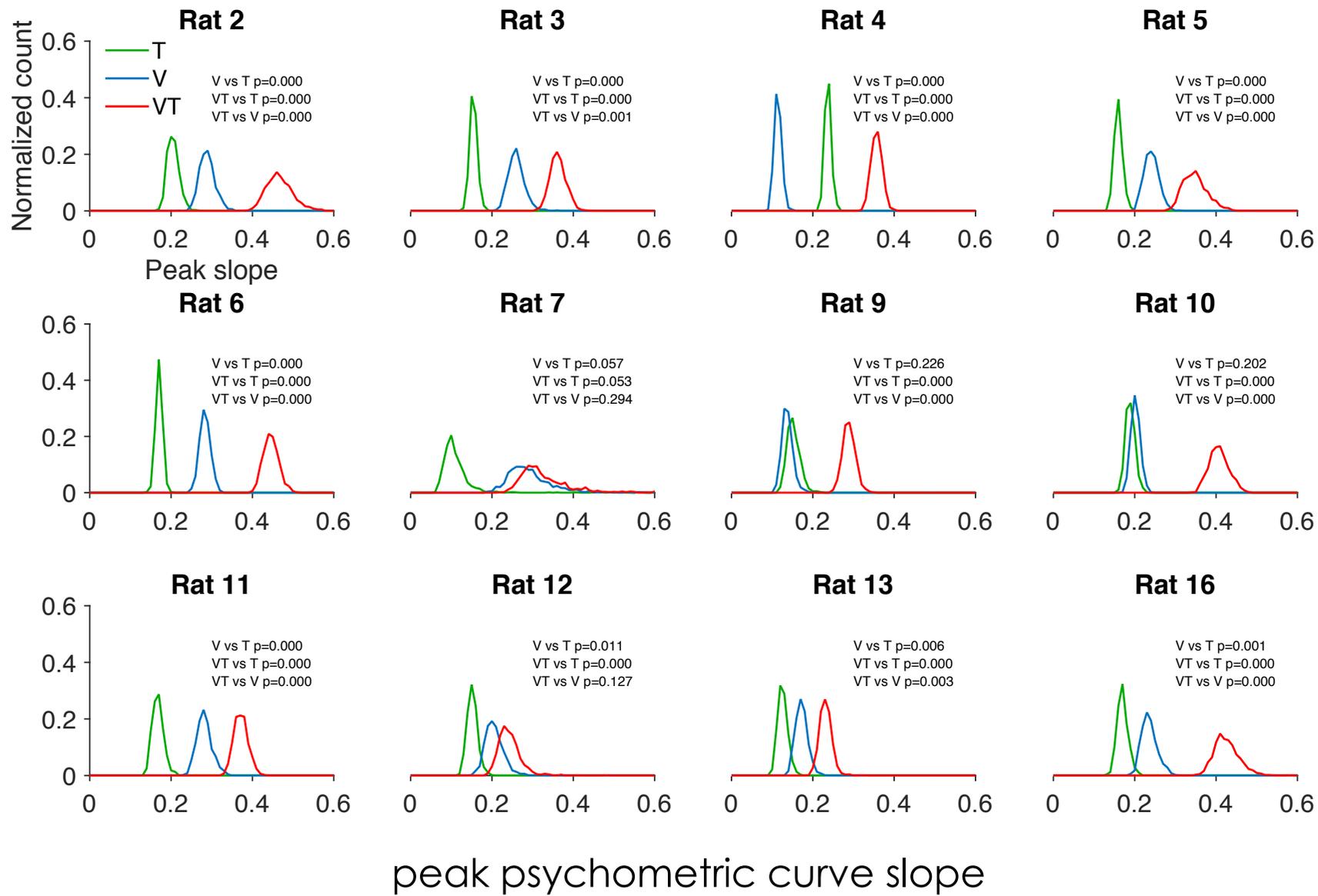


unimodal capacities vary among individual rats...  
... but always better under VT than V or T.



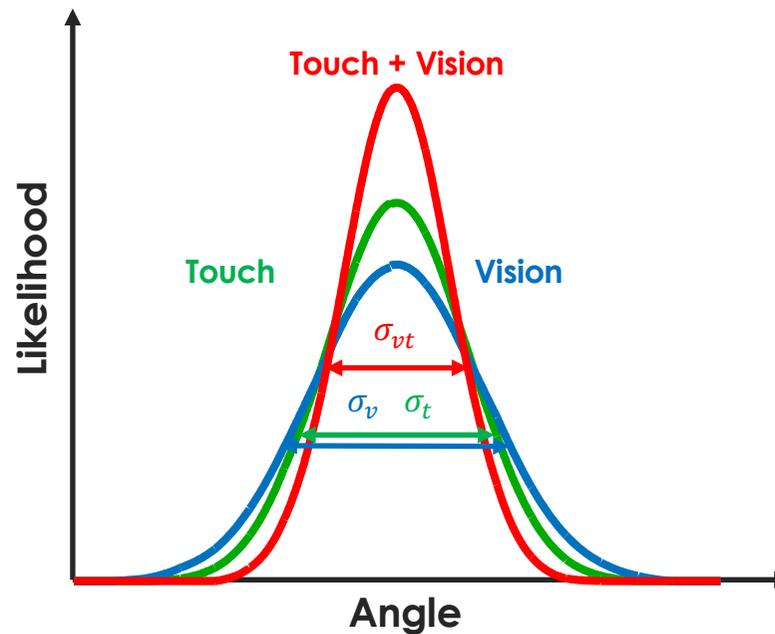
peak psychometric curve slope as single measure for of performance



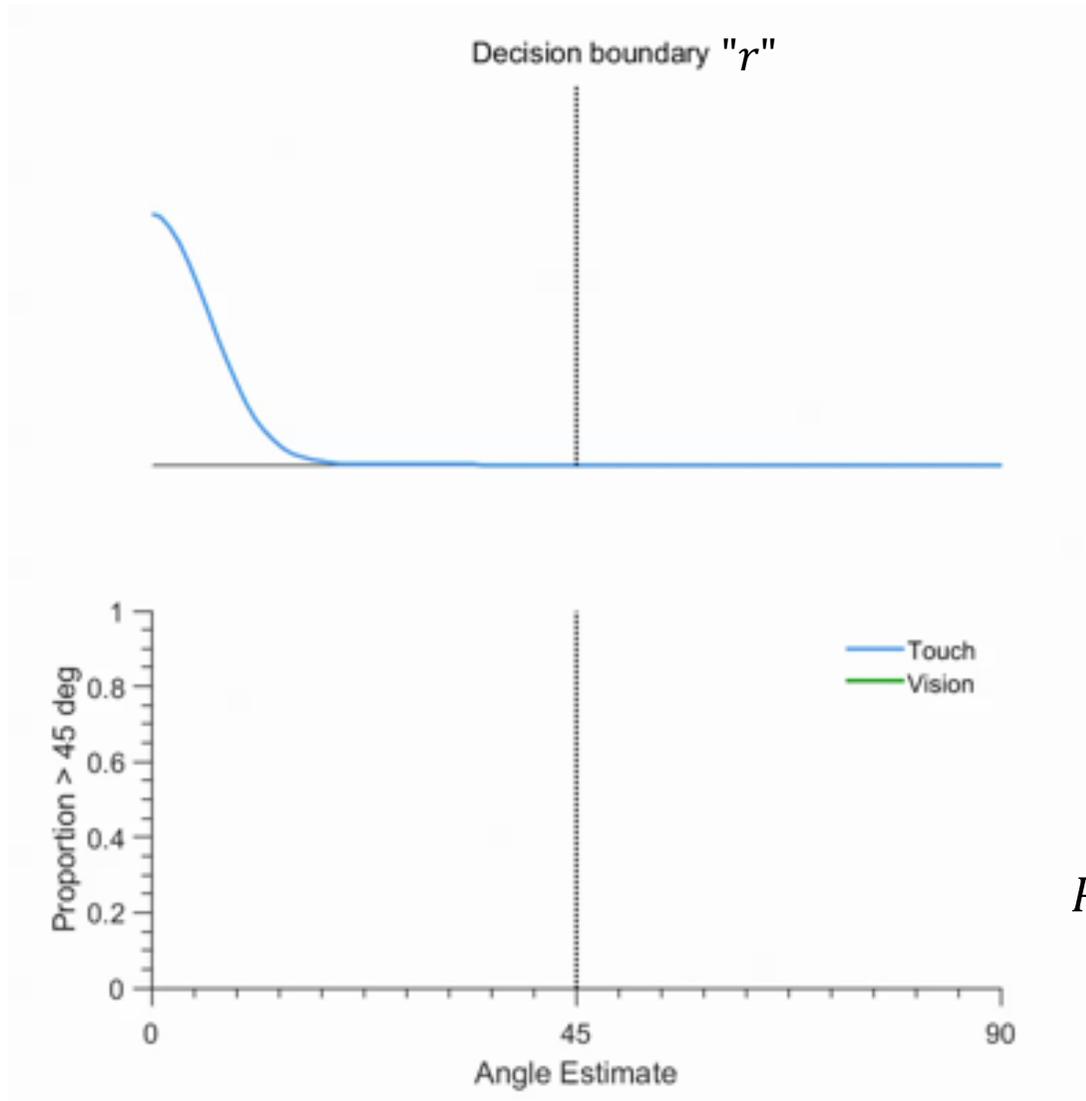


information received through the senses is inherently probabilistic

- subject is presented with a cue:  $s$
- he **estimates** some feature of that cue:  $\hat{s}$
- $\hat{s}$  is noisy and Gaussian-distributed:  $\hat{s} \sim N(\mu, \sigma^2)$
- reliability can be defined as the **inverse of variance**:  $\frac{1}{\sigma^2}$

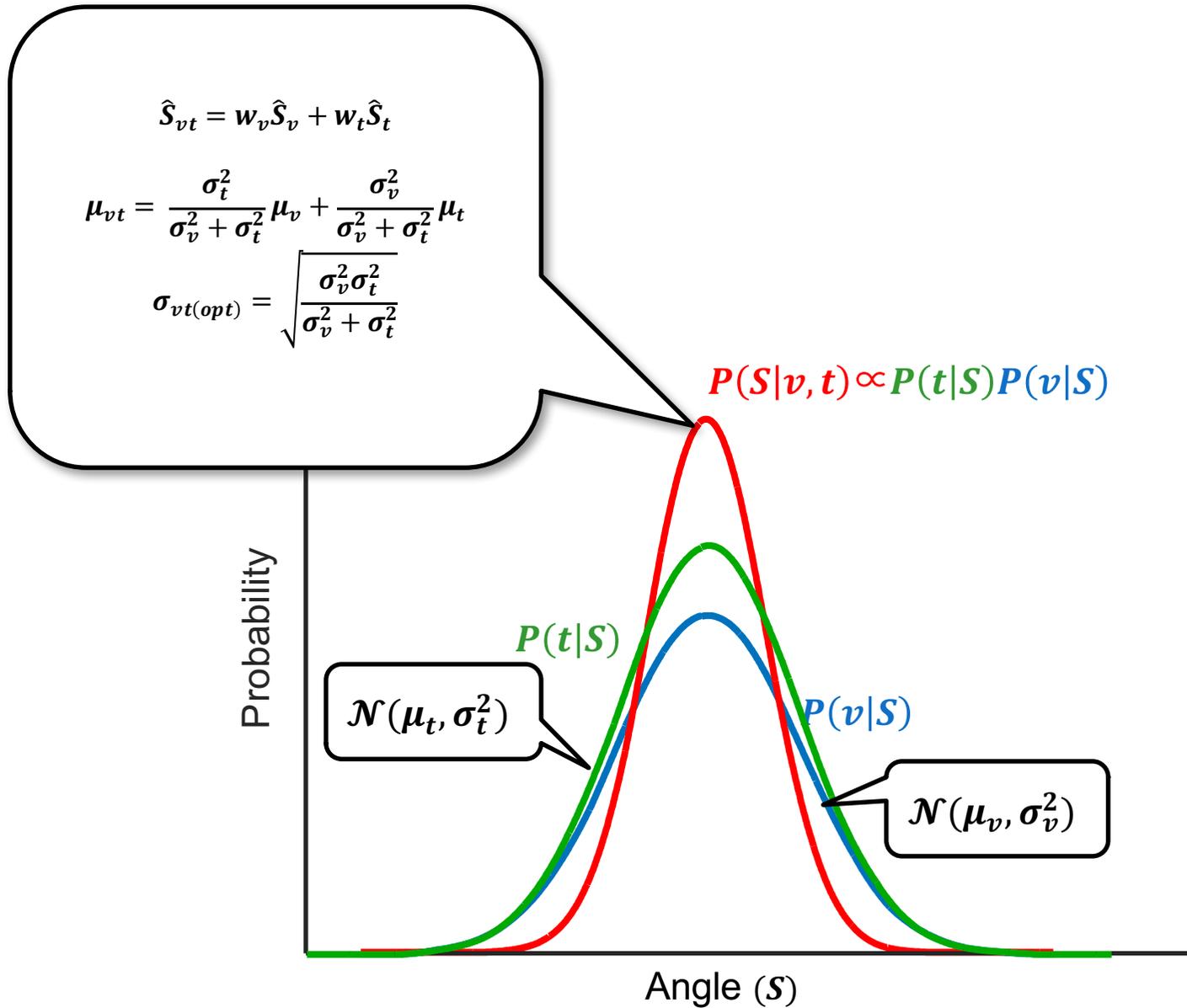


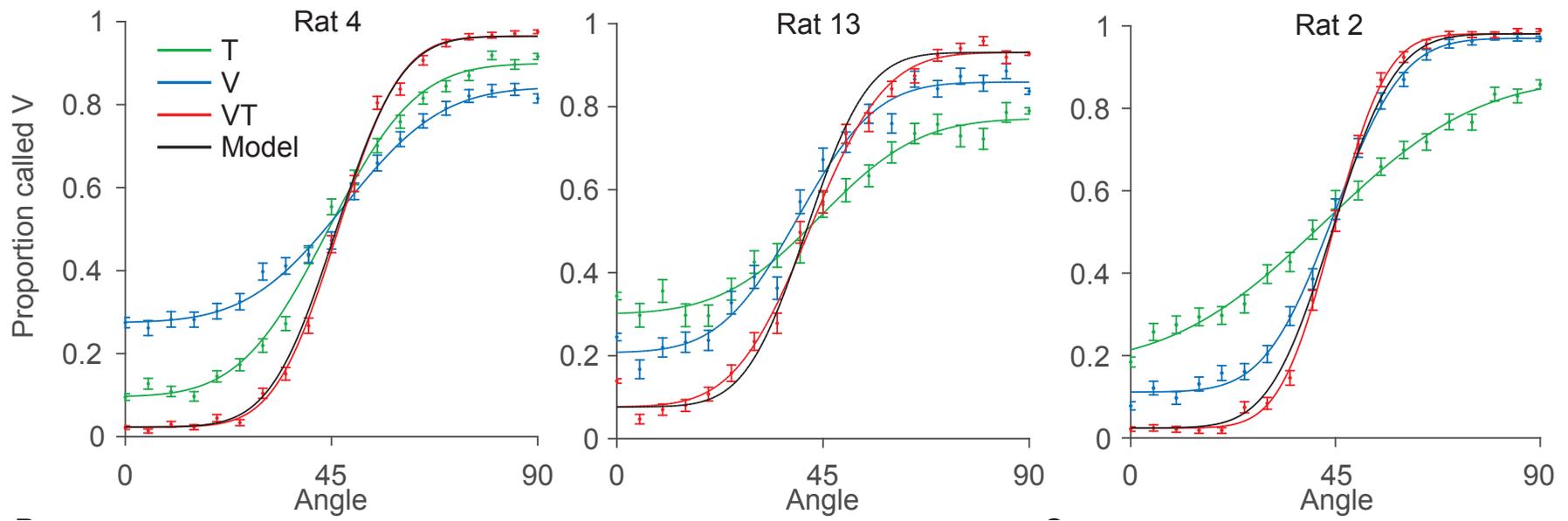
calculation of the brain is on  $\hat{s}$ : comparison between  $\hat{s}$  and a “fixed” reference: “ $r$ ”

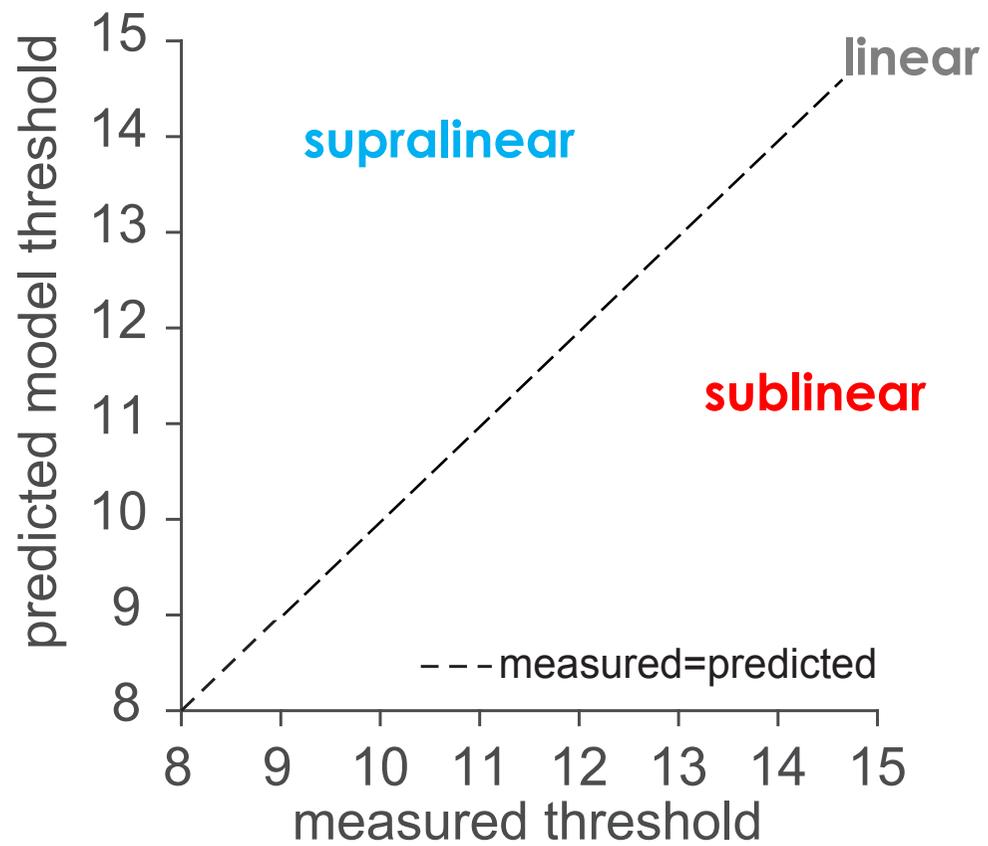


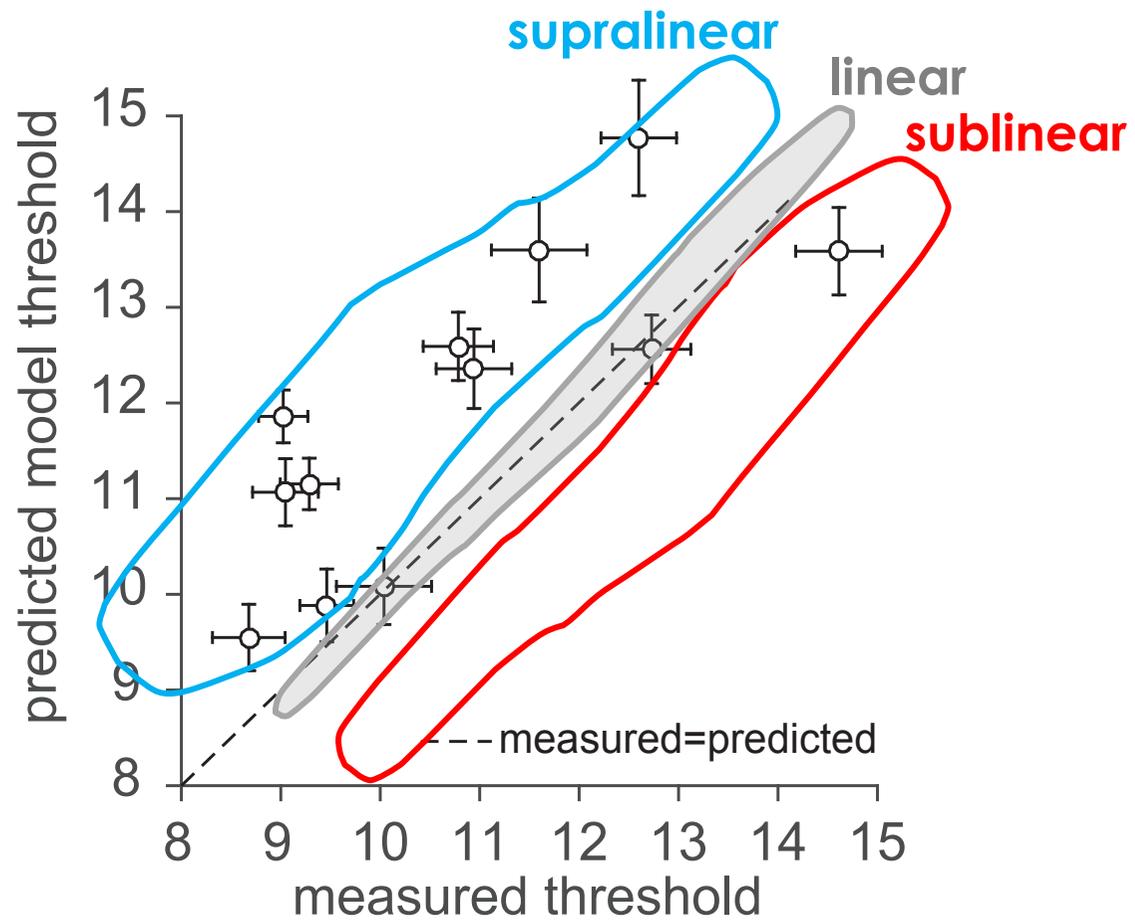
$$P(s \geq r) \equiv CDF(\hat{s}) = \int_r^{\infty} P(s) ds$$

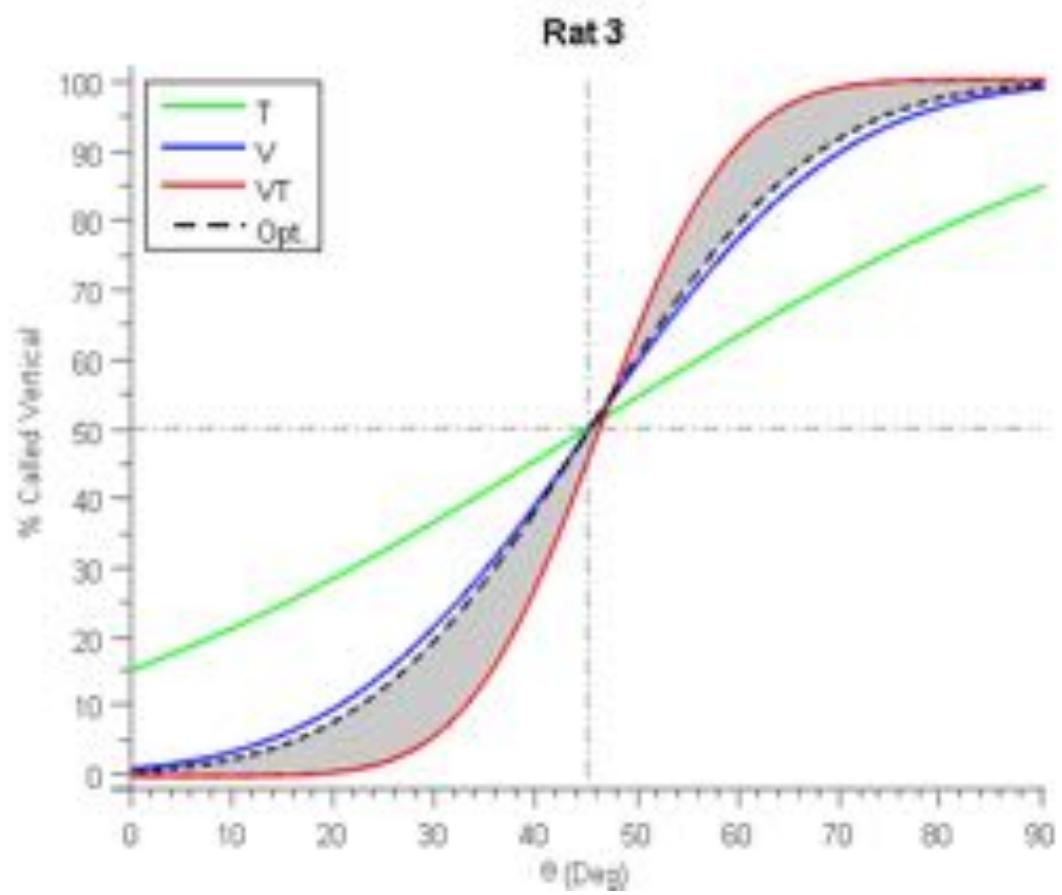
# Bayesian approach







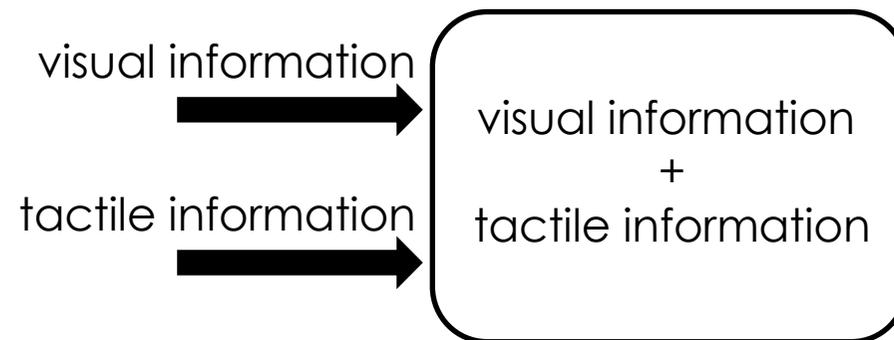




**a second approach to testing linearity**

we treat V and T as two channels that provide the rat with streams of information

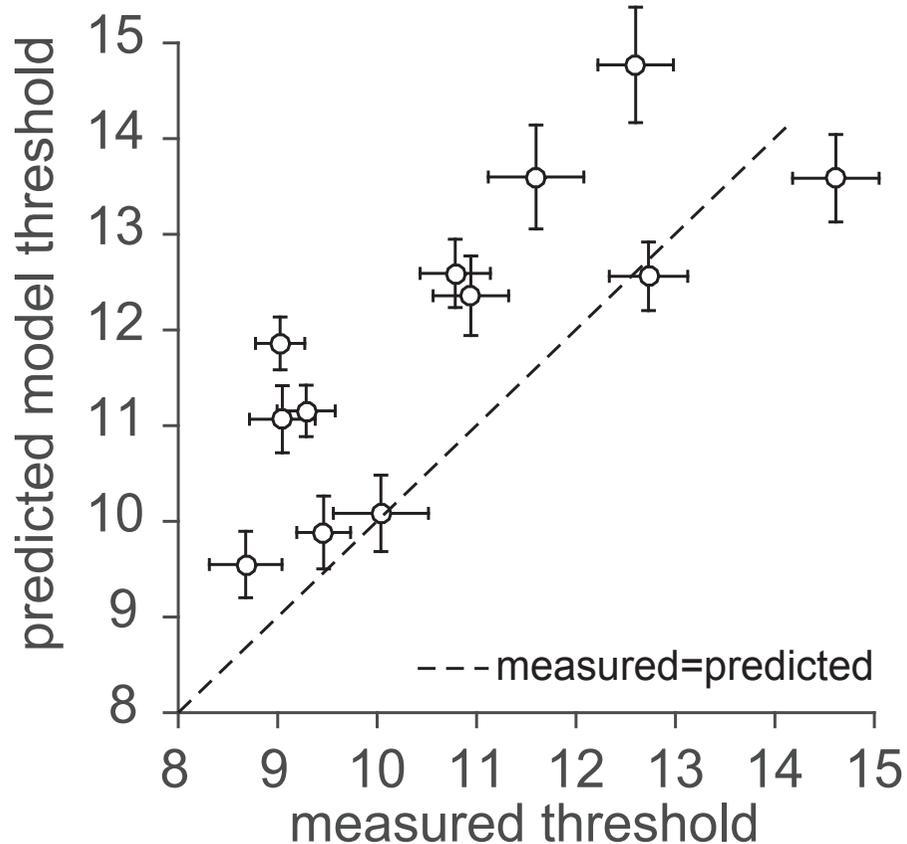
- assumes that the <sup>1</sup>information present within the sensory channels is converted directly into a choice.
- compute Shannon's Mutual Information between stimulus category (horizontal or vertical) and behavioral choice in each modality separately, V and T. Thus, 100% behavioral accuracy implies 1.0 bits of sensory information, 50% (chance) accuracy implies 0 bits.
- then we compute the quantities predicted by the linear combination of V and T signals.



# Information channel model

*within-rat consistency across models*

## Bayesian model



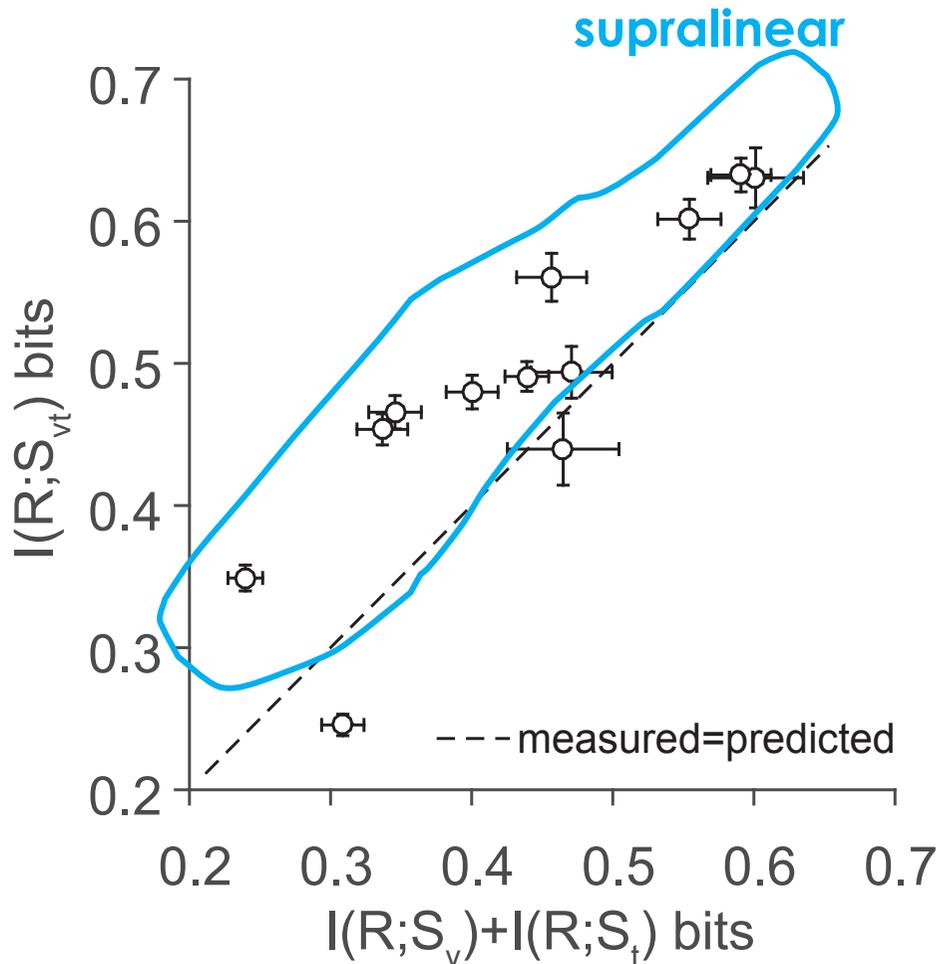
visual information



tactile information



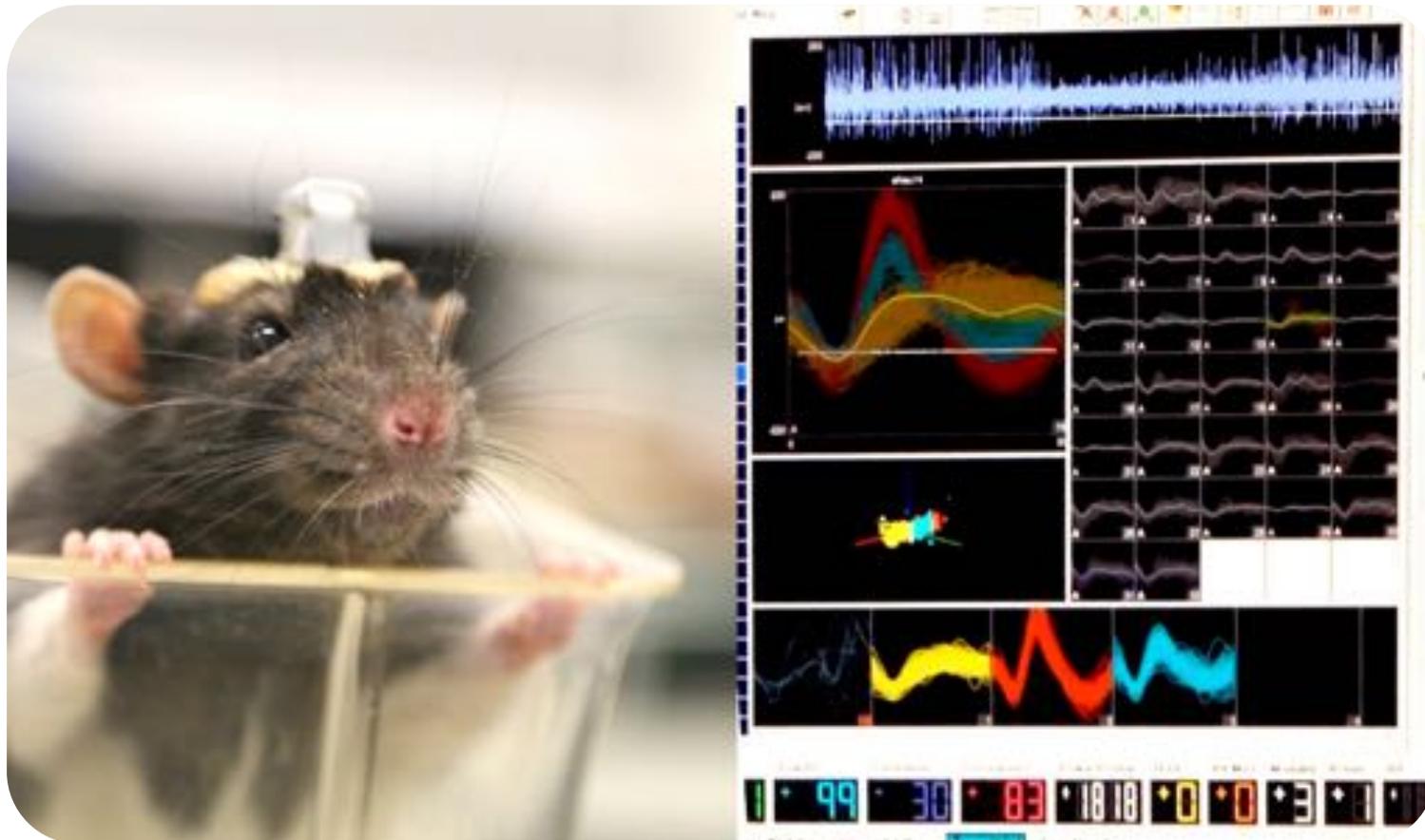
visual information  
+  
tactile information

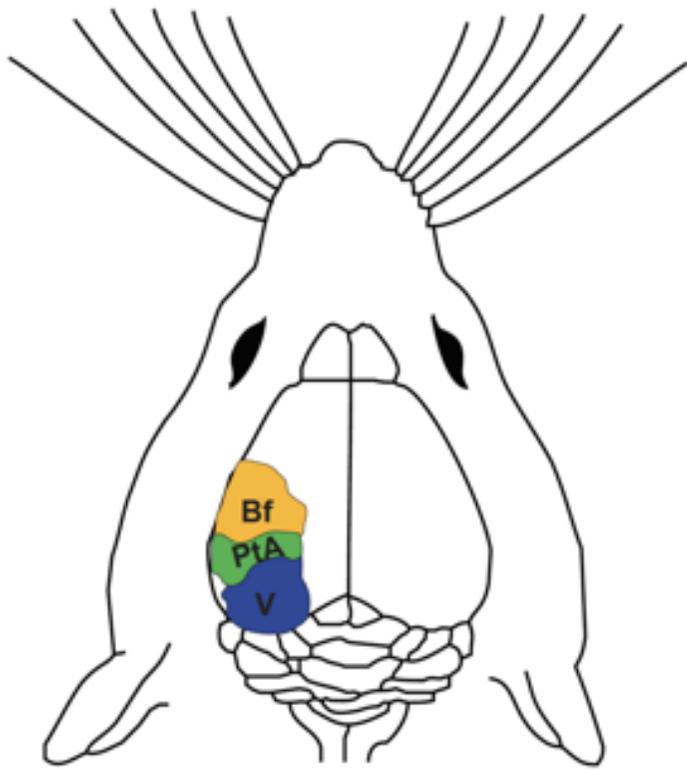


How can performance achieve supralinearity?

# Behavior

# Neurons





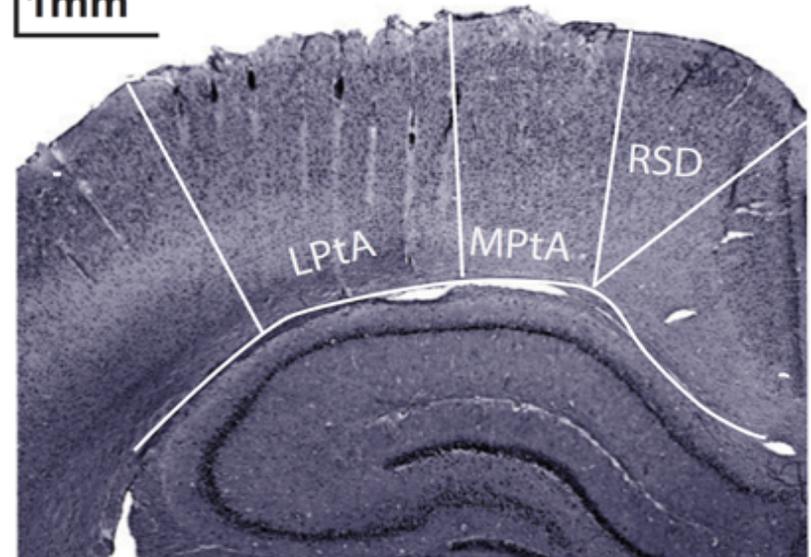
Bf: Barrel Field

PtA: Parietal Association Area

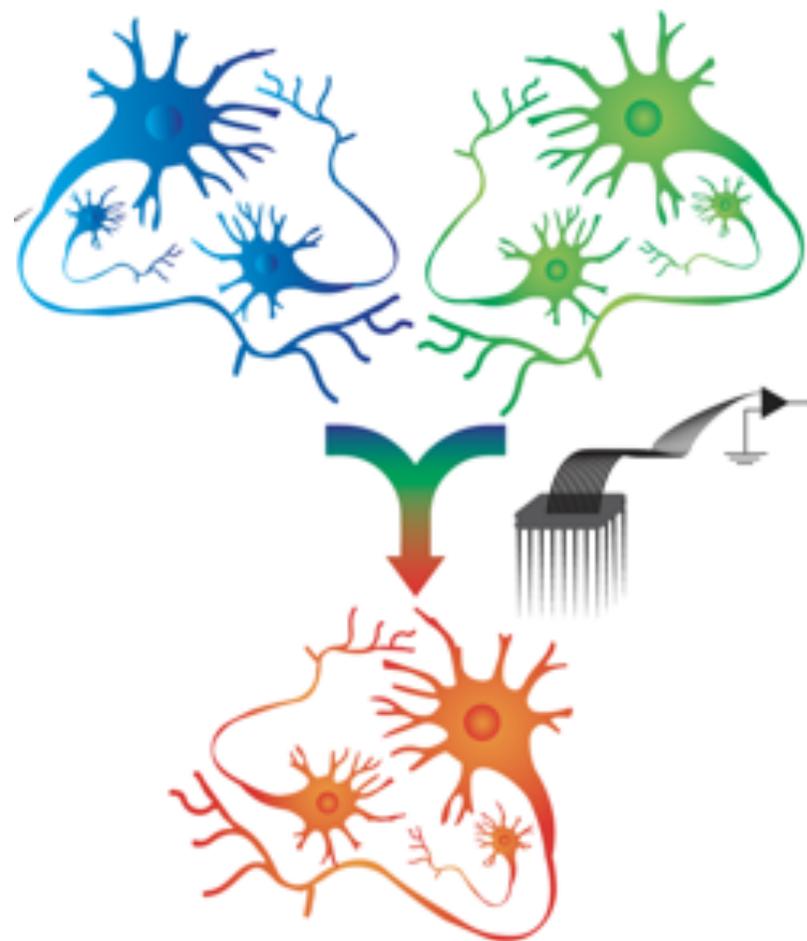
V: Visual Cortex



1mm

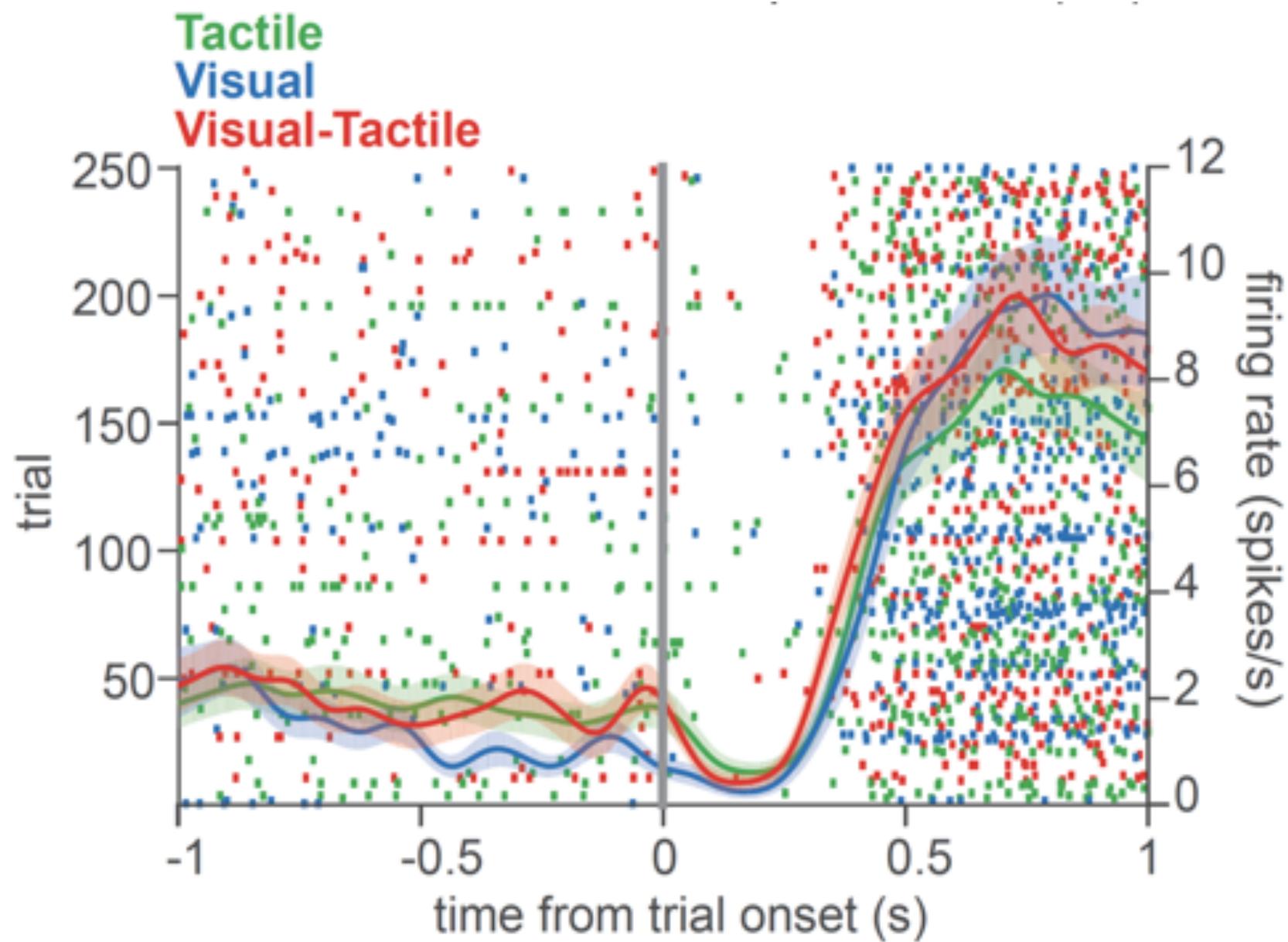


622 neurons from 5 animals

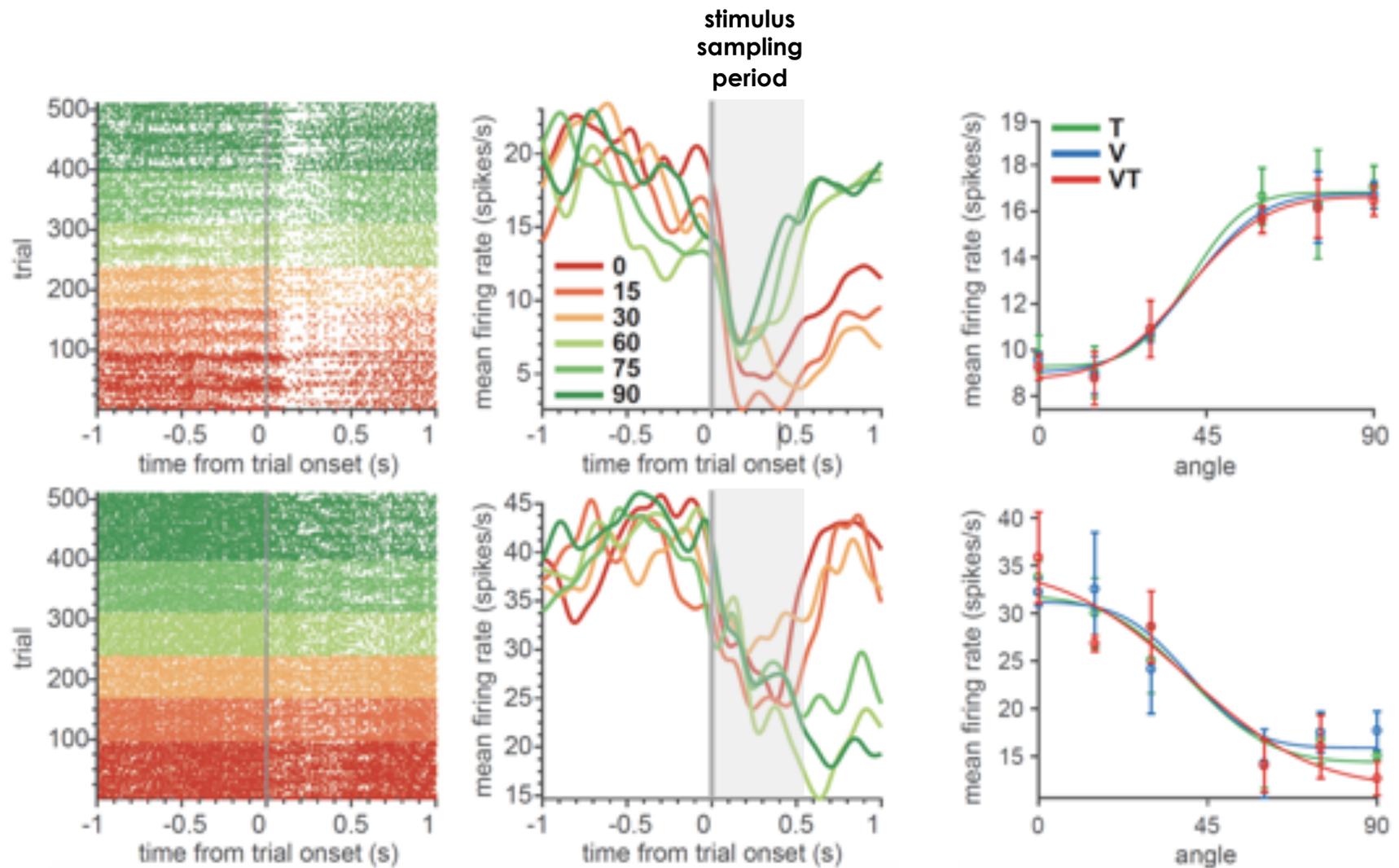


unimodal cortical  
representations

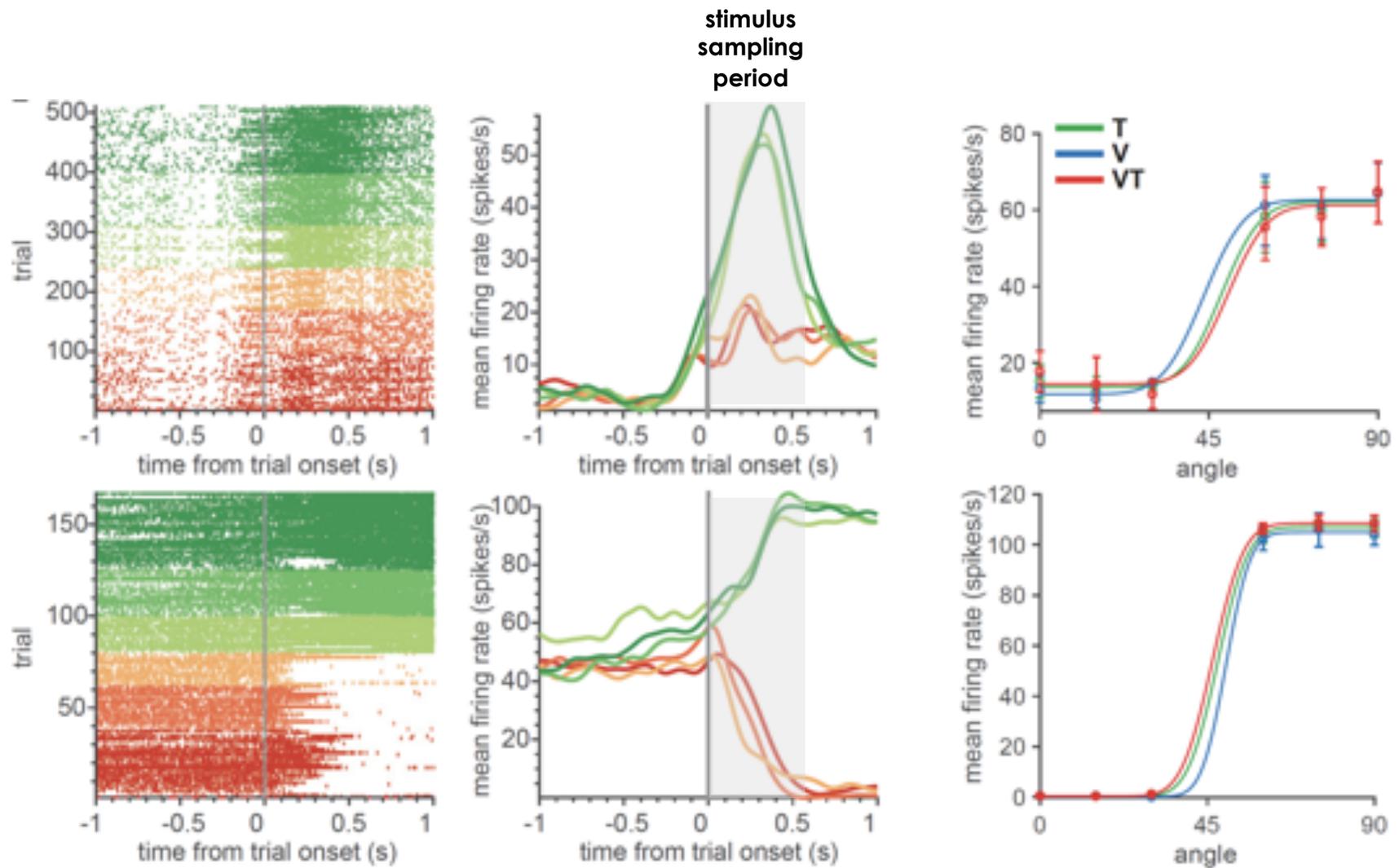
modality-shared  
representation of  
orientation and  
category in PPC



in 185 out of 622 neurons, trial-to-trial firing rate variations were best accounted for by stimulus orientation.

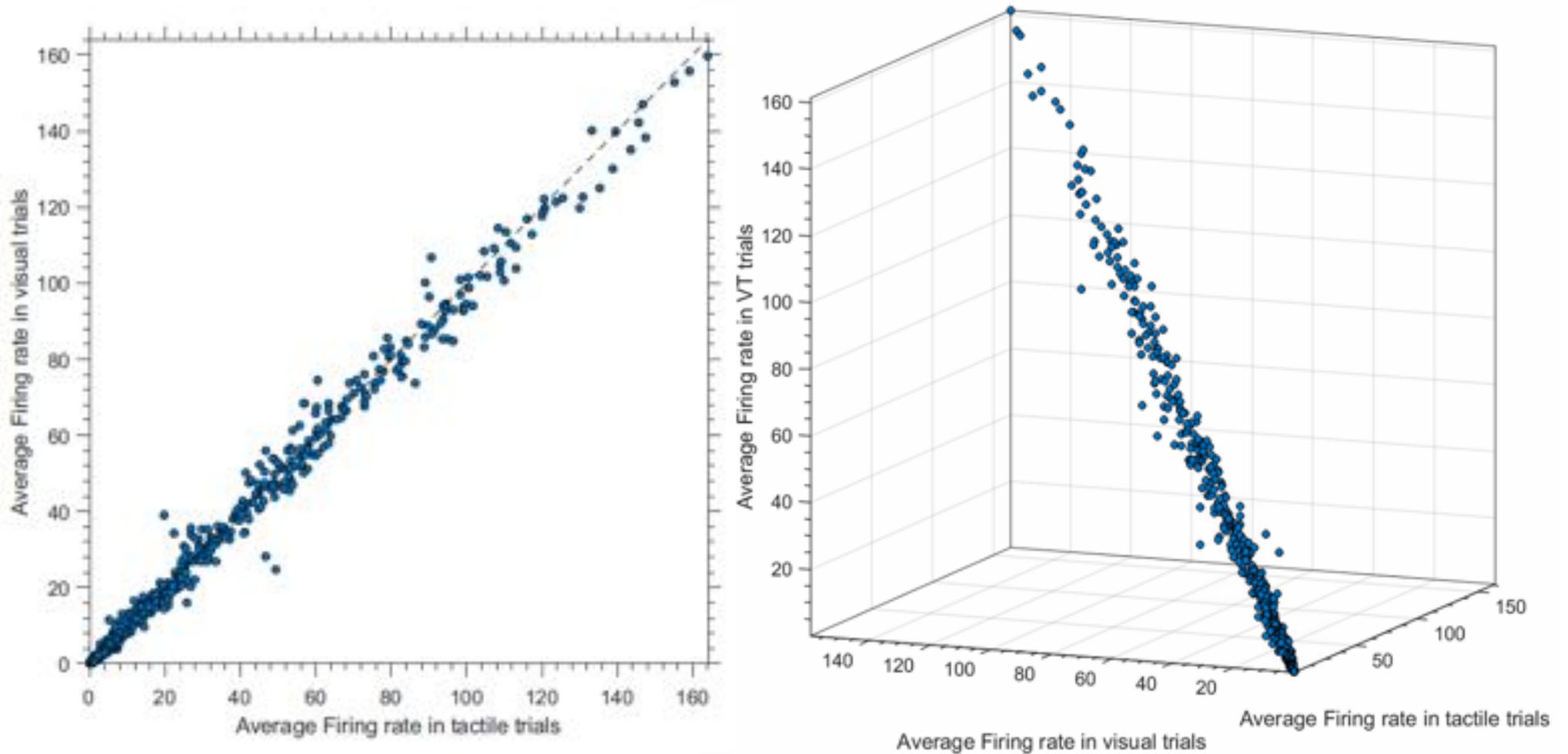


in 251 out of 622 neurons, trial-to-trial firing rate variations were best accounted for by upcoming behavioral choice.

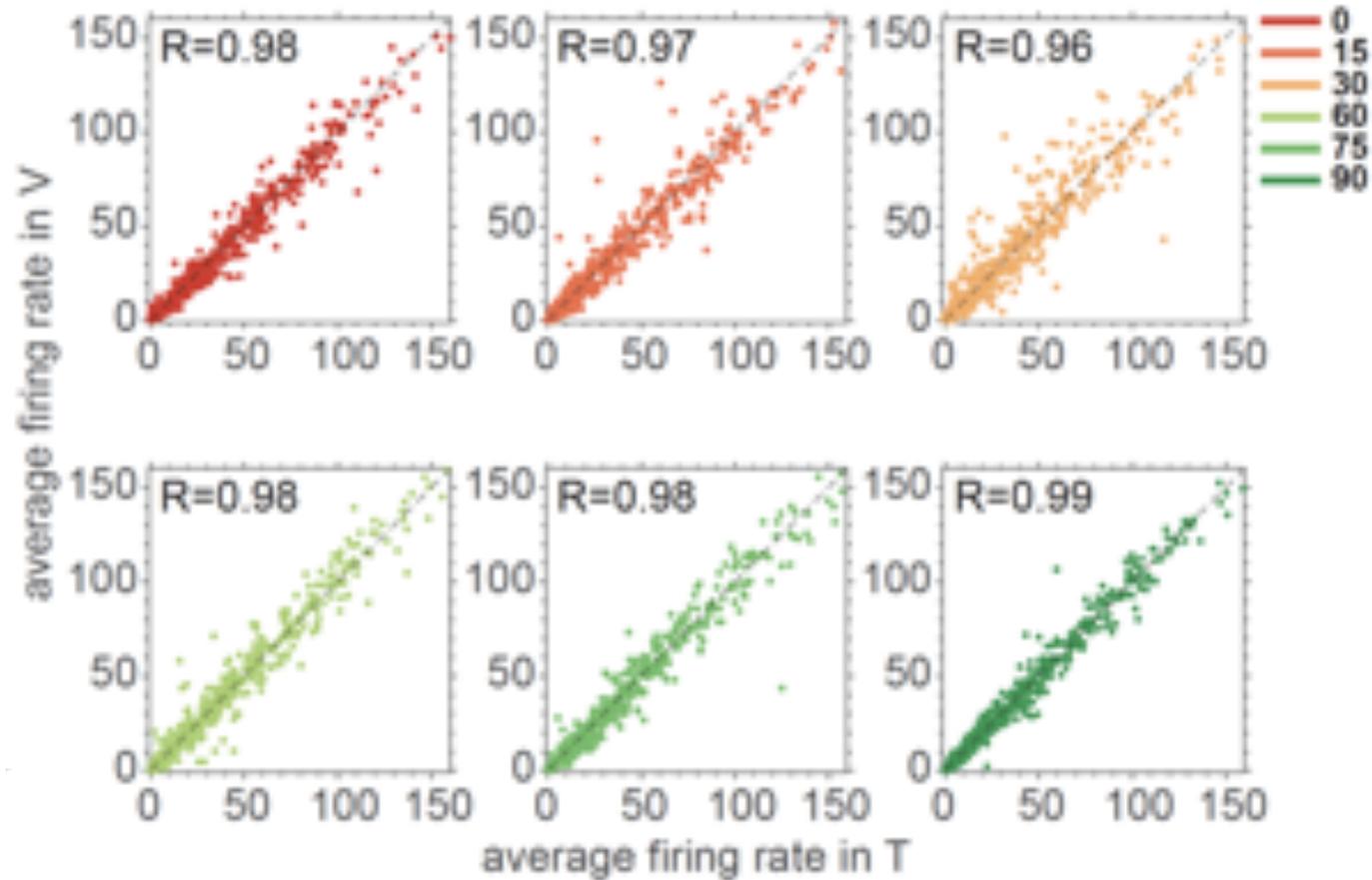


# neuronal responses are supramodal

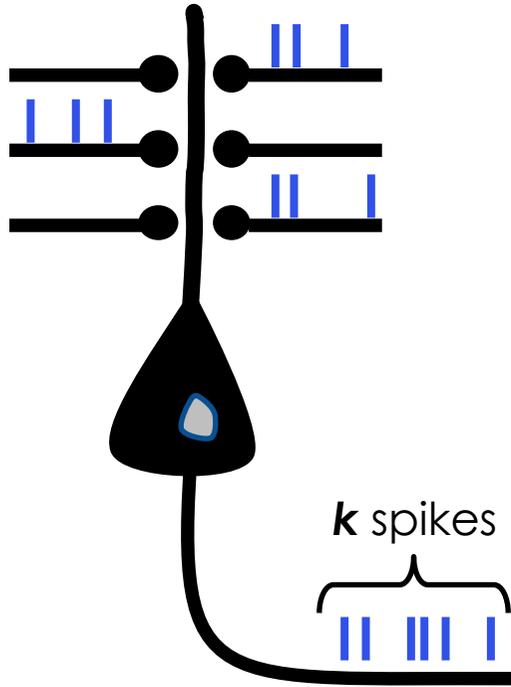
average FR in 400 ms window preceding the response lick



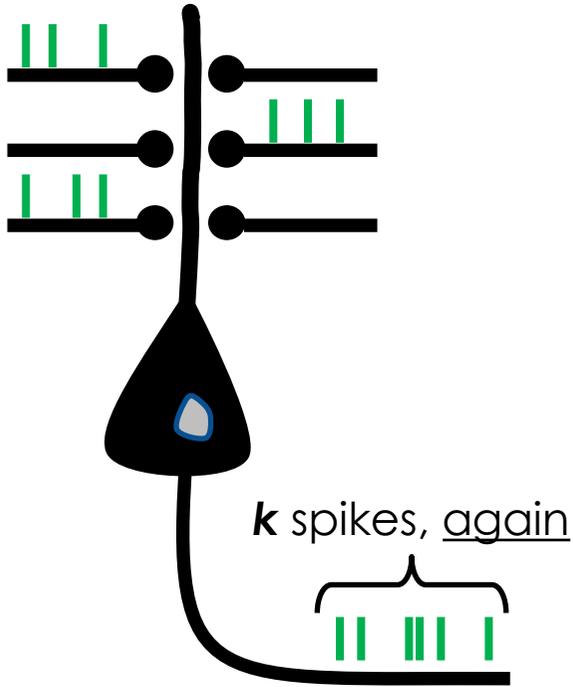
... neuronal responses are supramodal across all angles



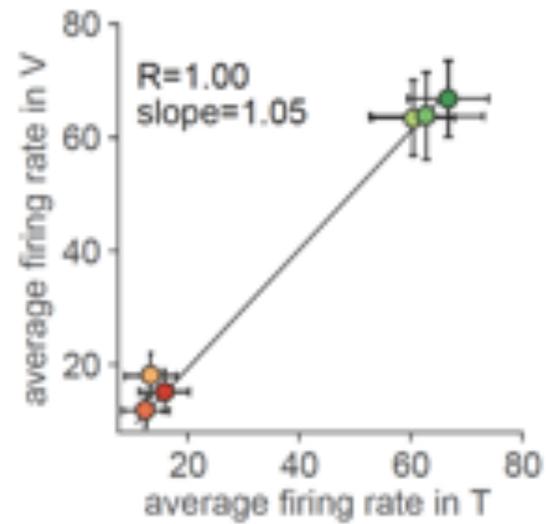
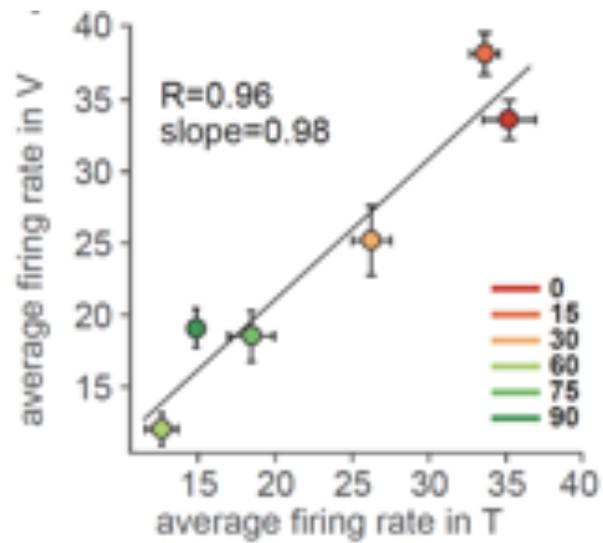
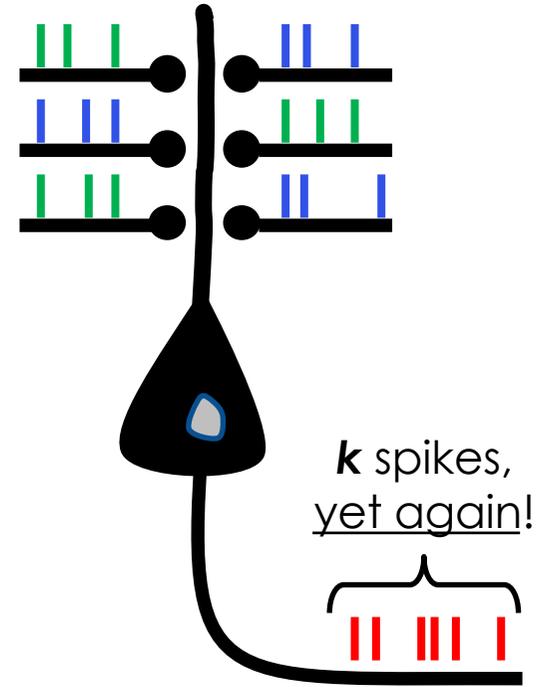
visual trial



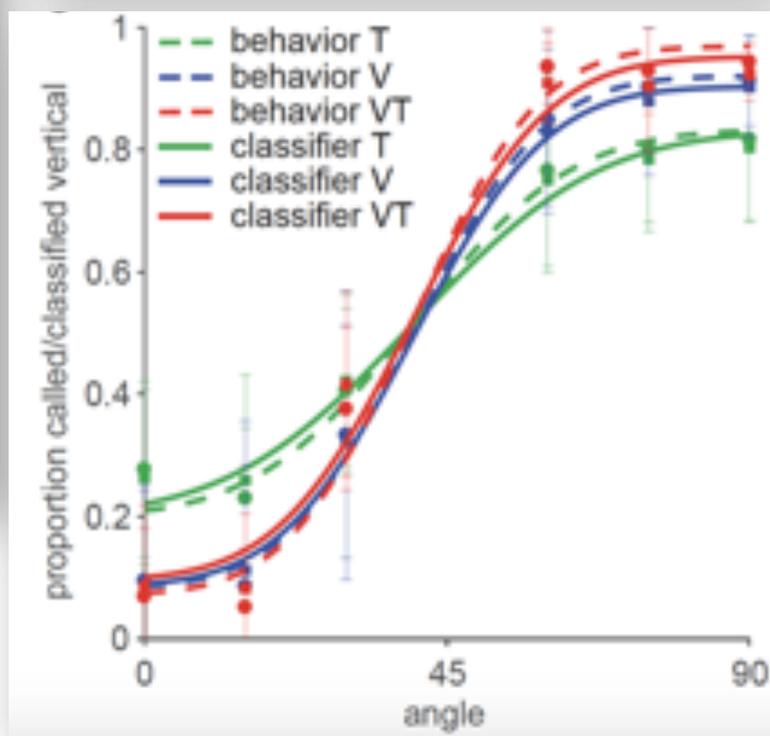
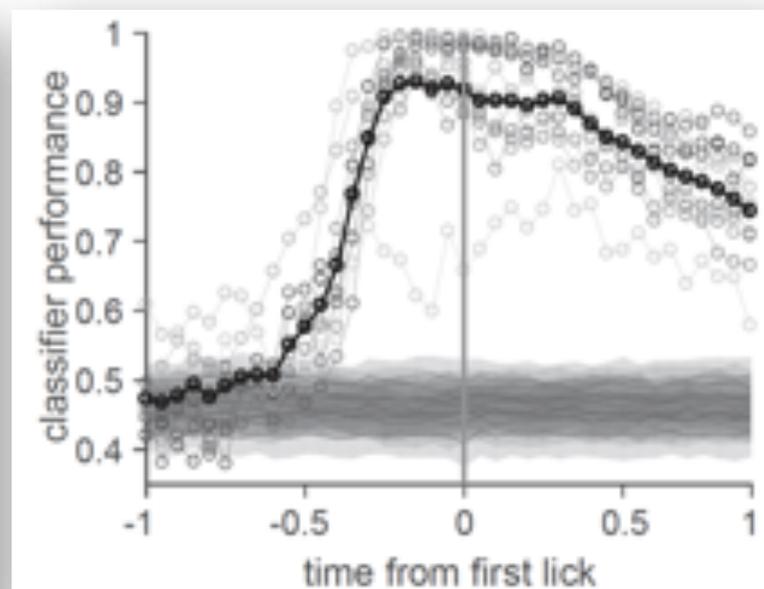
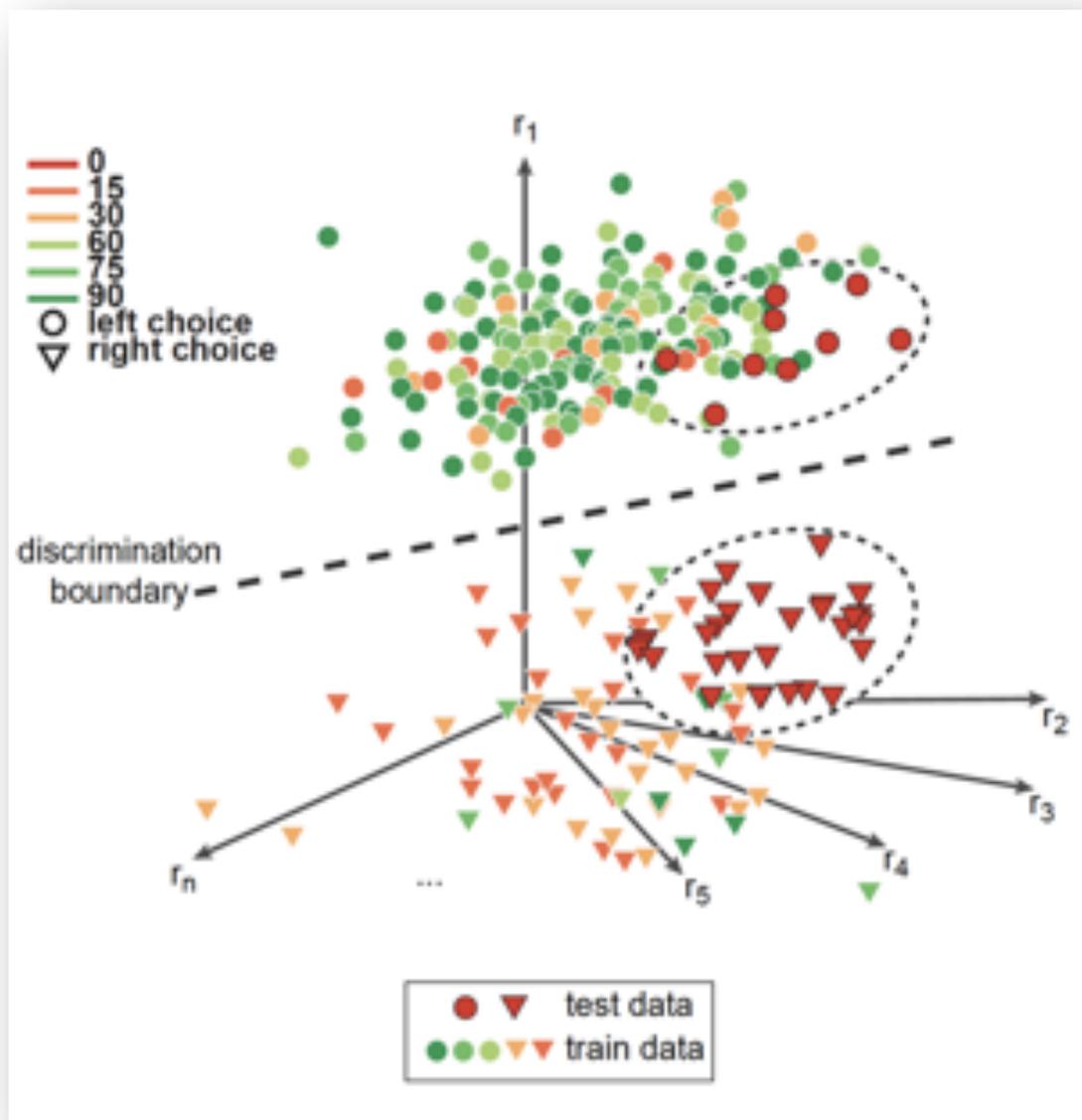
tactile trial



visual tactile trial



are these neurons merely correlated with sensory inputs but not truly the basis for multimodal integration and decision making?



How can  $1 + 1 > 2$ ?  
How can synergy occur?

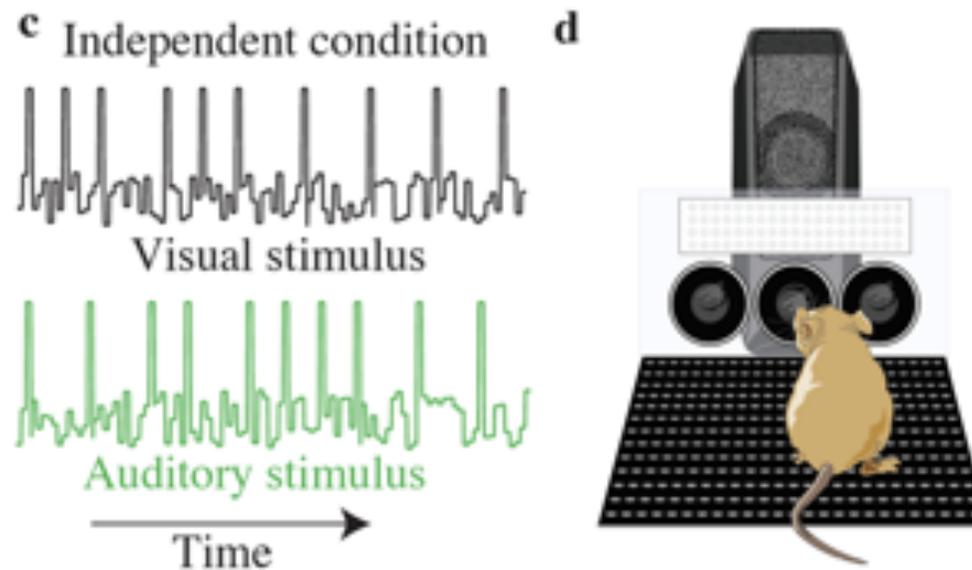
Two hypotheses come to mind:

- sensorimotor interaction
- intracortical interaction

# A category-free neural population supports evolving demands during decision-making

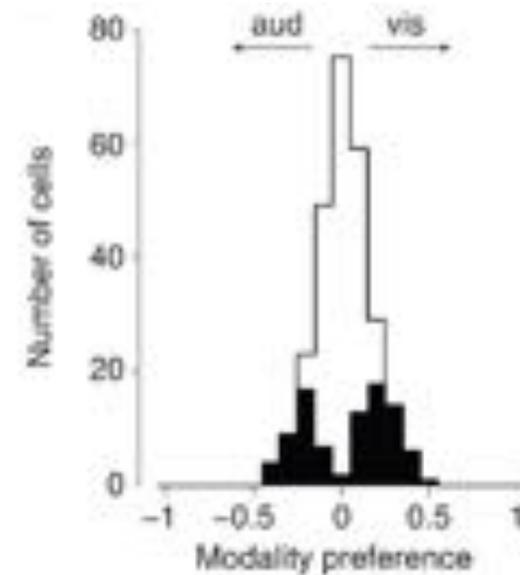
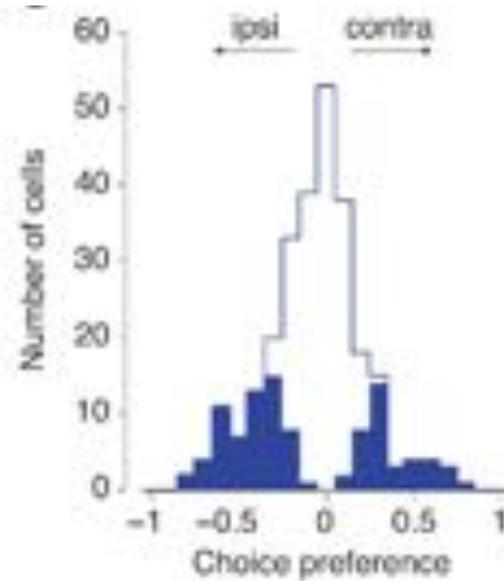
David Raposo, Matthew T Kaufman & Anne K Churchland

count uncorrelated trains of visual and auditory pulses

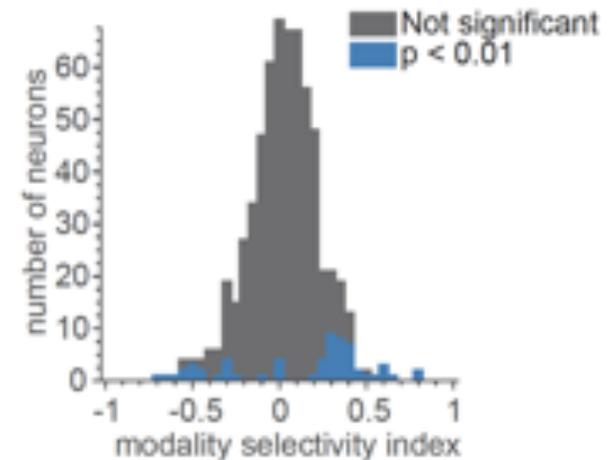
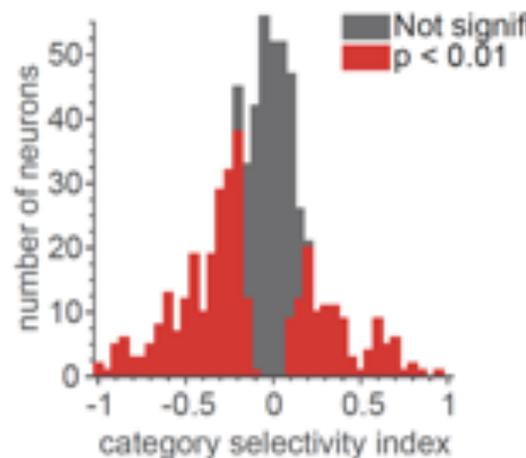


# A category-free neural population supports evolving demands during decision-making

David Raposo, Matthew T Kaufman & Anne K Churchland

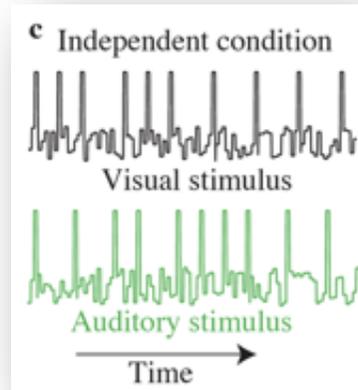


**our study**



Raposo et al.

count independent  
visual and auditory  
pulse trains



Nikbakht and Diamond

see and touch real thing



sensory tuning (code)?

not really

yes

category (choice)?

yes

yes

modality synergy  
(supralinearity)?

spotty

robust

modality specificity?

yes

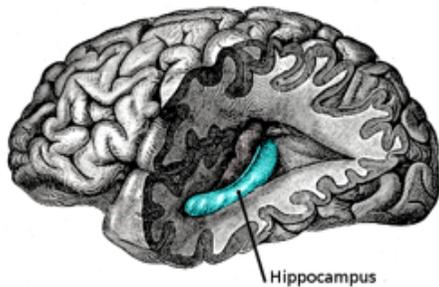
no

While these findings speak to the question of augmenting the reliability of unimodal signals – a means for reducing uncertainty – they also speak to the question of how modality-independent knowledge is created.

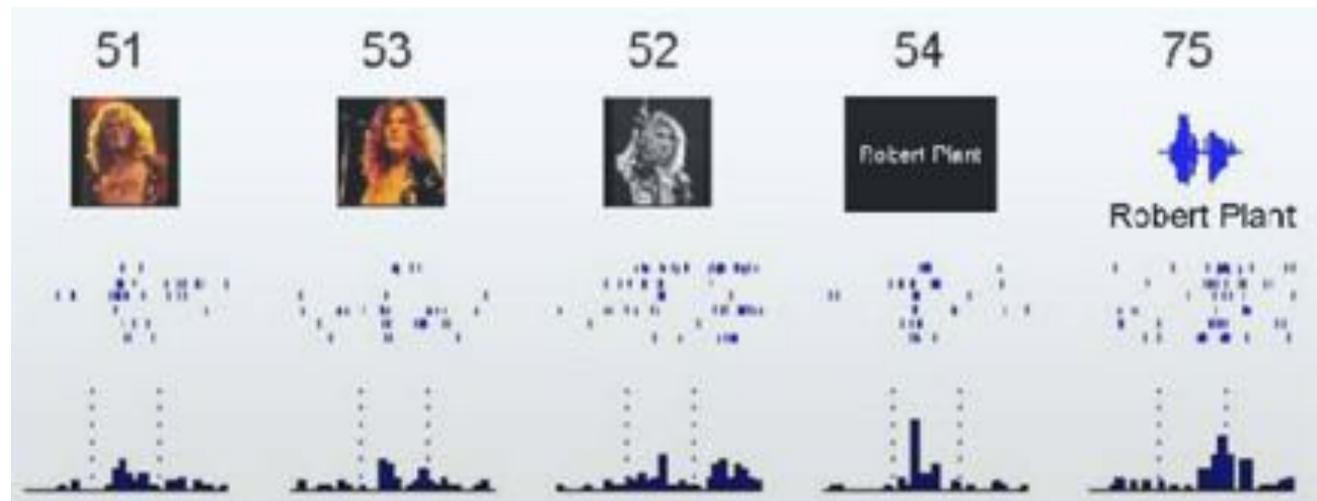
## KNOWLEDGE

Most of the things we know, we come to know through multiple modalities

### *human hippocampus*

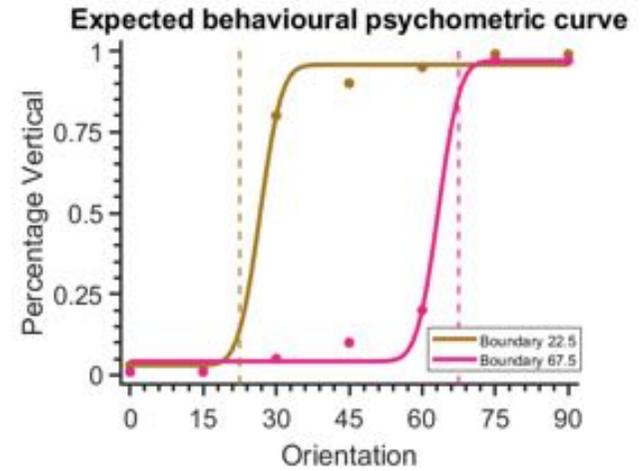
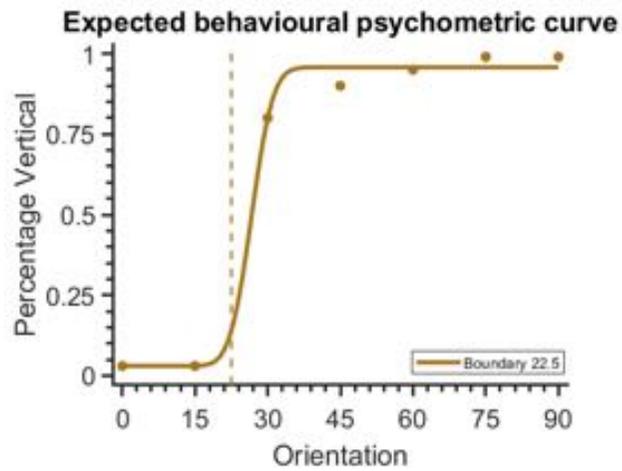


Henry Gray (1918)  
*Anatomy of the  
Human Body*



Quiroga et al. (2010)



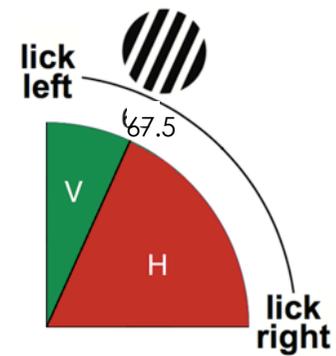
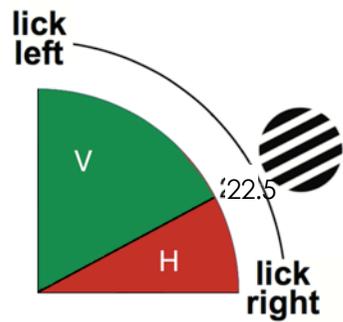


SHIFT

0

n

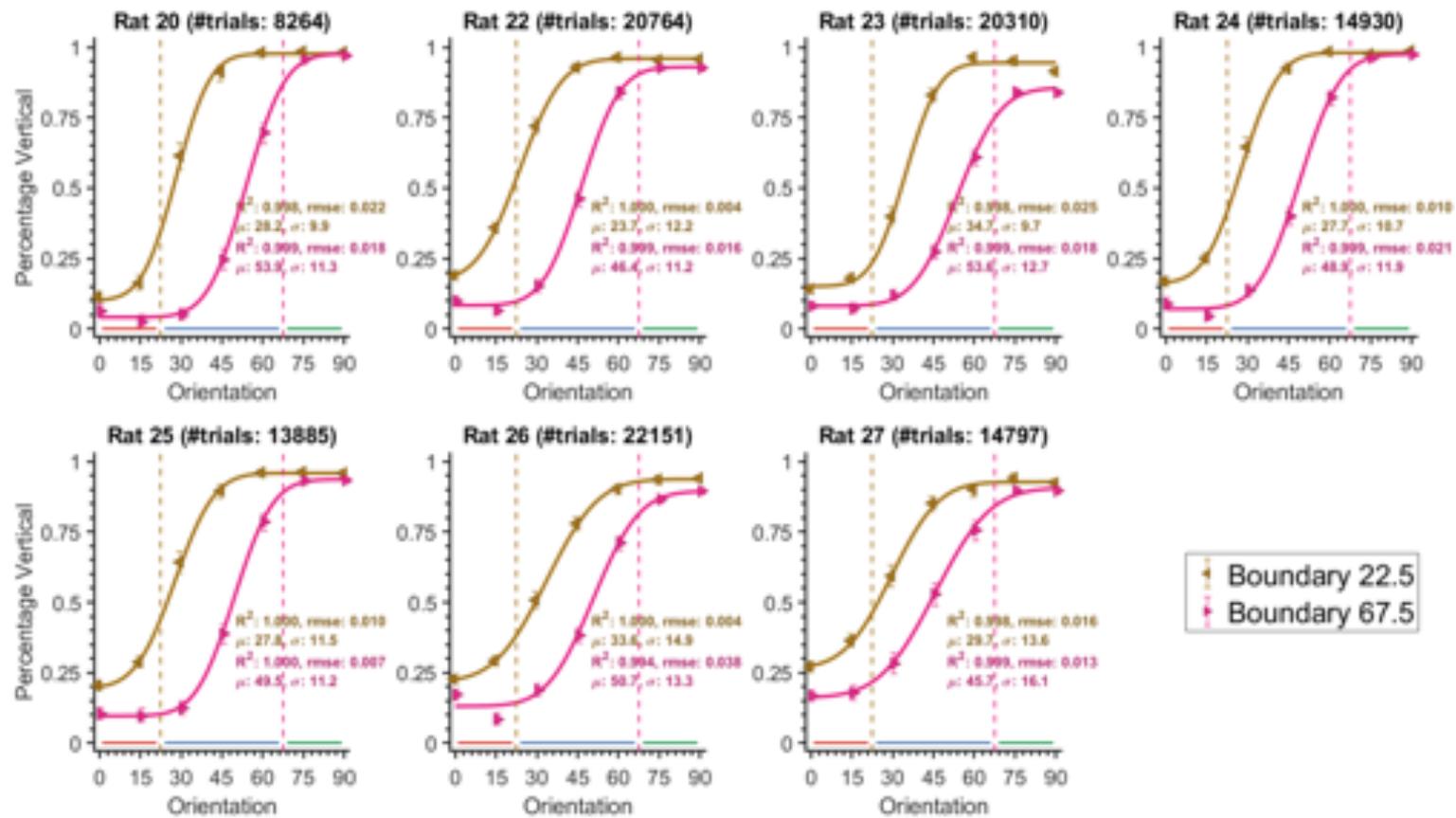
trials



Marco Bigica



# Behavioral performance



## reflections...



- modality convergence can reduced single-modality uncertainty
- modality invariance – a step in the abstraction of stimuli from sensory domains ('Robert Plant')??
- not hardwired... emerges from interaction with real things
- besides supramodal knowledge, PPC circuitry also might shed light on the percept-to-action transformation.