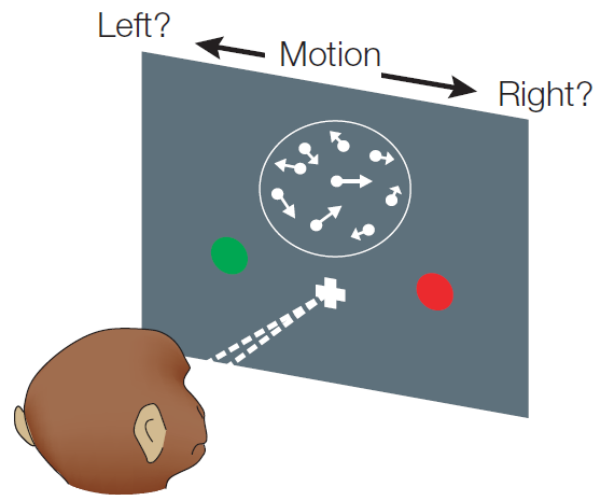


A vibrant fruit market stall with various tropical fruits. The stall is filled with a wide variety of produce, including mangoes, dragon fruit, pineapples, watermelons, and papayas. The fruits are arranged in neat piles and baskets, creating a colorful and appetizing display. The background shows more fruit hanging from the stall's structure.

Decision-making & behavior

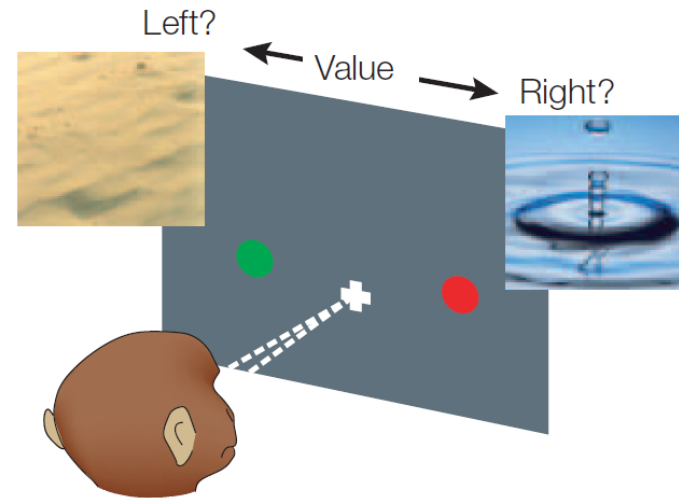
Decision-making & behavior

Perceptual judgment



- Sensory evidence

Value-based decisions



- Cost/benefit
- Value (utility)

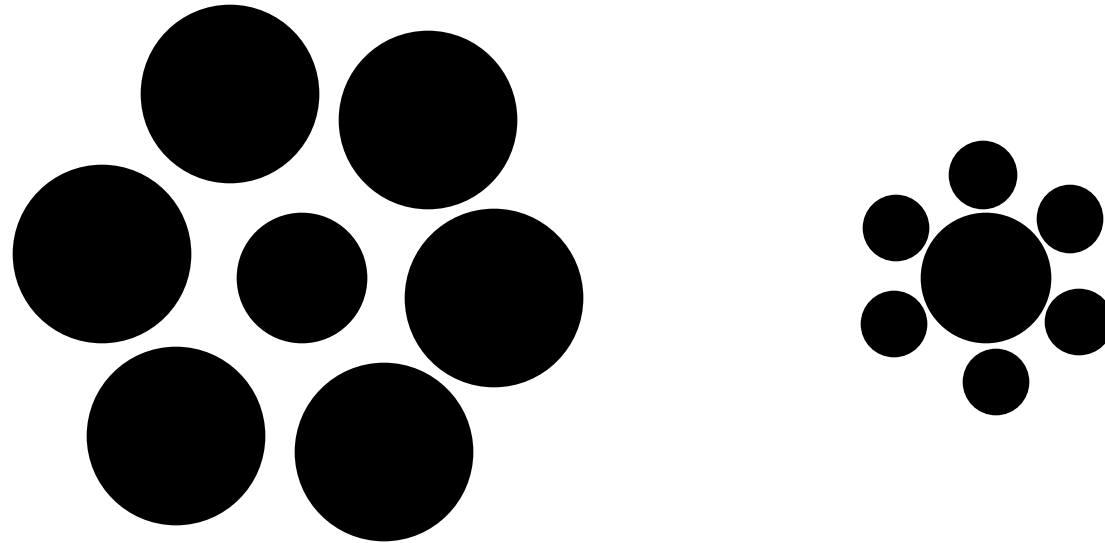
Perception, neural activity, decisions:

- How do neurons respond to sensory stimuli?
- What is the relationship between our perception and neural activity?
- How do sensory responses drive behavior?

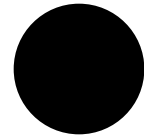
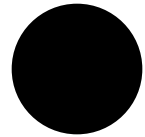
Goals of studying sensory processing with decision making:

- basic principles of how the brain “processes” information – *can you draw the pathways involved (vision; from the retina to visual cortex)* – and how perception changes decisions
- quantitative ways to analyze neural activities: *how would you design an experiment and compute a tuning curve of a neuron? How would you design an experiment to test perception on decisions?*

Perceptions shape beliefs (decisions)

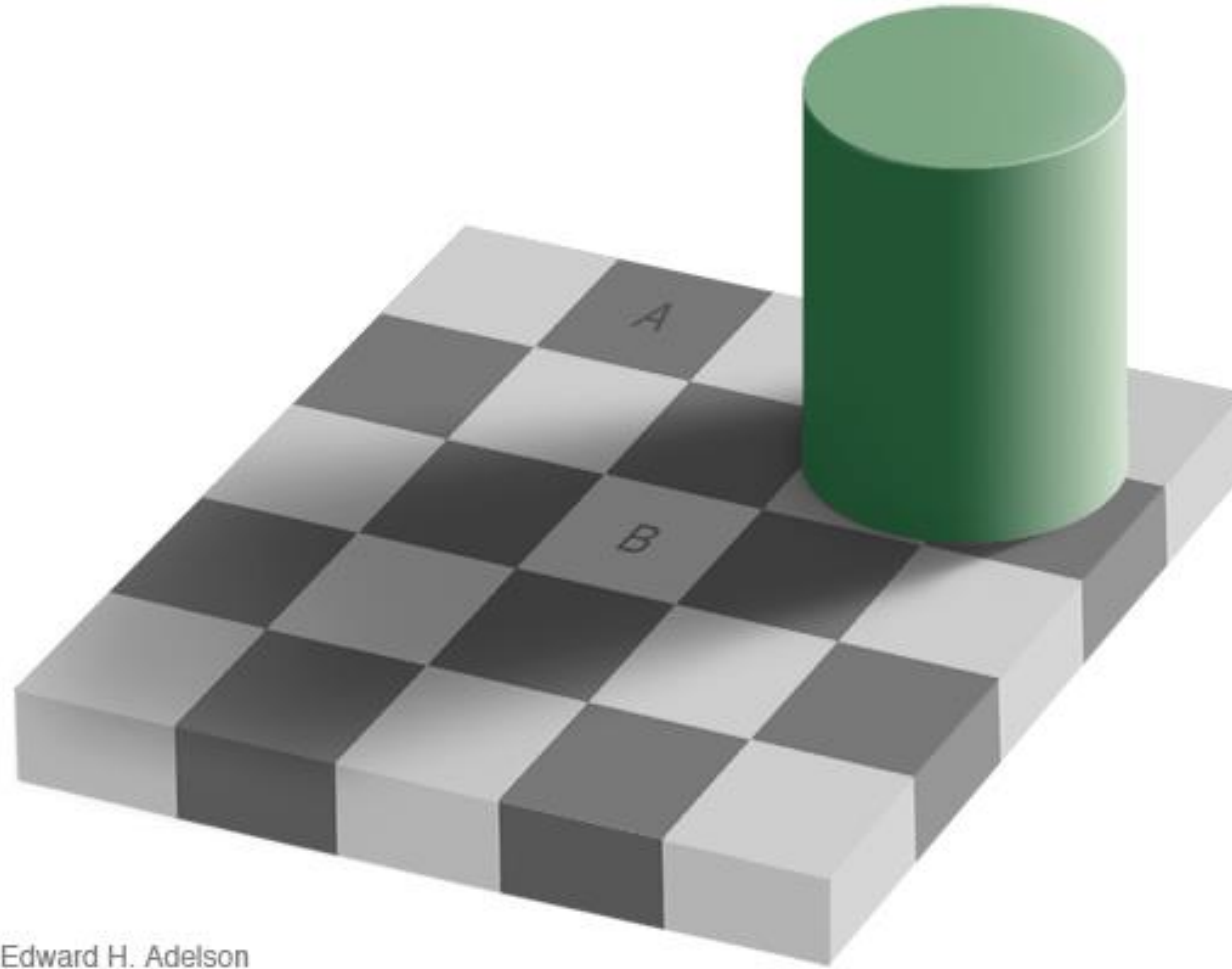


Is the center circle the same size on the left and the right?



Is the center circle the same size on the left and the right? (YES)

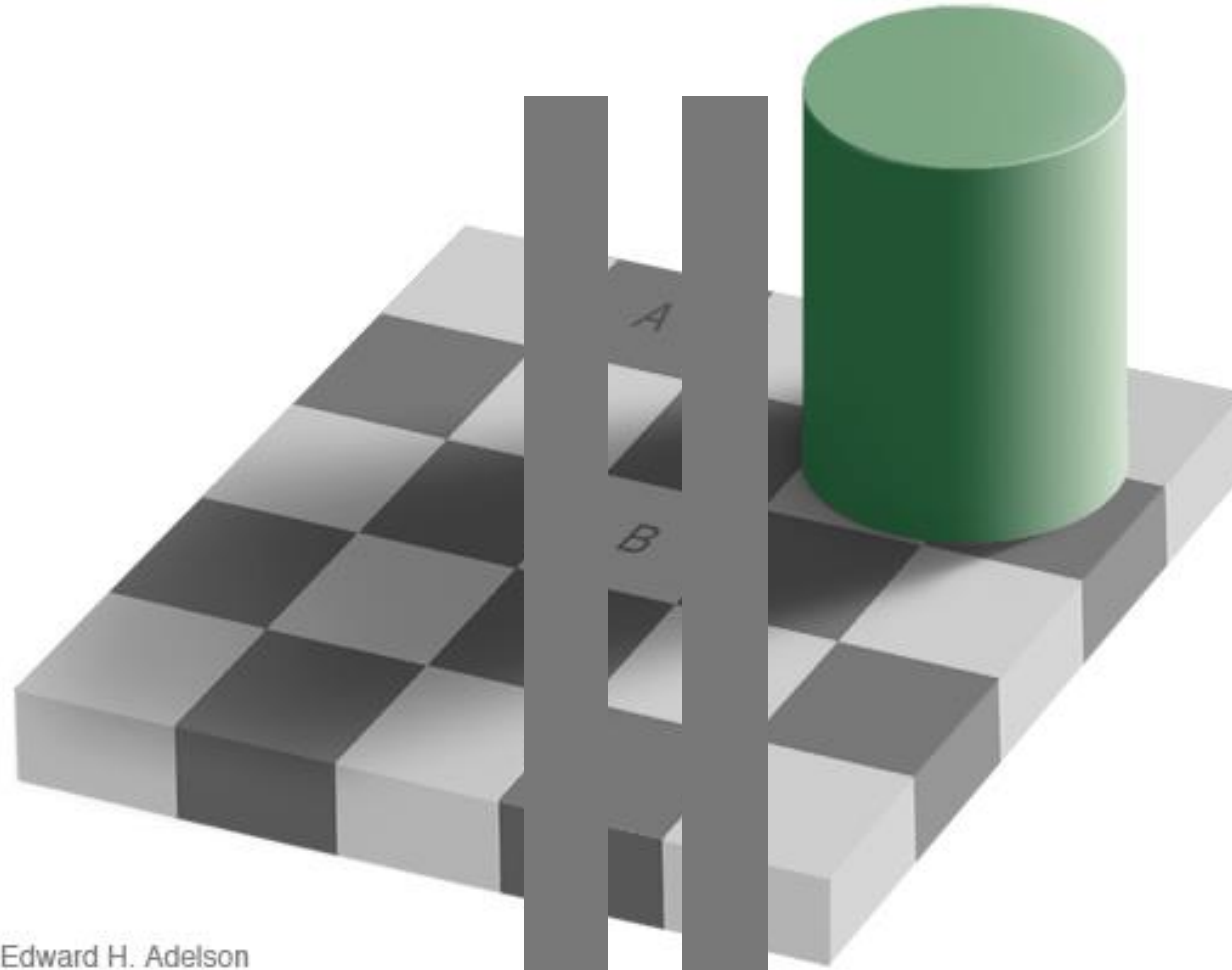
Perceptions shape beliefs (decisions)



Edward H. Adelson

Is A and B the same color?

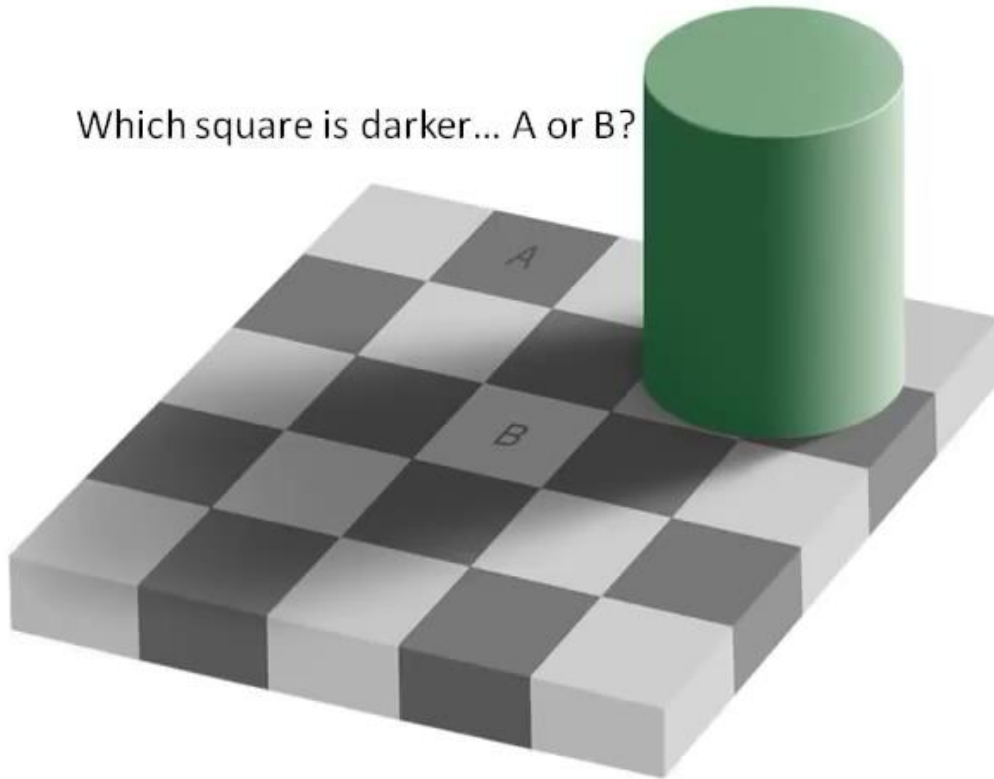
Perceptions shape beliefs (decisions)



Edward H. Adelson

Is A and B the same color? (YES)

Which square is darker... A or B?



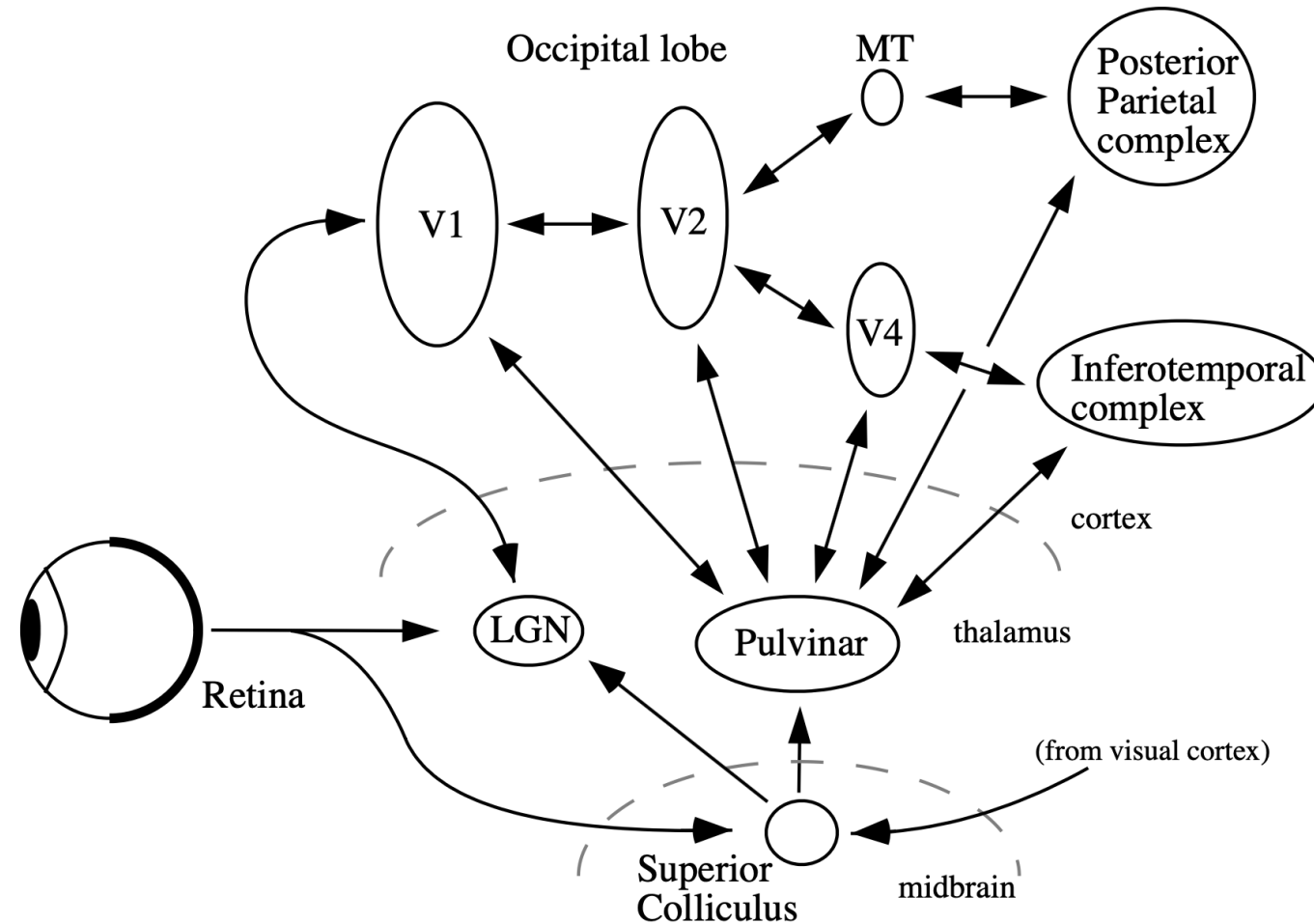
How does this illusion work?

- **Local contrast:** the light check in shadow is surrounded by darker checks. Thus, even though the check is physically dark, it is light when compared to its neighbors.
- **Edges:** The visual system tends to ignore gradual changes in light level, so that it can determine the color of the surfaces without being misled by shadows. *The shadow looks like a shadow, both because it is fuzzy and because the shadow casting object is visible.*

Neural circuits?

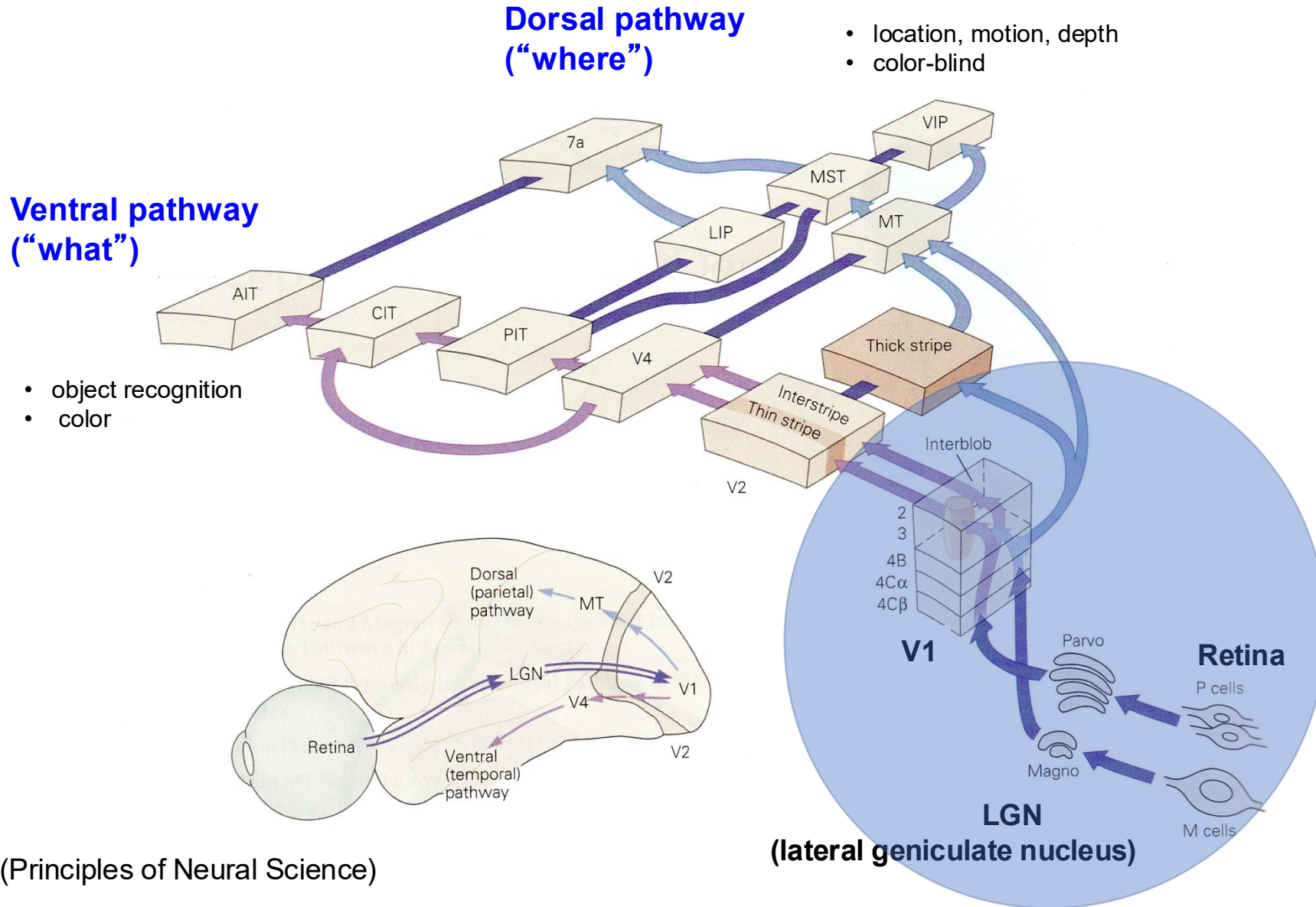
- perception of complex stimuli is presumably driven by the joint activity of neuronal populations, and it is not currently clear how population neuronal activity is integrated to give rise to lightness perception! ... some clues are arising, but this is not a “solved” circuit.

Visual information processing pathways



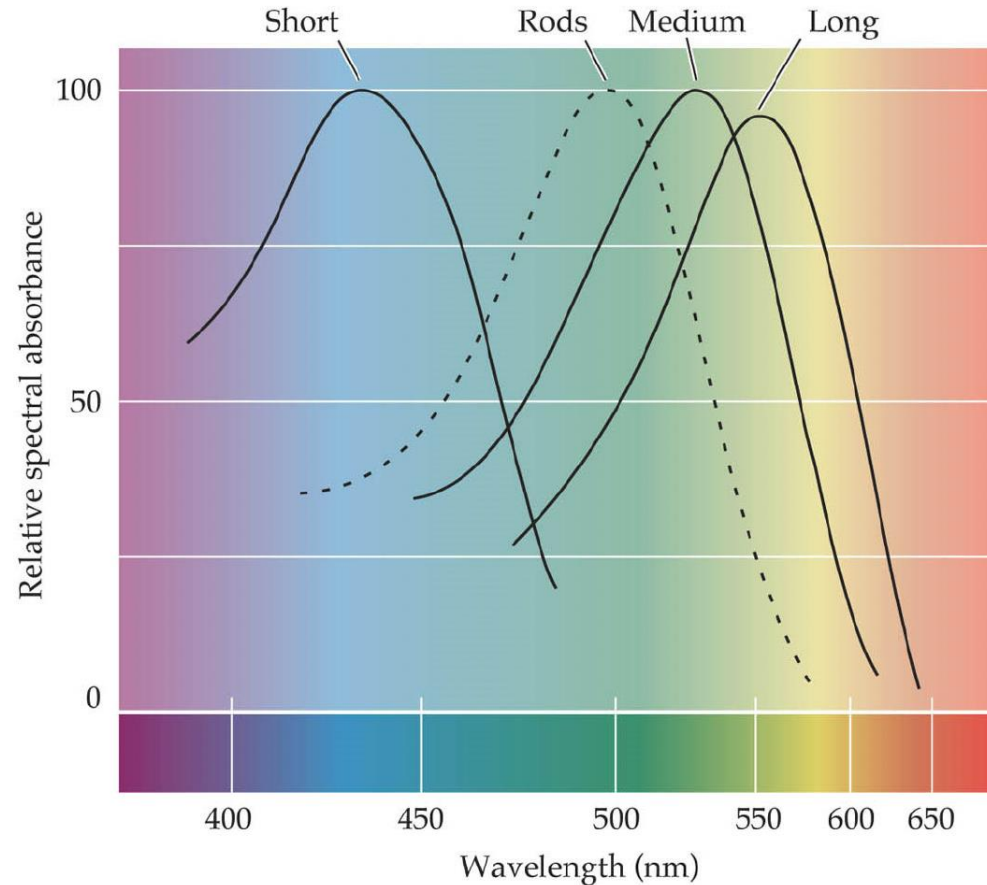
Slide courtesy of Prof. Bruno Olshausen

Visual pathway

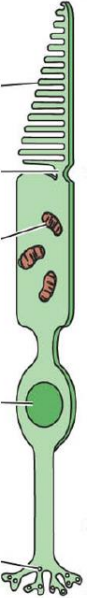


In primates, 3 types of cones exist, containing photopigments with different spectral sensitivity: S (short) M (medium) L (long) wavelength

- Human color perception depends on the neural representation of the spectral properties of light reaching the eye.



Thus:
S-cones
M-cones
L-cones



Purves Fig. 11.14

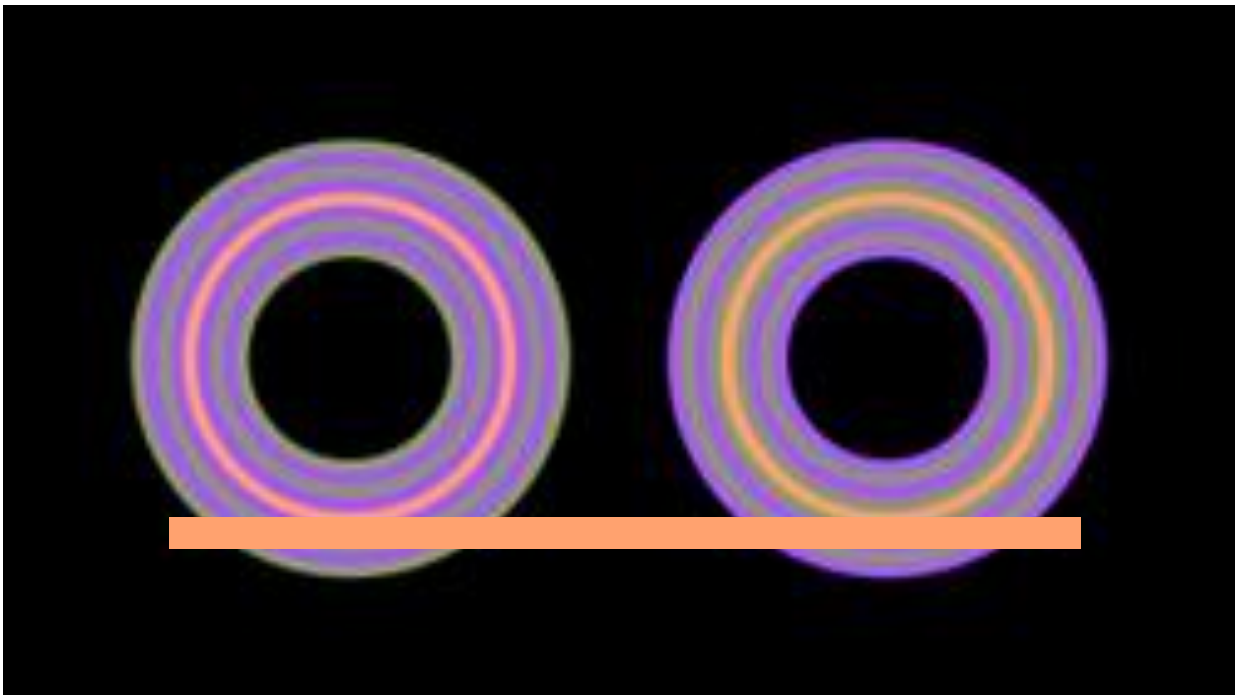
* => Tri-chromatic colour vision
in primates and humans

All other mammals:
Dichromats (S- and L-cones)



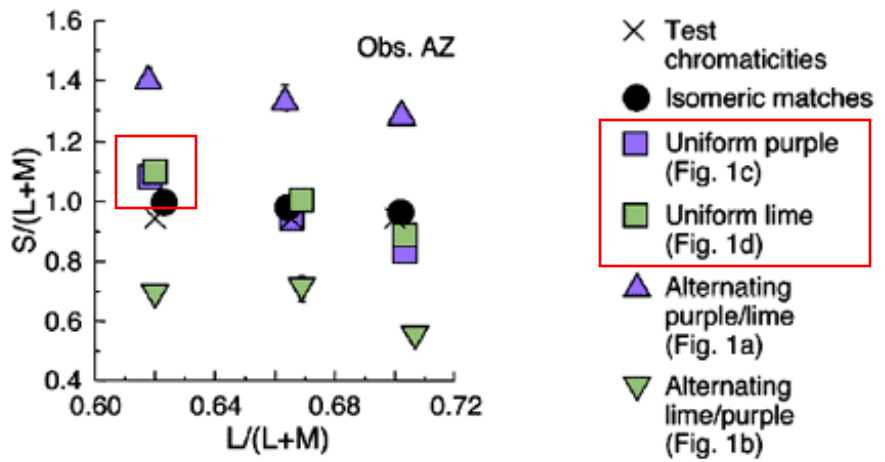
- The perceived color of a light varies with the background on which it is seen!
- HERE: patterned backgrounds composed of two different chromaticities caused larger shifts in perceived color than did a uniform background at either chromaticity within the pattern.
- **Cortical receptive-field organization, but not optical factors or known retinal neurons, can account for the color shifts from patterned backgrounds.**

Monnier P, Shevell SK.
Large shifts in color appearance from patterned chromatic backgrounds.
Nat Neurosci. 2003 Aug;6(8):801-2.



Whether the cause was the optics of the eye or neural processes?

- **not** explained by color contrast from the immediate surround or by diminished spatial resolution due to optics of the eye or neural processes ...
- **Detailed evidence:** the negligible $S/(L+M)$ shift induced by 0.70/0.62 variation in $L/(L+M)$ implies also that known retinal ganglion cells cannot explain these shifts in appearance
- The shifts must depend on signals from **S cones**, which are carried at the retinal level by small bistratified ganglion cells
- The color shifts from patterns can be explained by a neural receptive field with S-cone spatial antagonism (for example, +S center and -S surround).
- BUT, no known retinal neuron has +S/-S antagonism, so the model implicitly posits a class of neuron in visual cortex ...



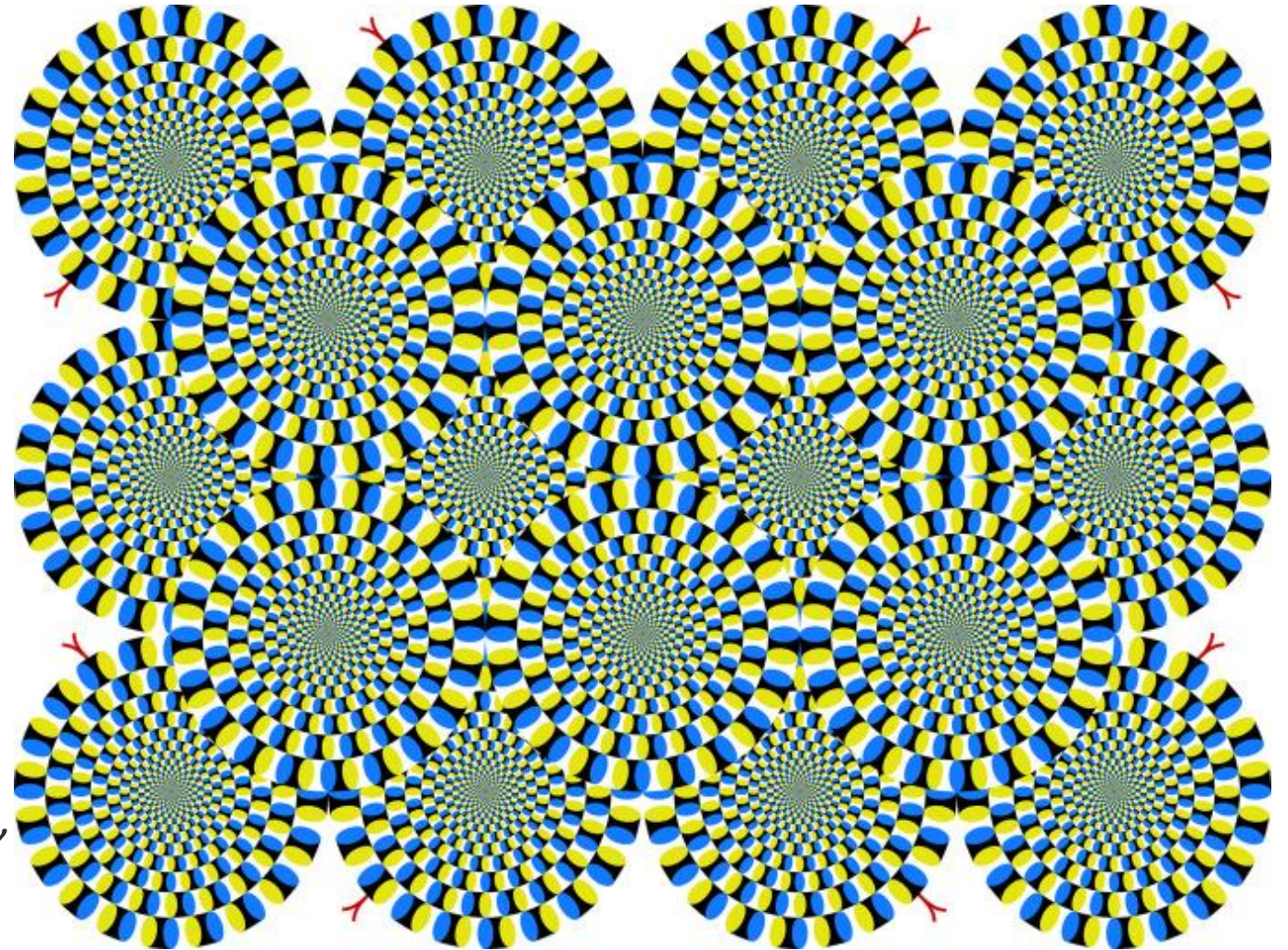
Monnier P, Shevell SK. Large shifts in color appearance from patterned chromatic backgrounds. Nat Neurosci. 2003 Aug;6(8):801-2.

Perceptions shape beliefs (decisions)

There are countless examples of visual illusions which can be grouped into categories such as those involving:

- geometry or angles
- luminance
- contrast or color
- size constancy
- motion

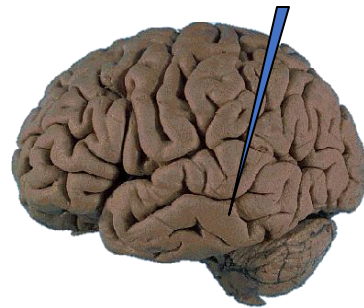
Bach and Poloschek, 2006; Bachmann et al., 2011; Schapiro and Todorović, 2017



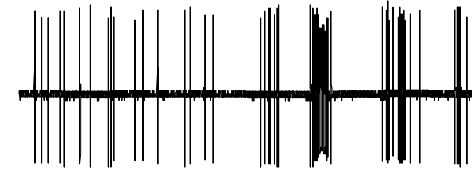
Motion illusion: The precise mechanism underlying the illusory perception of movement is not clear but a plausible suggestion is that it arises from differences between the visual latencies in the processing of the light and dark parts of the image (Kitaoka and Ashida, 2003; Kitaoka, 2017).

Encoding

Stimulus

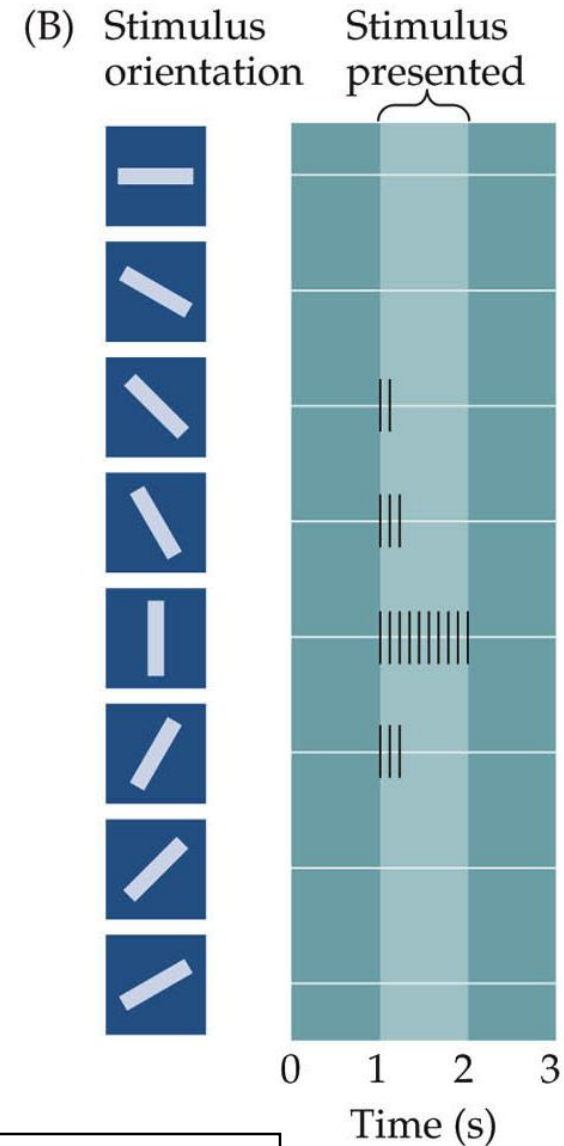
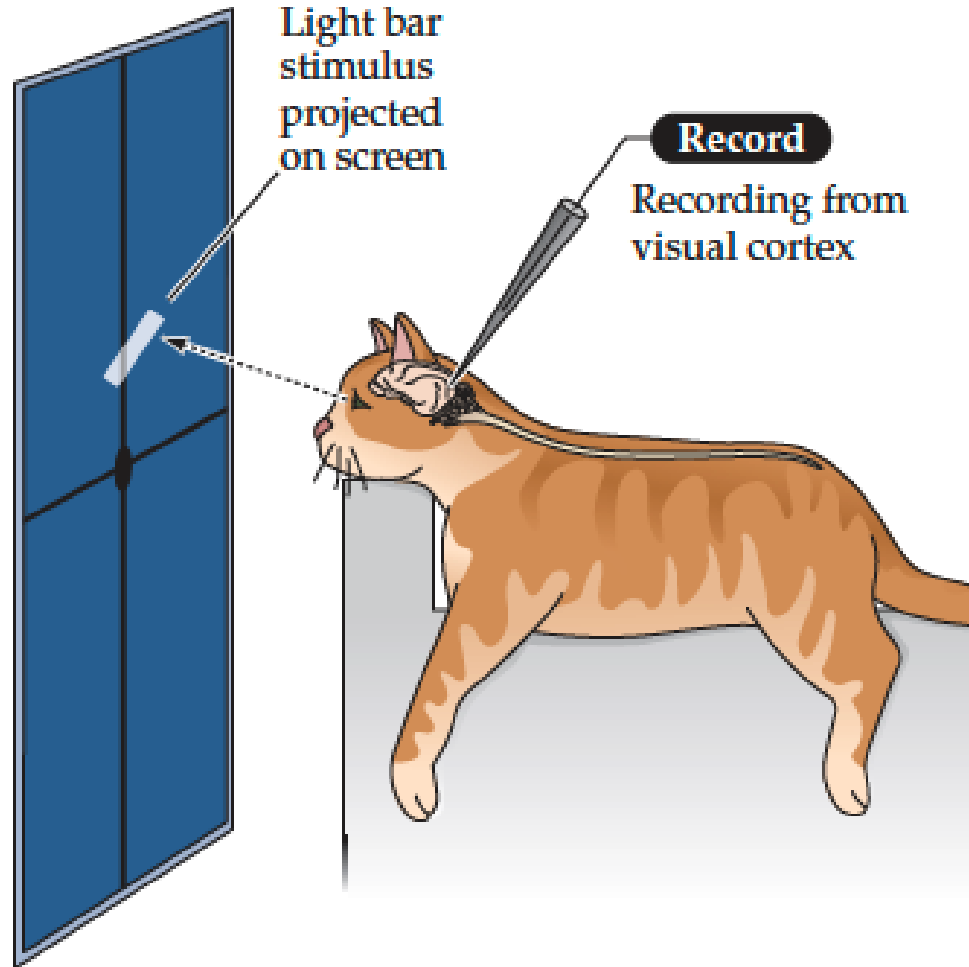


Spikes



- How do neurons respond to a certain stimulus?

Organization of receptive field of neurons in the primary visual cortex

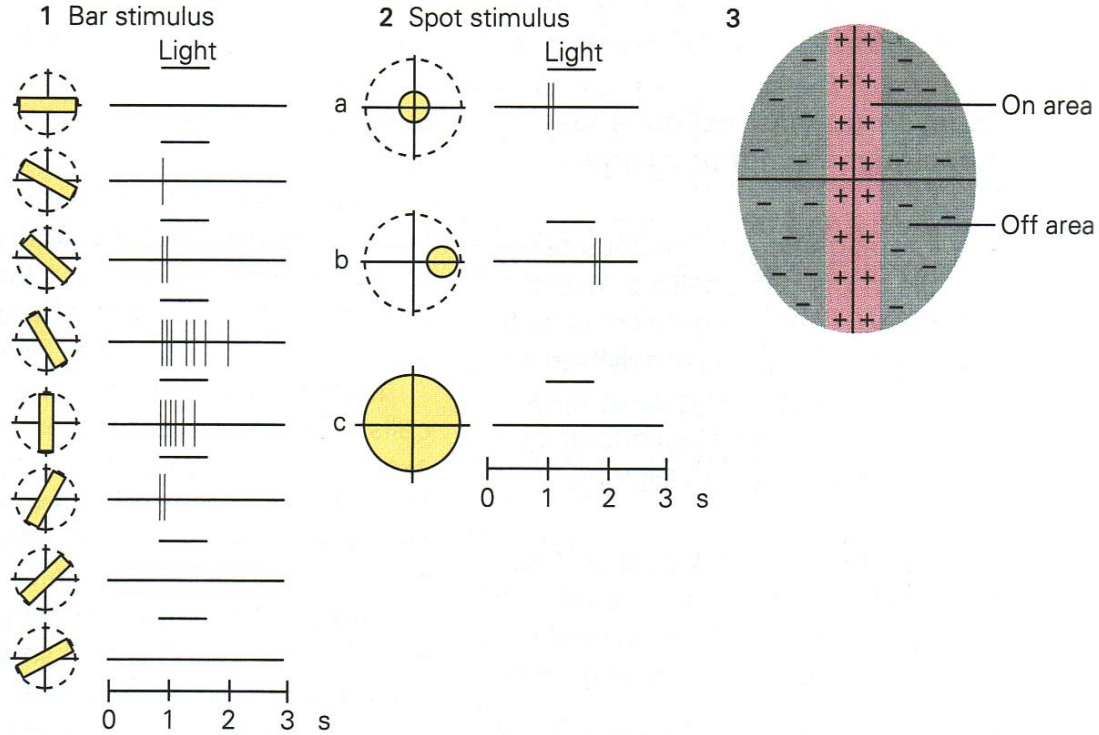


Example for a V1 neuron with a "simple" (bar-like) receptive field

V1 simple cell

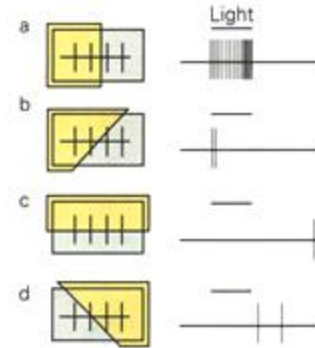


V1 simple & complex cell

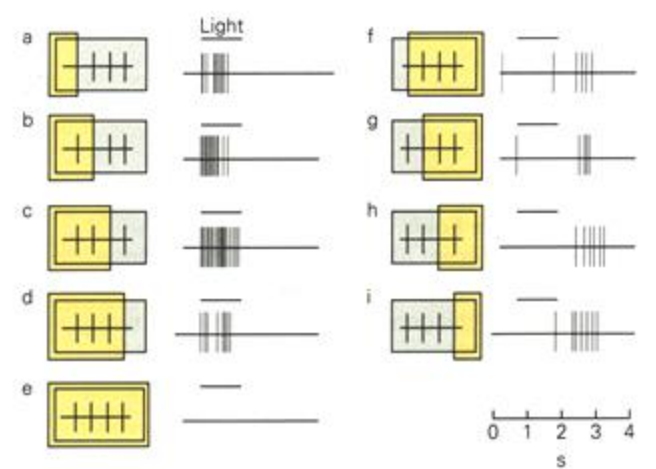


- Orientation specificity!

A₁ Response to orientation of stimulus

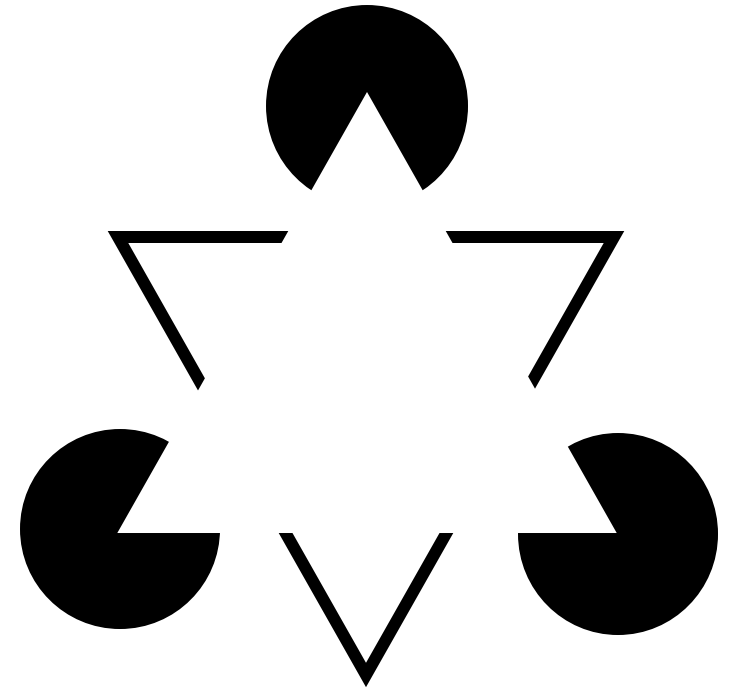


A₂ Response to position of stimulus



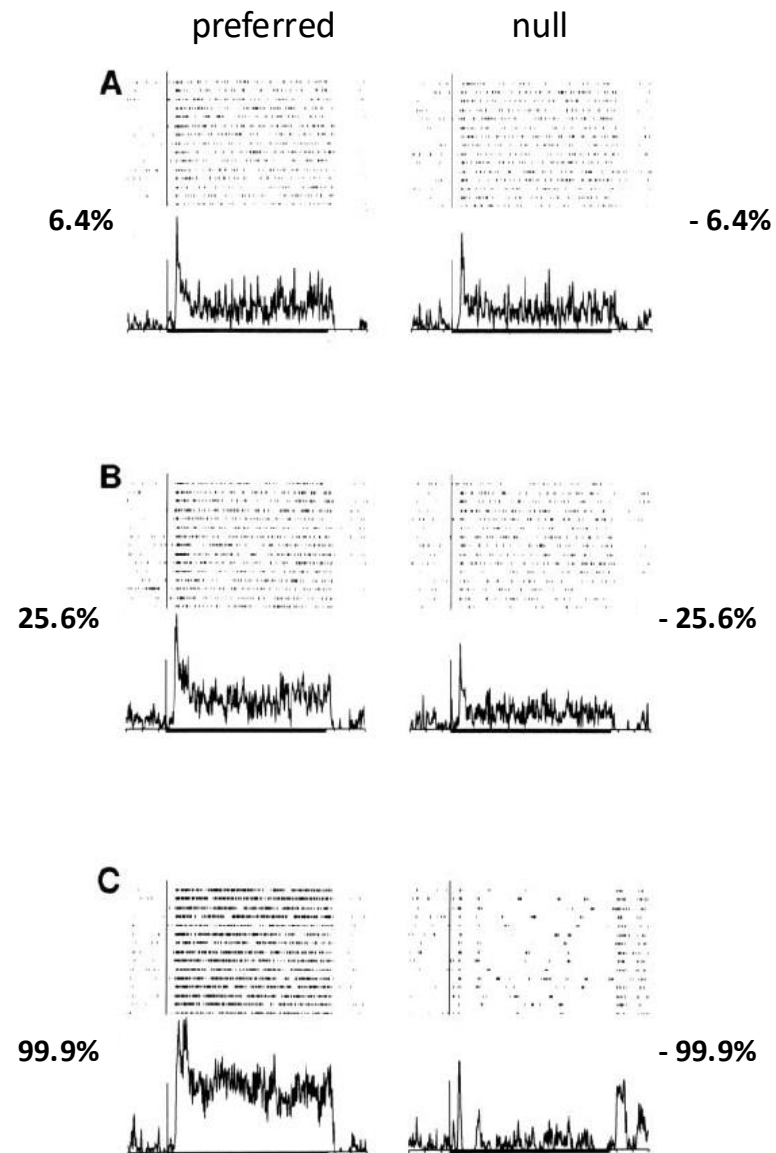
- Orientation specificity!
- Less sensitive to exact locations

Edge detector



(Kanizsa, 1955)

Neural responses are often stochastic



Establishing the causal link between neurons and perception (criteria)

1. The responses of the neurons and of the perceiving subject should be measured and analyzed in directly comparable ways.
2. The neurons in question should signal relevant information when the organism is carrying out the chosen perceptual task: Thus, the neurons should have discernable differences in their firing patterns in response to the different external stimuli that are presented to the observer during the task.
3. Differences in the firing patterns of some set of the candidate neurons to different external stimuli should be sufficiently reliable in a statistical sense to account for, and be reconciled with, the precision of the organism's responses.
4. Fluctuations in the firing of some set of the candidate neurons to the repeated presentation of identical external stimuli should be predictive of the observer's judgment on individual stimulus presentations.
5. Direct interference with the firing patterns of some set of the candidate neurons (e.g. by electrical or chemical stimulation) should lead to some form of measurable change in the perceptual responses of the subject at the moment that the relevant external stimulus is delivered.
6. The firing patterns of the neurons in question should not be affected by the particular form of the motor response that the observer uses to indicate his or her percept.
7. Temporary or permanent removal of all or part of the candidate set of neurons should lead to a measurable perceptual deficit, however slight or transient in nature.



Newsome

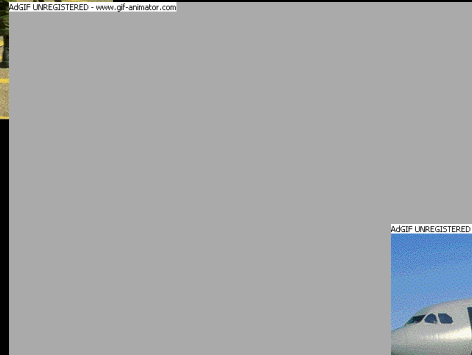
conscious perceptual experience:
Change blindness



Isn't the brain good at detecting a change?



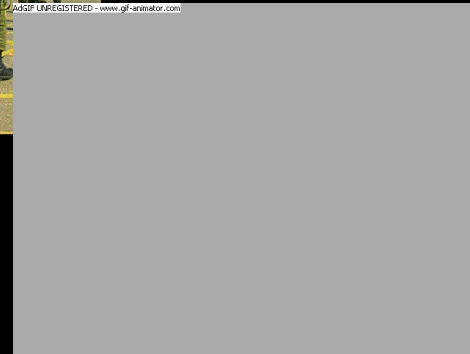
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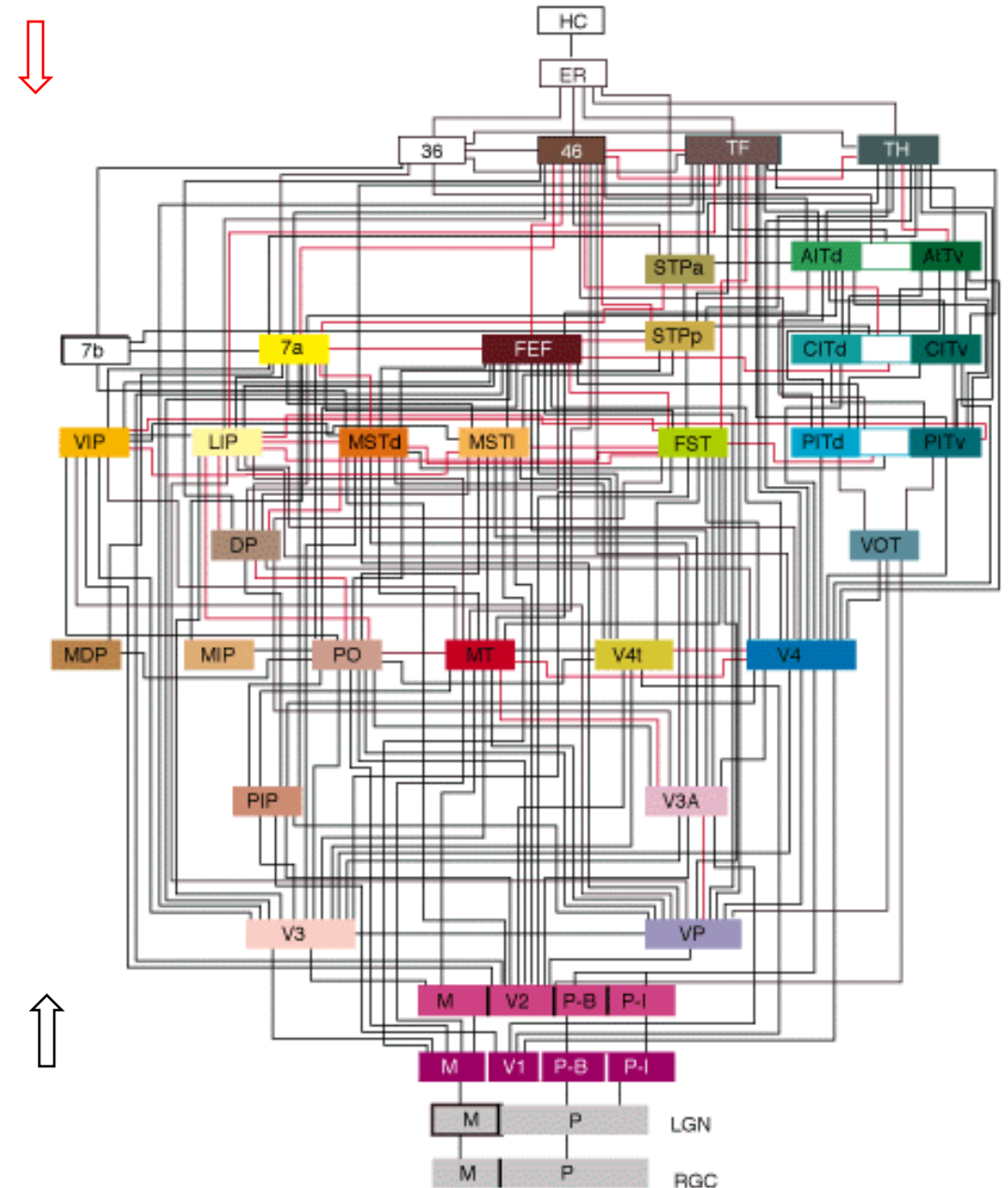
0.25 sec

Strong prior beliefs on what could/would change...



According to the **theory of predictive processing**, our brains use an **internal model of the world to make predictions that are fed back from higher to lower levels** of the processing hierarchy, thereby enabling inferences about the hidden causes of the sensory input data.

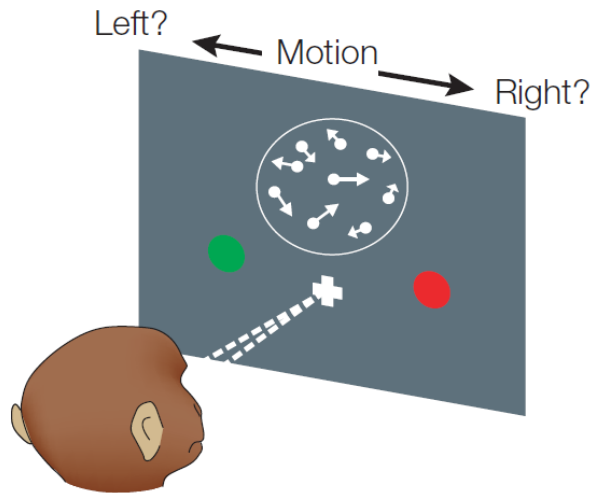
(Friston, 2005; Rao & Ballard, 1999)
(Adapted from Kemedade, 2021)



Van Essen Diagram

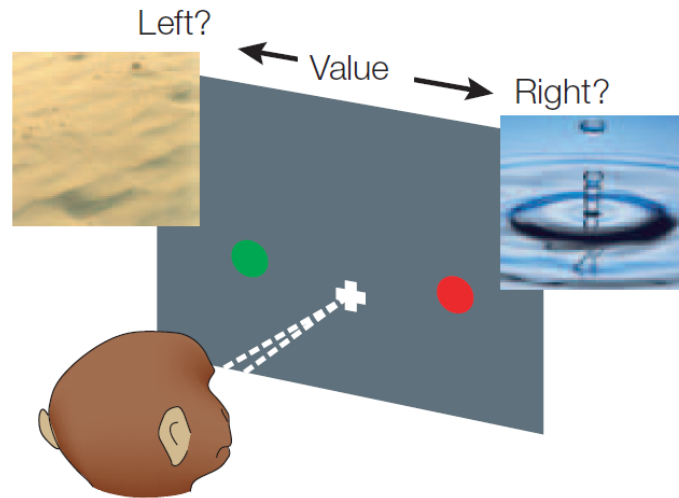
Decision-making & behavior

Perceptual judgment



- Sensory evidence

Value-based decisions



- Cost/benefit
- Value (utility)

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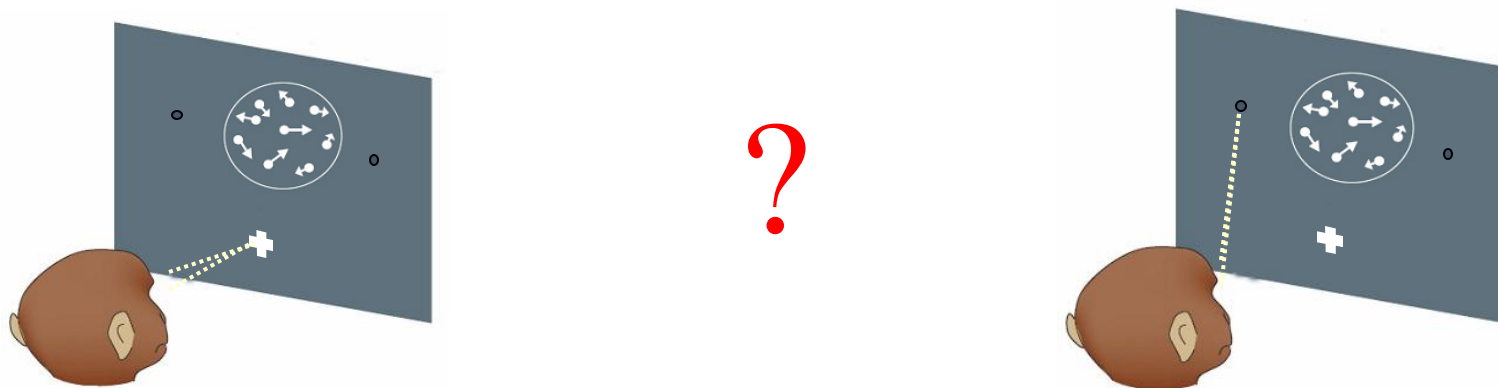
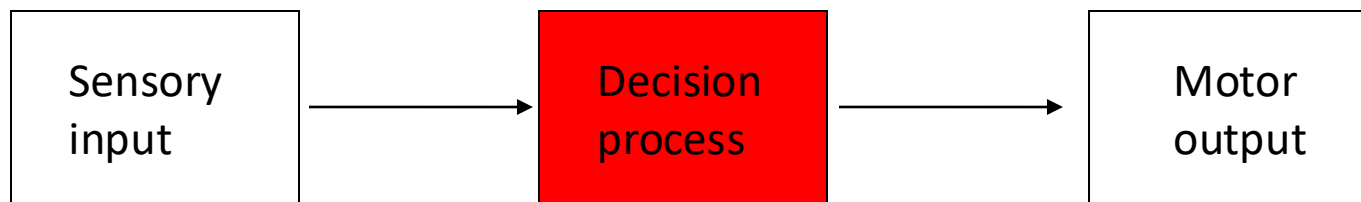
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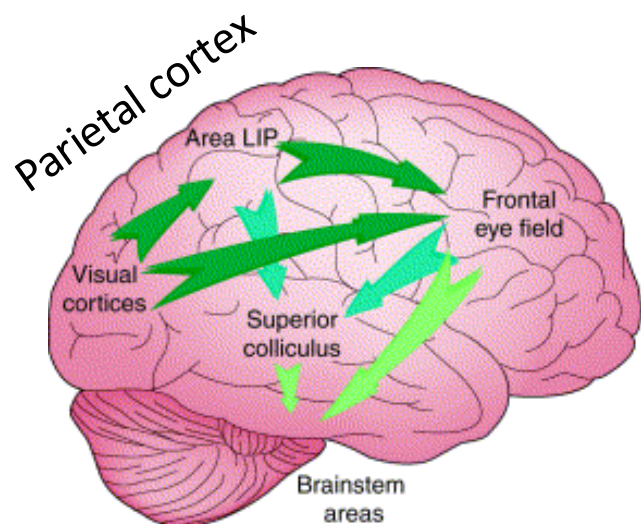
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?



Random dot motion task

- It takes up to 1-2 seconds to make a decision
 - Decisions unfold gradually by accumulating noisy evidence.
1. How does the brain accumulate evidence?
 2. How does the brain decide when to stop a decision process?

Decision-making

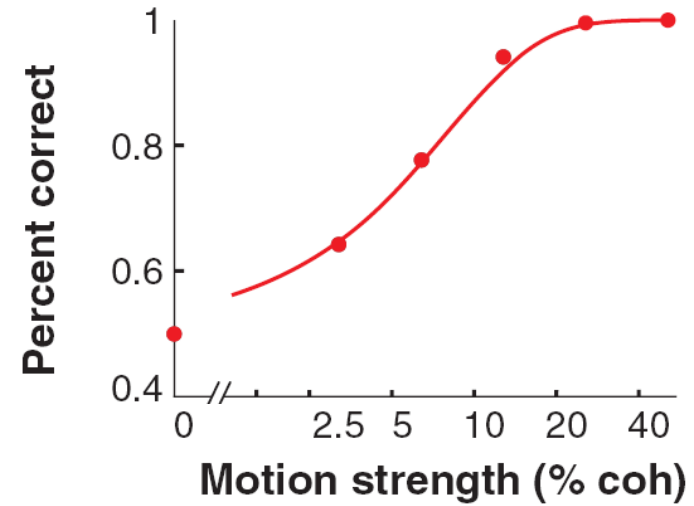
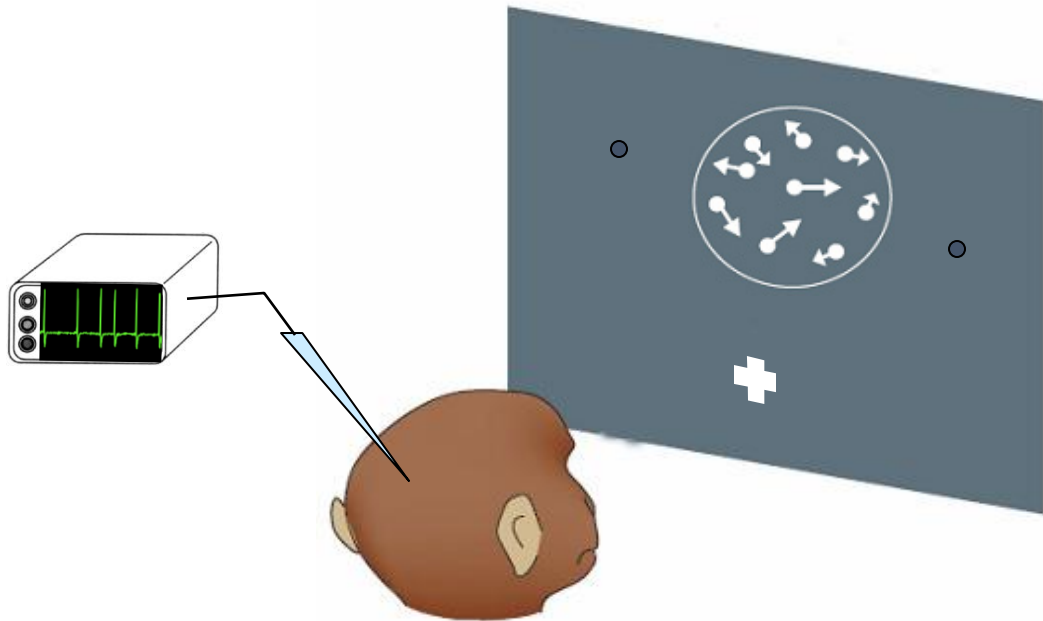
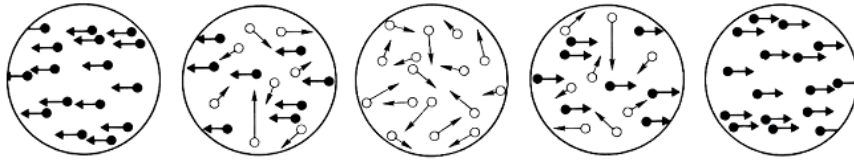


Newsome



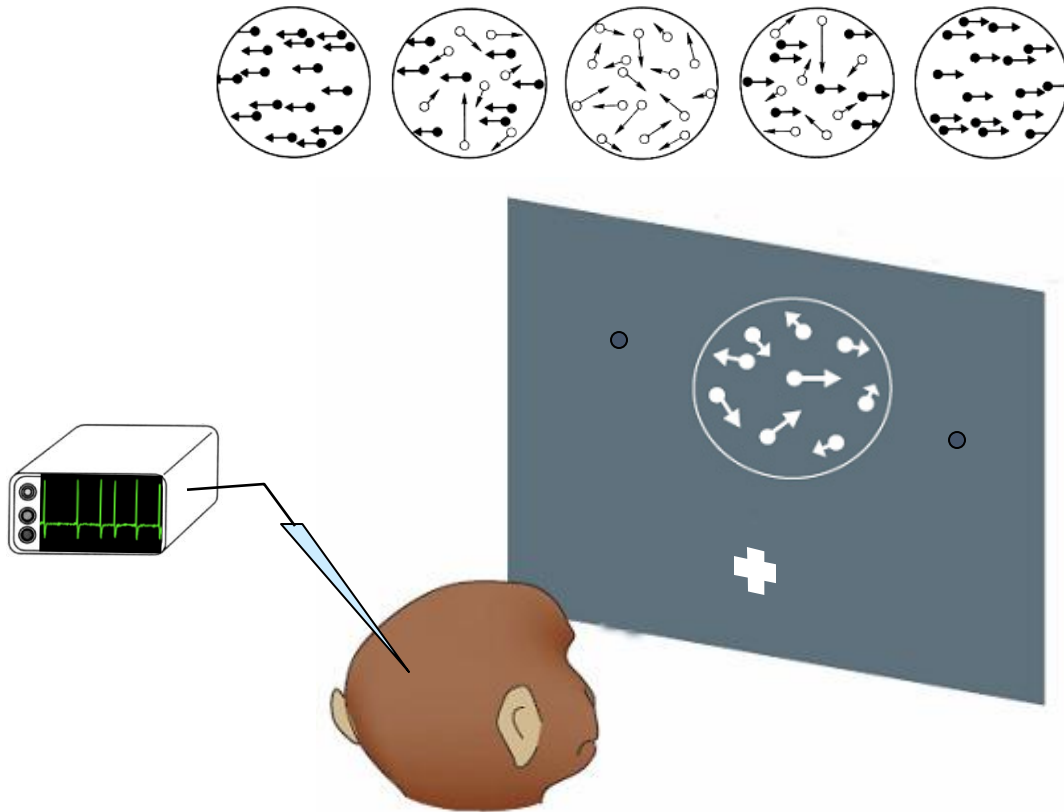
Shadlen

Random dot motion discrimination task

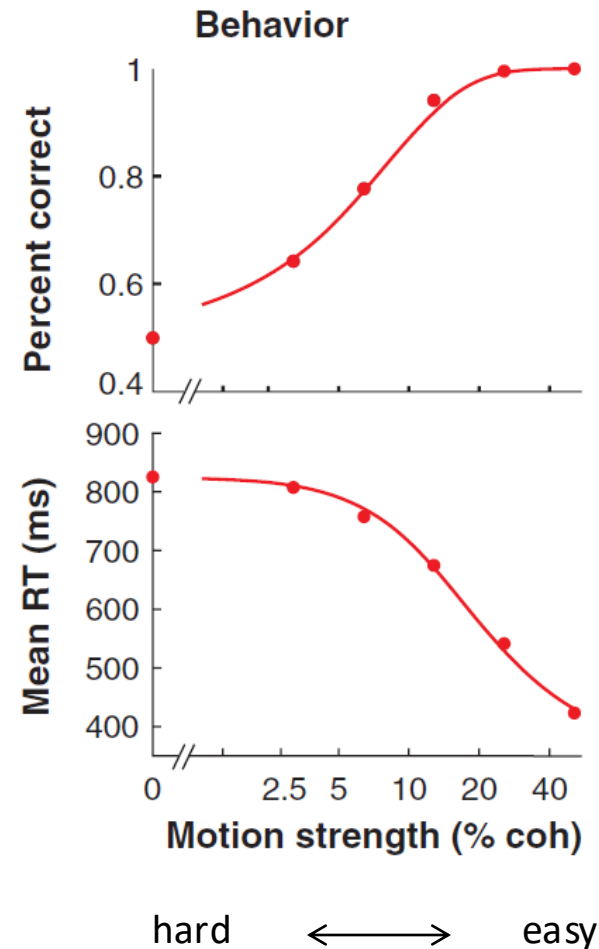


Temporal integration of sensory information

Motion discrimination task ([reaction time version](#))



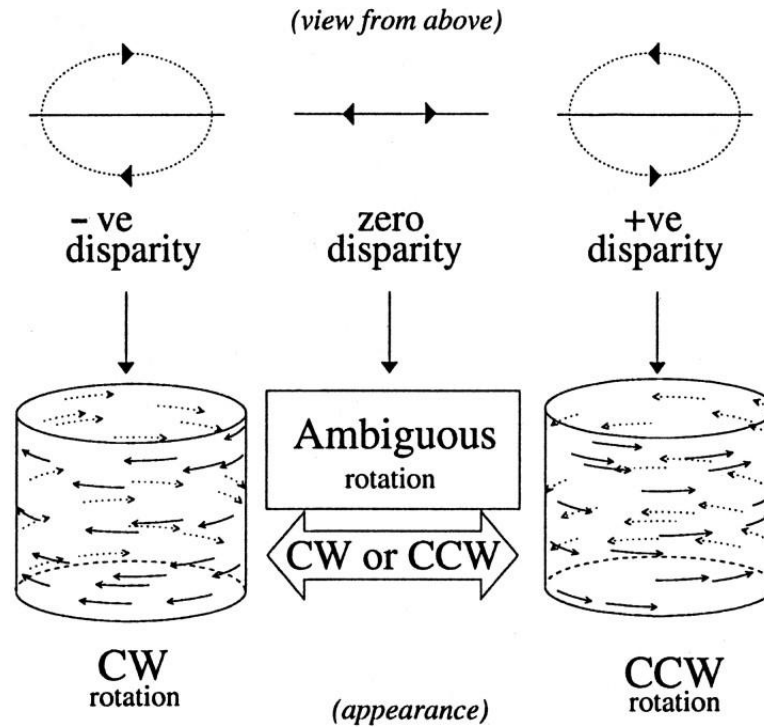
- Harder decisions → longer time to act



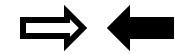
Cortical area MT (V5) in the macaque plays an important role in the perception of visual motion

- evidence suggests a role in the perception of stereo depth.
- MT contains an ordered map of binocular disparity ([DeAngelis and Newsome, 1999](#))
- -electrical microstimulation in MT influences the perceptual reports of monkeys in a stereo task ([DeAngelis et al., 1998](#)).

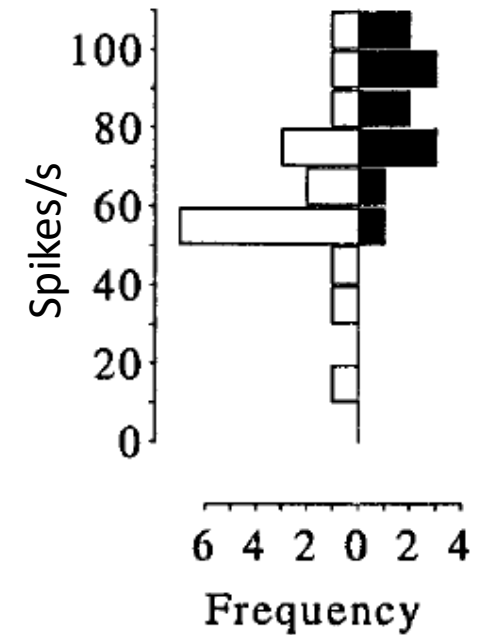
Bistable percept: which way is it rotating?



Monkey's behavioral report

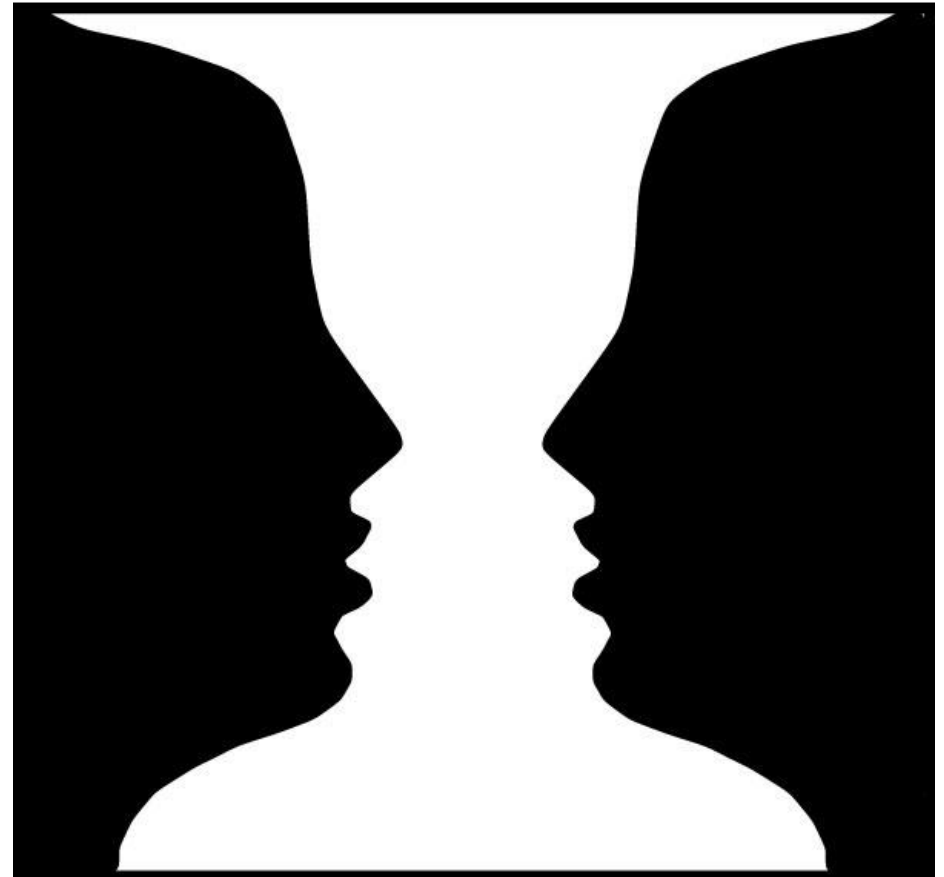


Neural activity (single neuron)



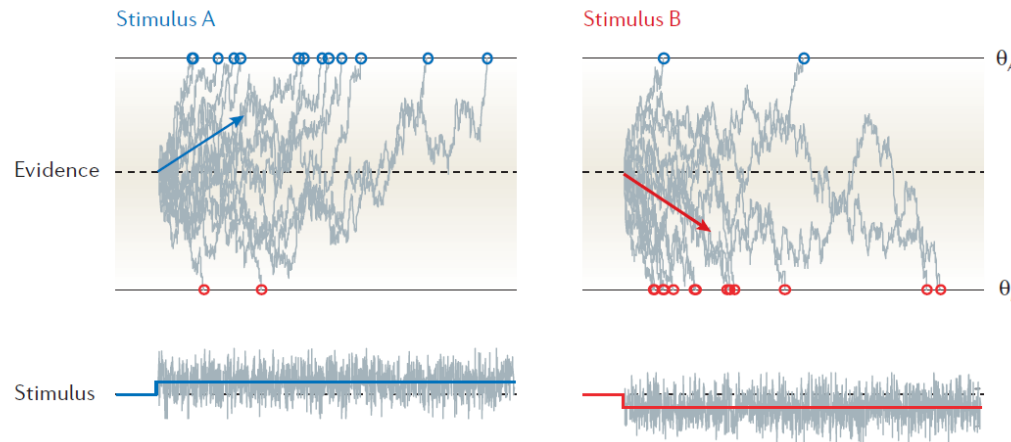
30 zero disparity trials:

Another example of bistable percept:
Rubin's vase

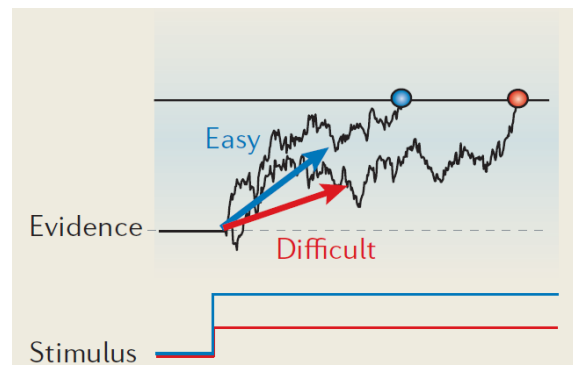


Drift diffusion models: accumulating noisy evidence

- Variability in response times and judgments

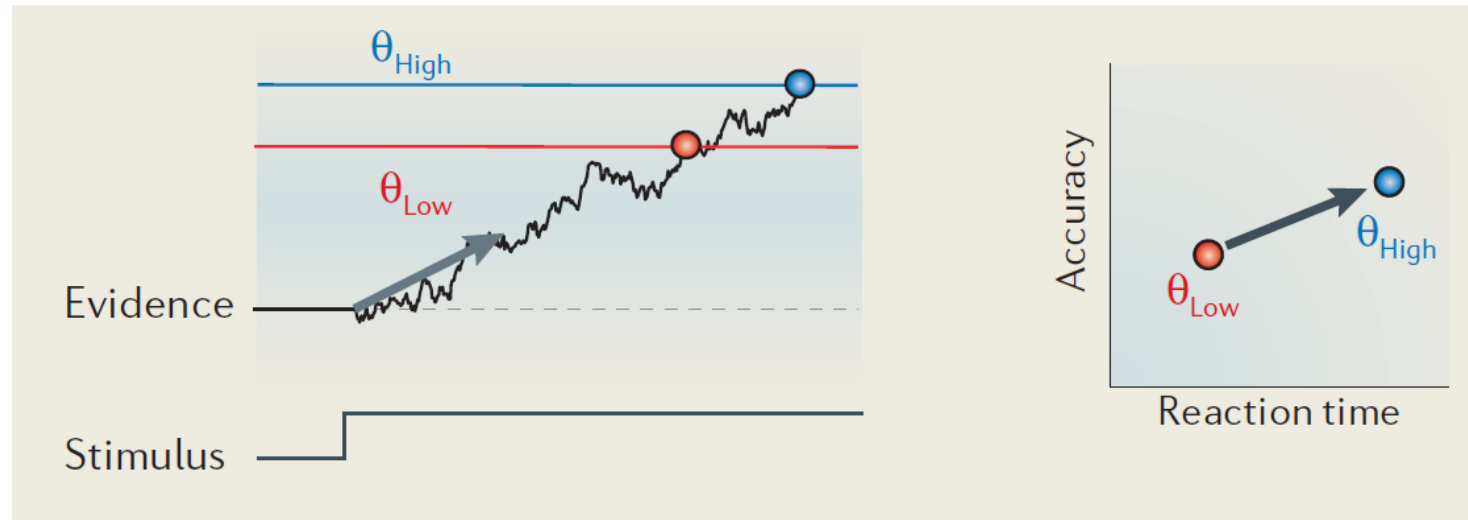


- Effect of difficulty on response times



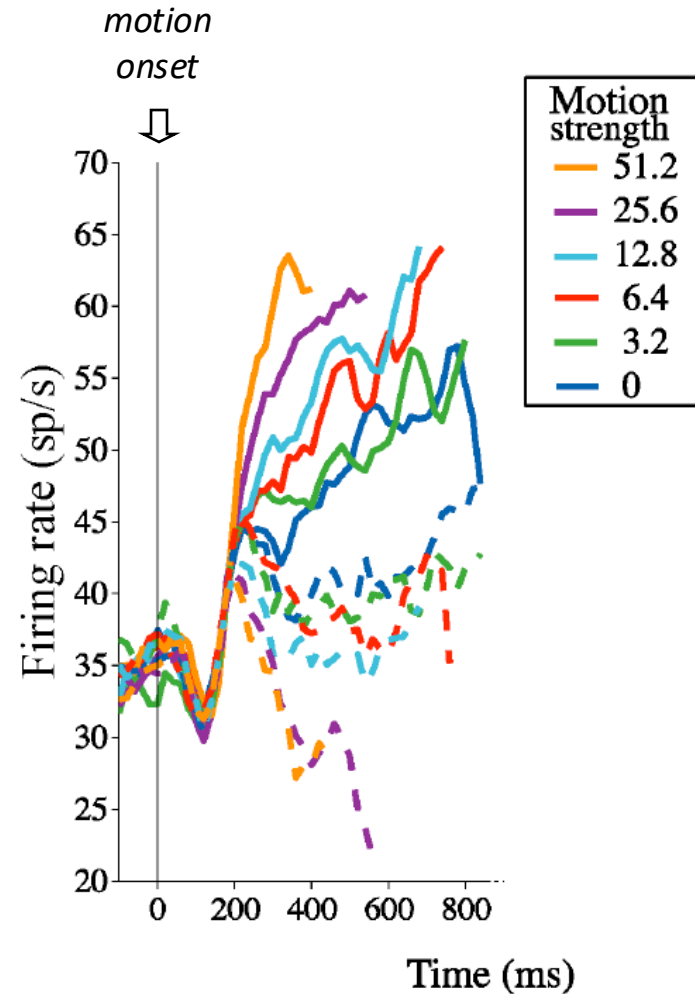
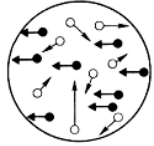
Drift diffusion models: accumulating noisy evidence

- Speed-accuracy tradeoff

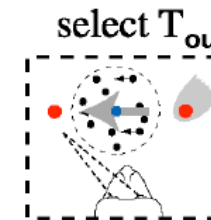
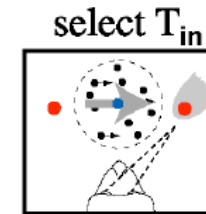


- Emphasis on accuracy \Rightarrow higher threshold (θ)
(higher accuracy)
- Changing criterion (*signal detection theory*)

LIP (sub-area of parietal cortex) neurons: accumulating evidence



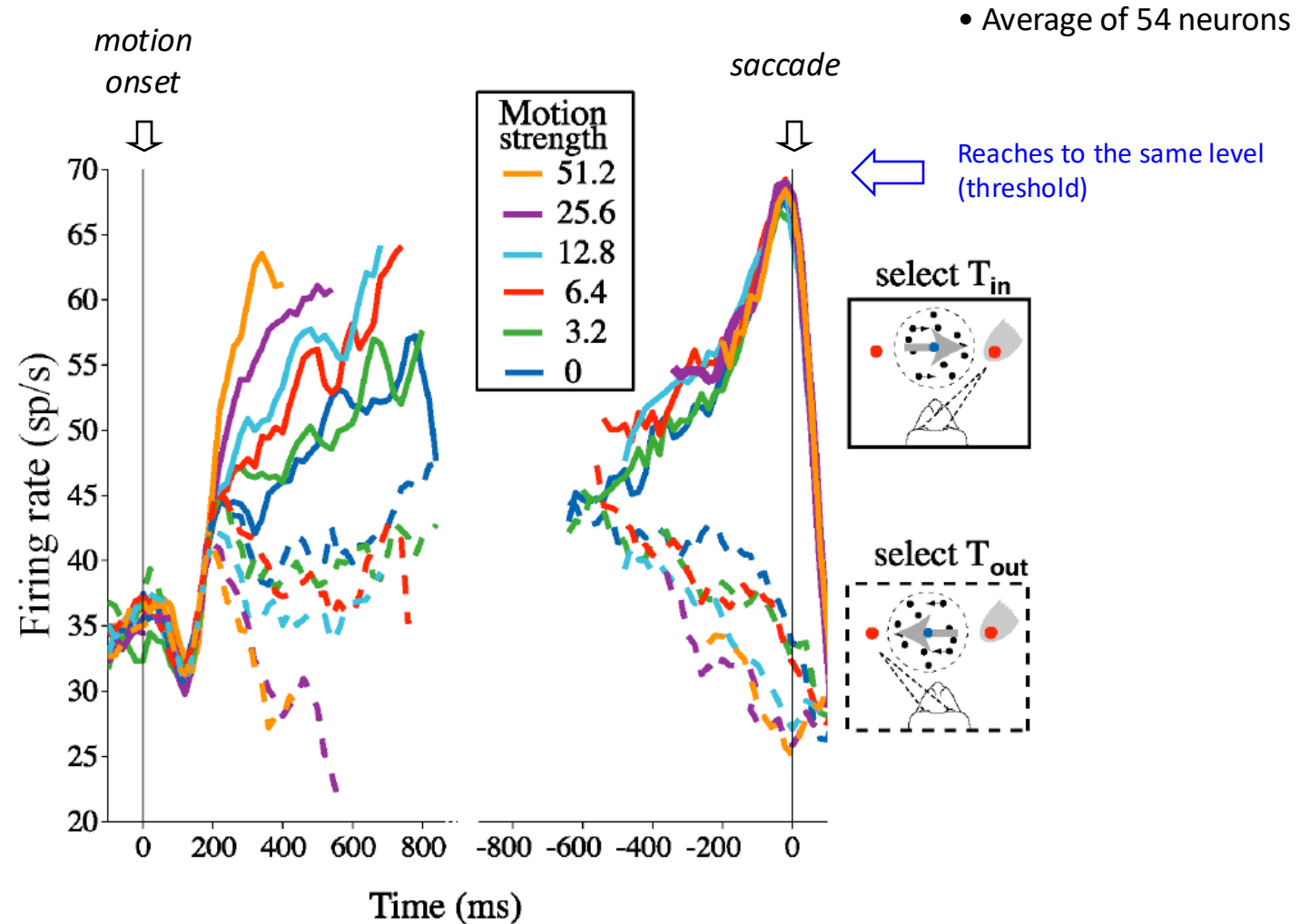
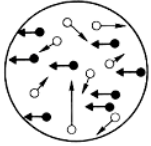
• Average of 54 neurons



• Strong signal \implies faster increase in firing rate

(Roitman & Shadlen, 2002)

LIP neurons: accumulating evidence

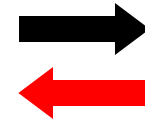
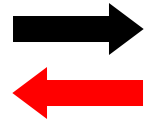


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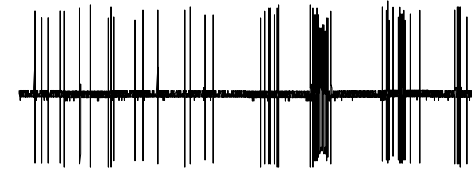
(Roitman & Shadlen, 2002)

Encoding and *decoding*

Stimulus

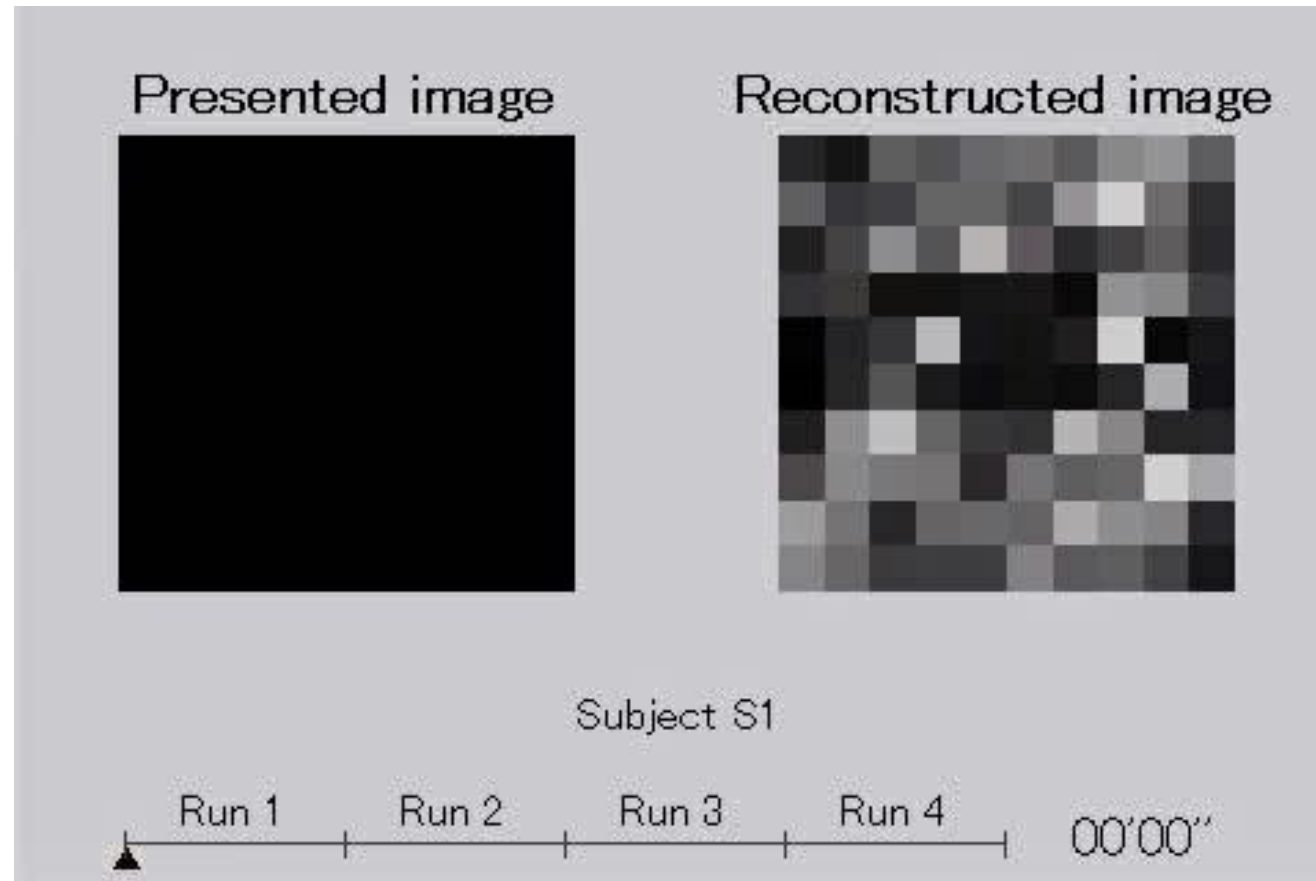


Spikes



- Our brain needs to determine what is going on in the real world from patterns of spikes.

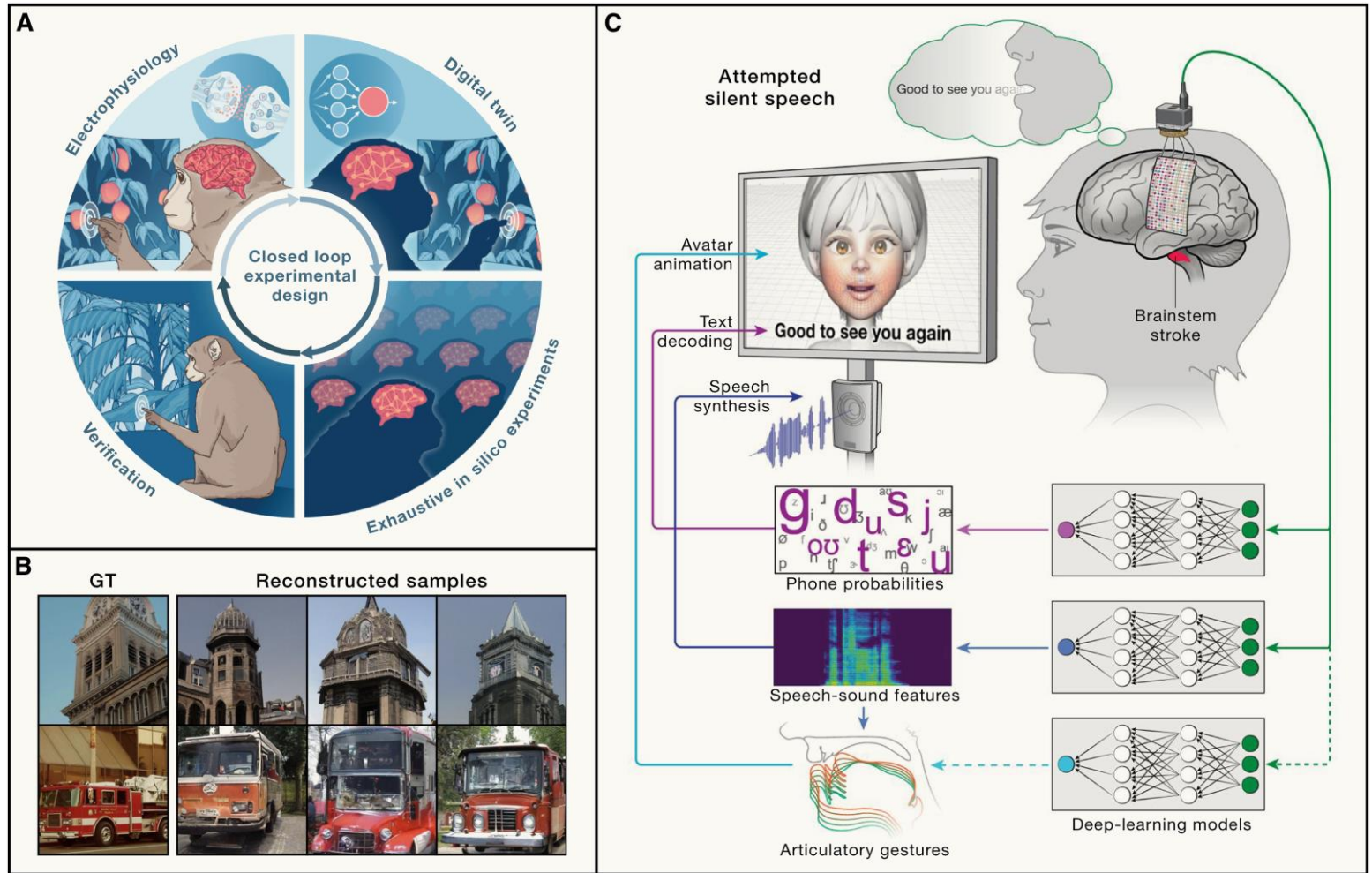
Real-time decoding of fMRI signals



(Miyawaki et al., 2008)

Visual image reconstruction from human brain activity using a combination of multiscale local image decoders

Decoding of neural signals



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Decoding the brain: From neural representations to mechanistic models

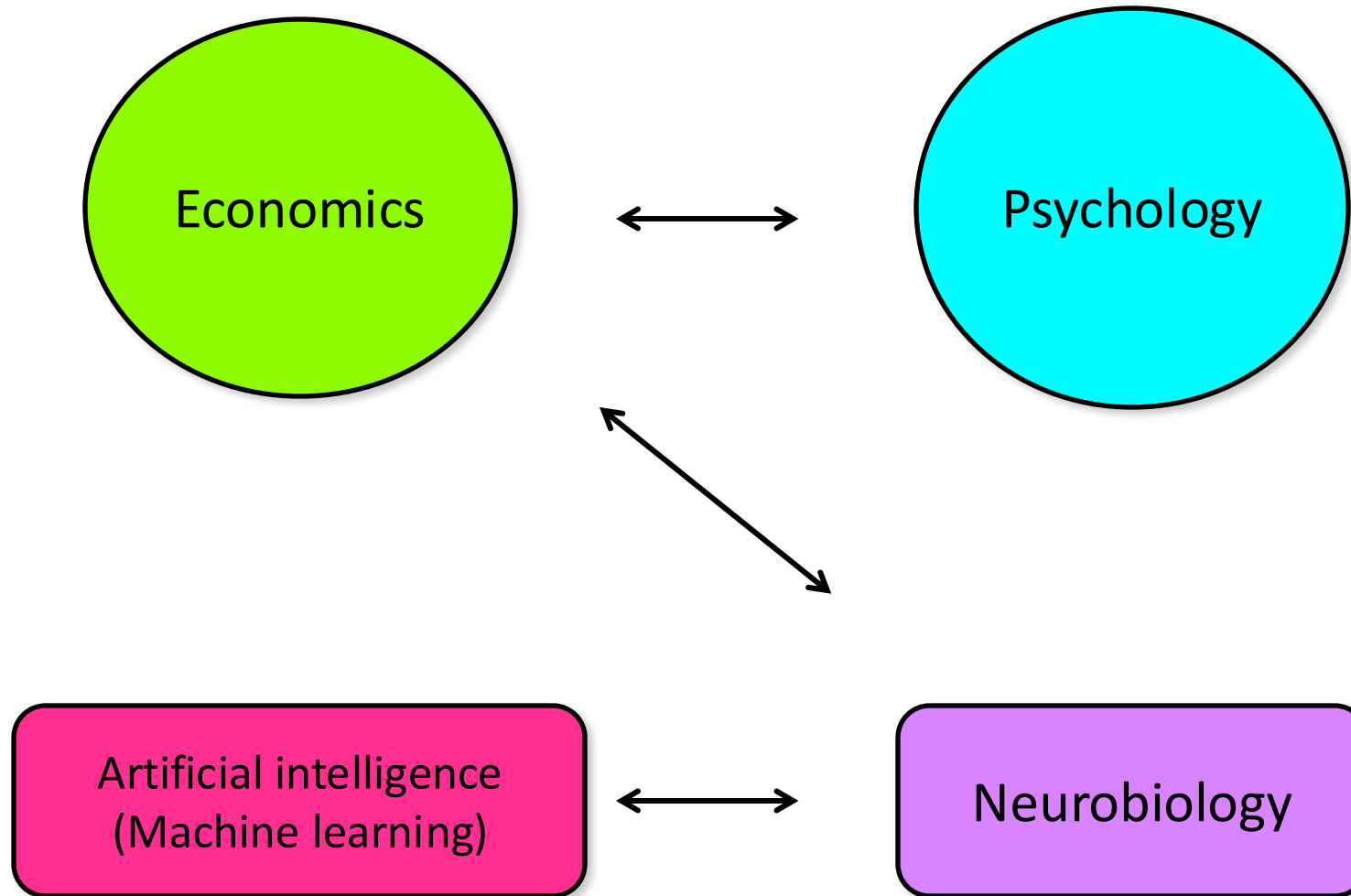
[Mackenzie Weygandt Mathis](#)^{1,2} · [Adriana Perez Rotondo](#)^{1,2} · [Edward F. Chang](#)³
[Andreas S. Tolias](#)^{4,5,6,7} · [Alexander Mathis](#)^{1,2}

(B) Illustration of decoded images from fMRI using diffusion models: ground truth (GT) vs. decoded images generated by Chen et al.⁹⁶ from human fMRI with a diffusion model. Note that decoded images share similar color, shape, and semantics.

Mini-Summary

- Drift diffusion models (accumulation of noisy signal) explain the relationships between the speed and accuracy in perceptual decision tasks.
- LIP neurons increase or decrease their firing rates as evidence accrues for or against the direction associated with the choice target in the response field of each neuron.
- The rate of increase (or decrease) correlate with motion strength.
- LIP neurons attain the same level of activity just before the saccade, independent of motion strength.
- Neural decoding can be used to “read out” perception/stimulus & modern approaches are leveraging AI models

Decision science



Theories of decision-making

- **Normative**: how we *should* decide.
 - **Expected utility theory**
 - Game theory
- **Descriptive**: how we *actually* decide.
 - Behavioral economics
 - Prospect theory
- **Prescriptive**: how can we improve

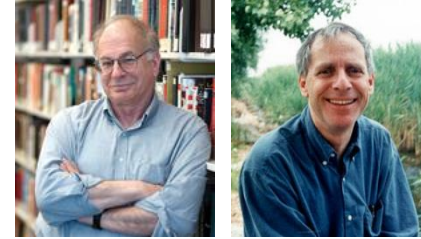
What is driving decisions?



Blaise Pascal

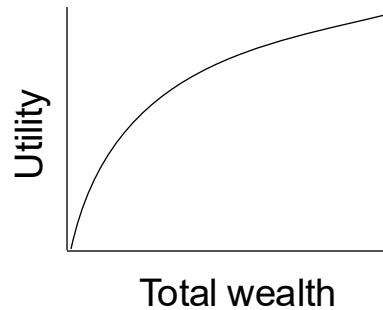


Daniel Bernoulli



Kahneman & Tversky

Probability x value

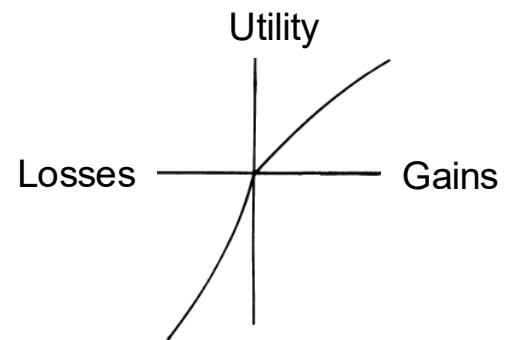


Expected value
(objective value)

Expected utility
(subjective value)

Expected utility theory

Explains risk-aversiveness



Gains and losses

Prospect theory

Explains reflection effect (framing effect)
loss aversion
Certainty effect, effect of low probability etc.

Expected value



Blaise Pascal

- One should select the option with the highest expected value.

Expected value = probability x value

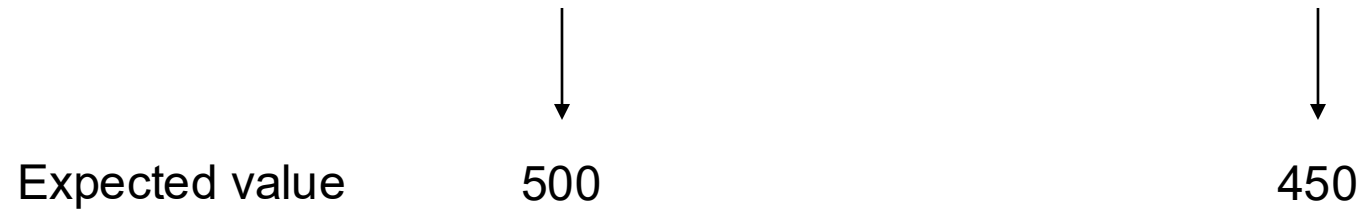


Risk aversion

Which of the following would you prefer?

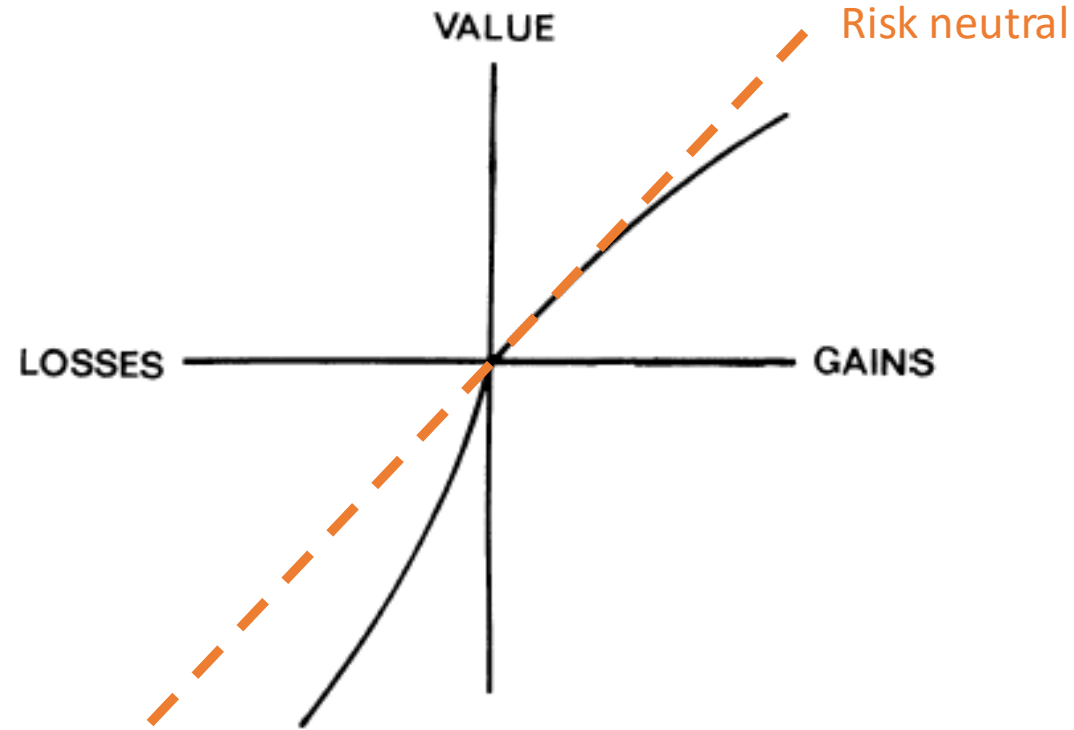
A: 50% chance to win 1,000,
50% chance to win nothing;

B: 450 for sure.



- But humans choose B more often...

Value function



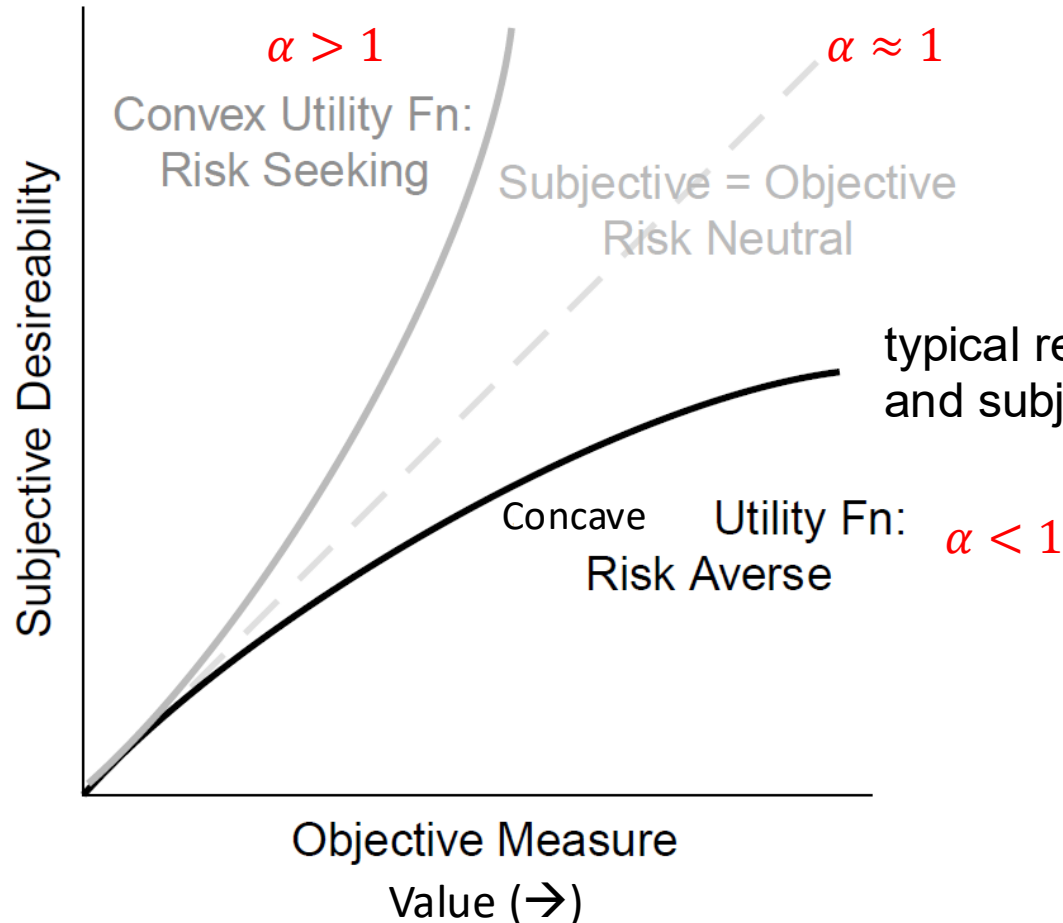
- Carriers of value are gains and losses (x-axis)
- Risk averse for gains \Rightarrow concave in gains
- Risk seeking for losses \Rightarrow convex in losses
- Loss aversion (more sensitive to losses) \Rightarrow (about 2 times) steeper in losses

subjective value grows more quickly than objective value

Risk preference and utility functions

Bernoulli's notion of subjective value or **utility**.

$$Utility = k \cdot (value)^\alpha$$



typical relationship between objective and subjective valuations of an action

As the objective value of a gain increases, the subjective desirability, or utility, grows more slowly.

Finding: humans are typically risk averse

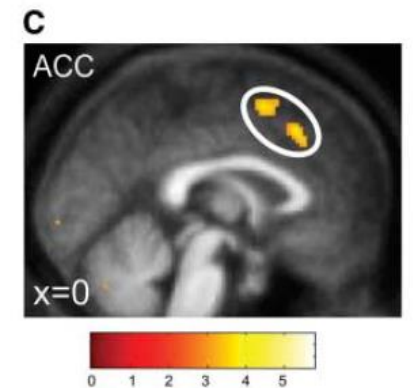
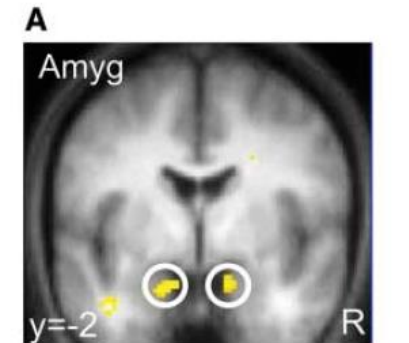
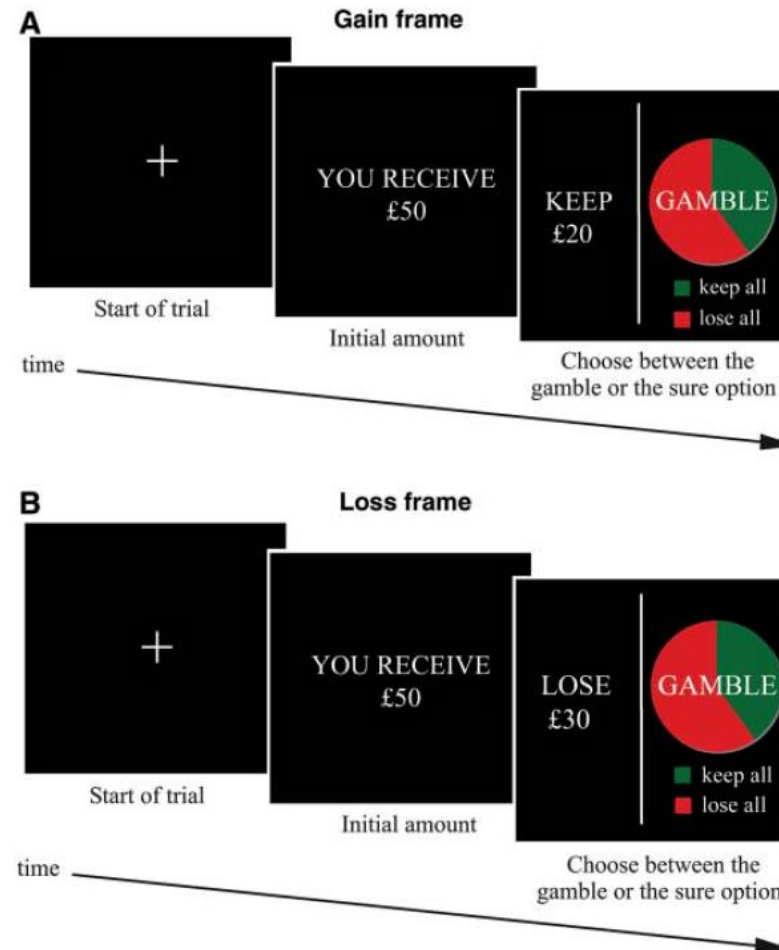
Frames, Biases, and Rational Decision-Making in the Human Brain

Benedetto De Martino,* Dharshan Kumaran, Ben Seymour, Raymond J. Dolan

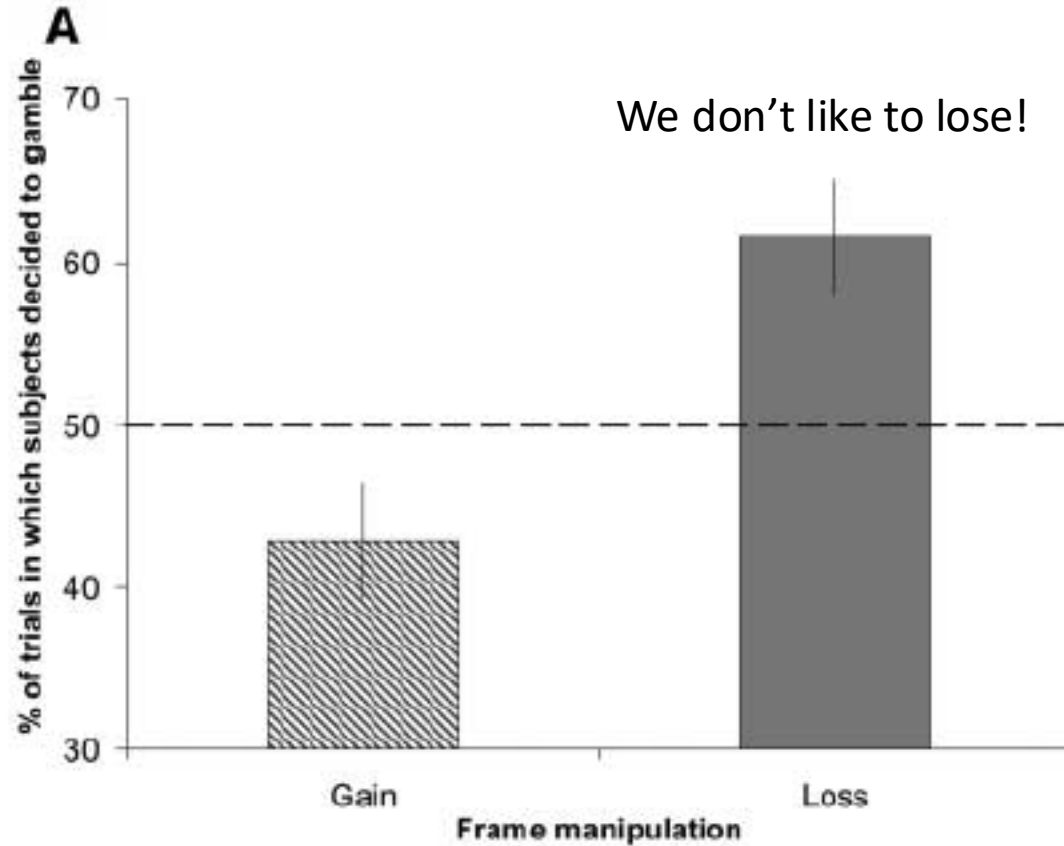
At the beginning of each trial, participants were shown a message indicating the starting amount of money that they would receive (e.g., “You receive 50”) (duration 2 s).

Subjects were instructed that they would not be able to retain the whole of this initial amount, but would next have to choose between a sure option and a gamble option (4 s).

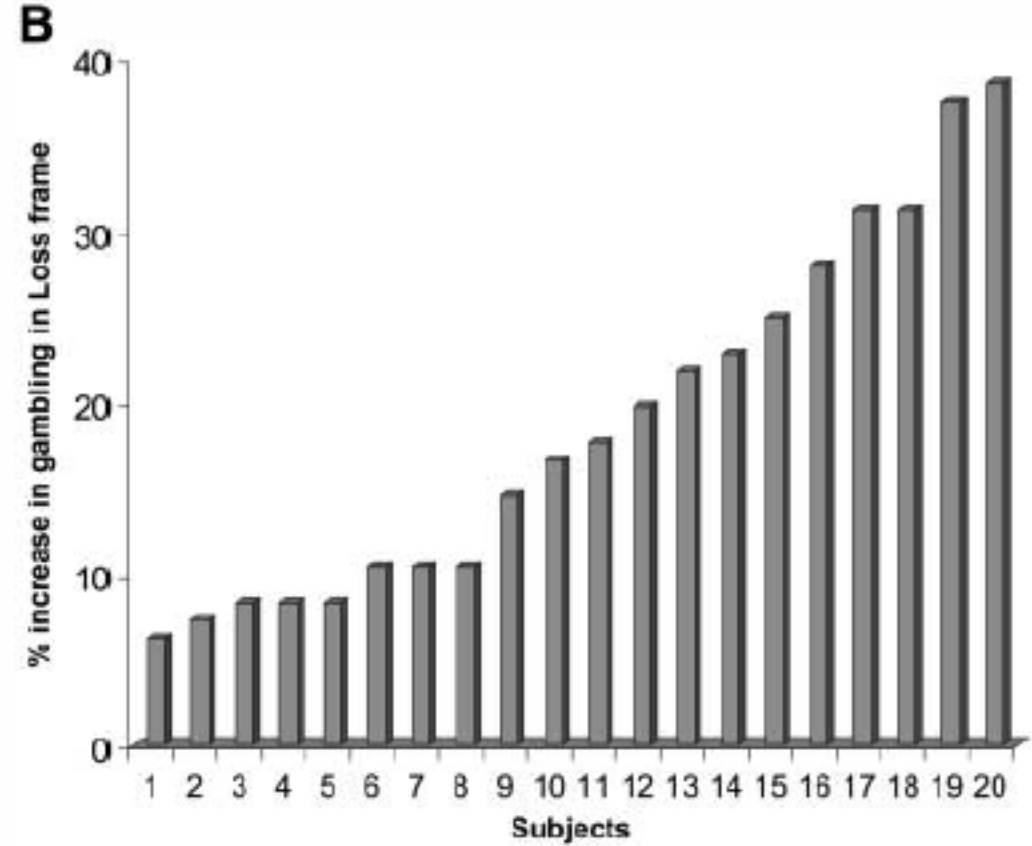
- The sure option was presented in the Gain frame trials as an amount of money retained from the starting amount (e.g., keep U20 of the U50)
- in the Loss frame trials as an amount of money lost from the starting amount (e.g., lose U30 of the U50).



Percentages of trials in which subjects chose the gamble option in the Gain frame and the Loss frame:

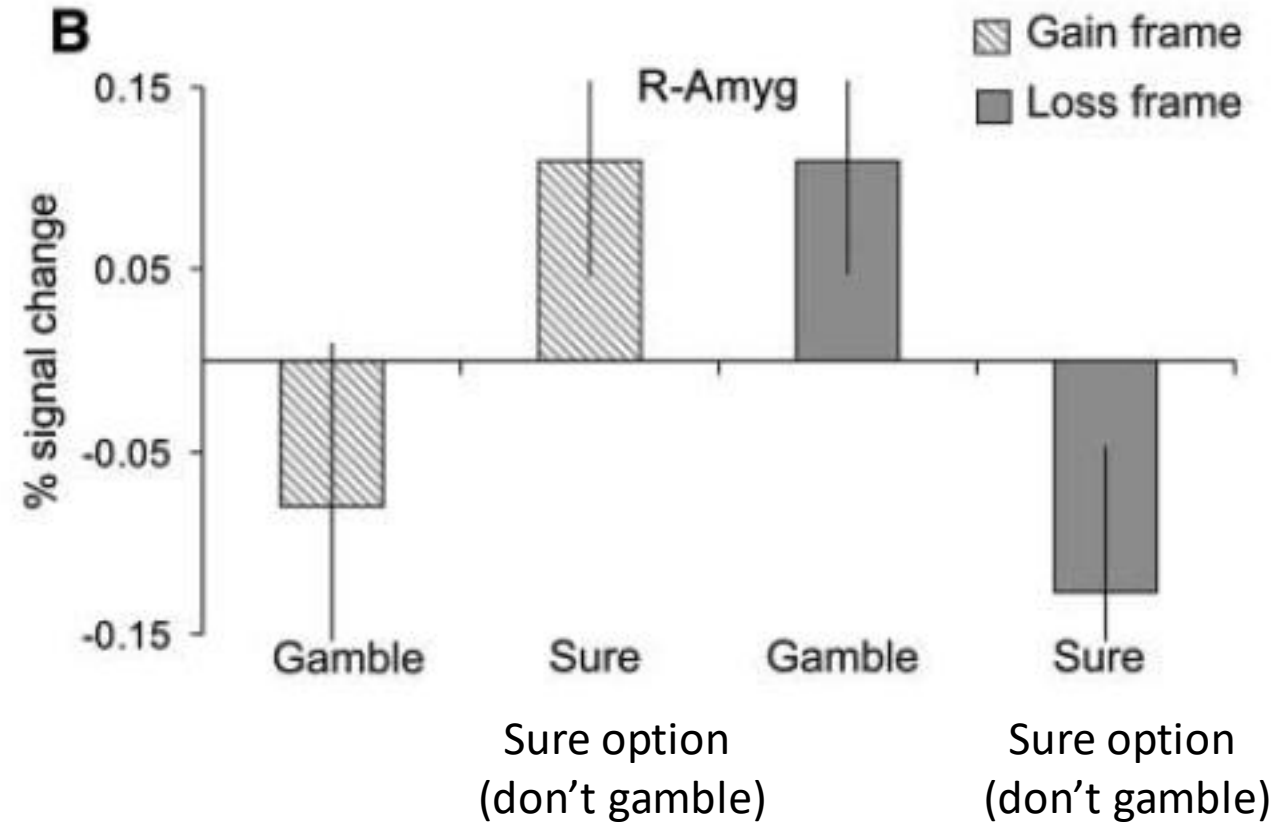
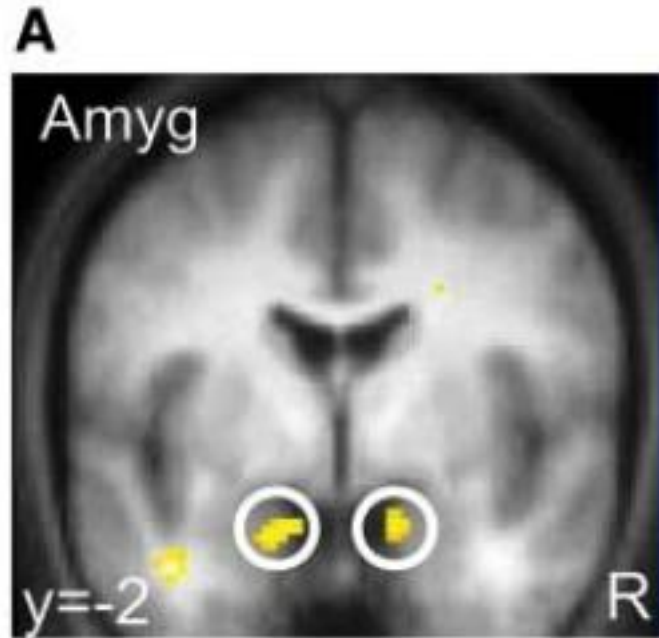


The dashed line represents risk neutral behavior (choosing the gamble option in 50% of trials)



All participants, to varying degrees, showed an effect of the framing manipulation!

Amygdala activated *differentially* depending on the framing:



If in a **gain framing**, amygdala increased activity **when not** gambling
But, if in the **loss framing**, amygdala increased activity **when** gambling

Can we quantify happiness?



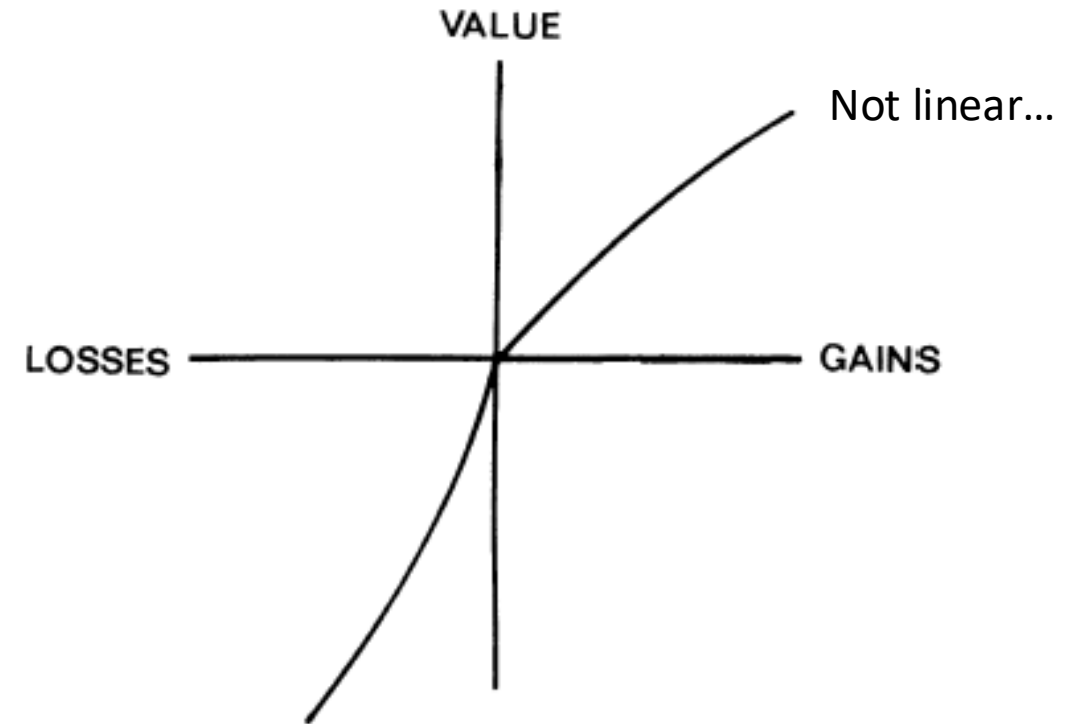
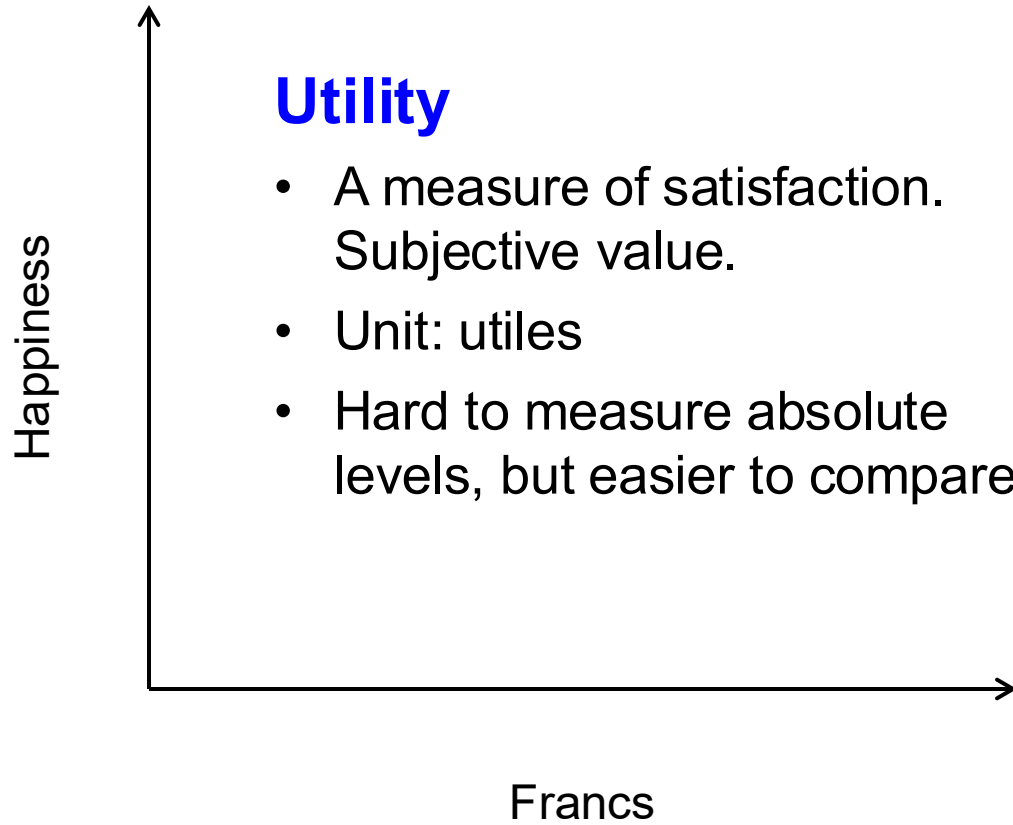
Suppose I were to tell you that I have a special fund and that I am going to give you each 10 CHF. That would make you happy.

How much would I have to give you to make you **twice** as happy?

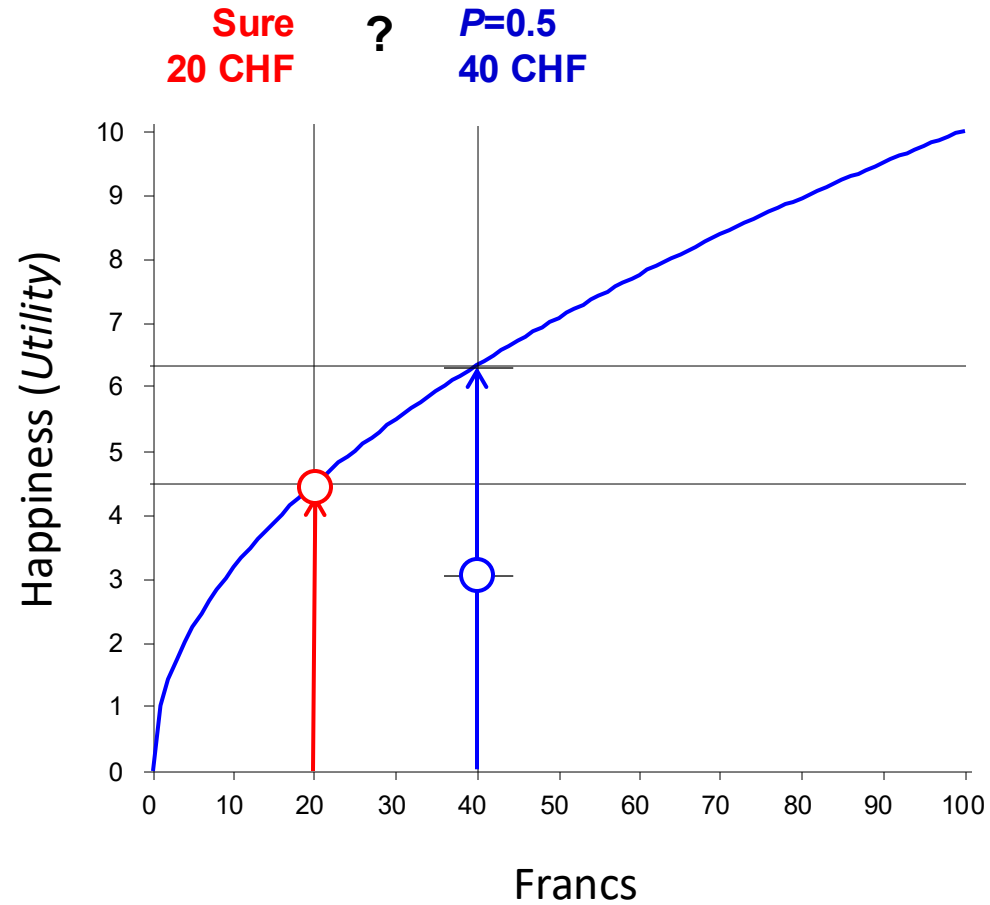
How does your “happiness” change as a function of money?

Utility

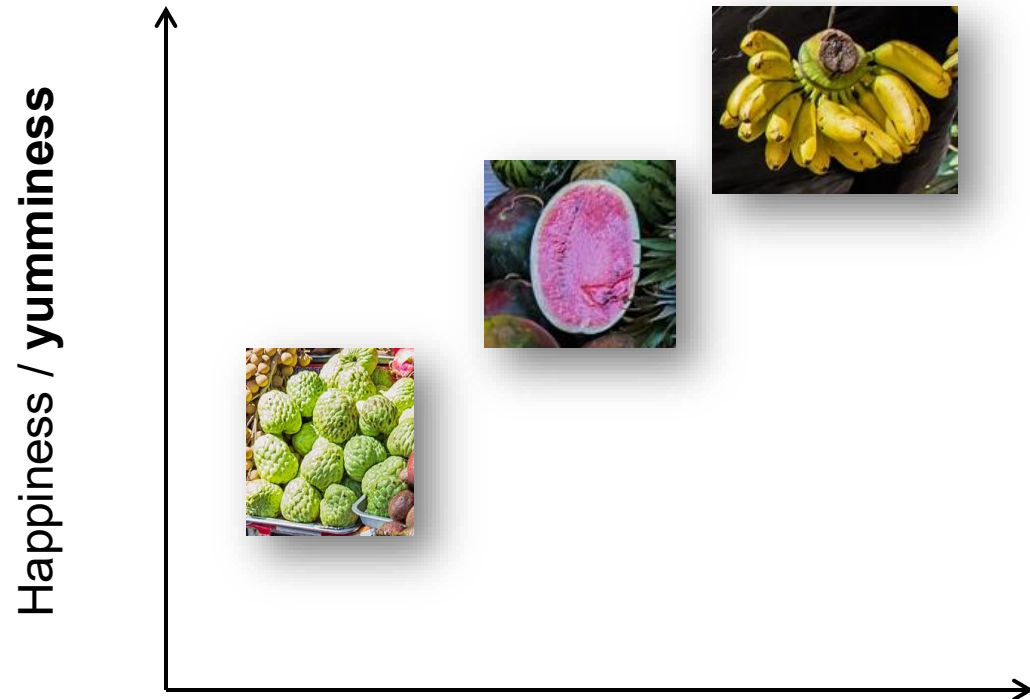
- A measure of satisfaction. Subjective value.
- Unit: utiles
- Hard to measure absolute levels, but easier to compare.



Concave utility function corresponds to risk-aversiveness



How do we learn and encode value?



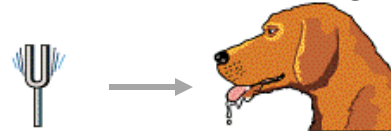
- What if you don't know the value (i.e., unknown foods)?
- Or, do you value variety? Sticking to what you like?

Pavlov Conditioning & Kamin's blocking experiment (1969)

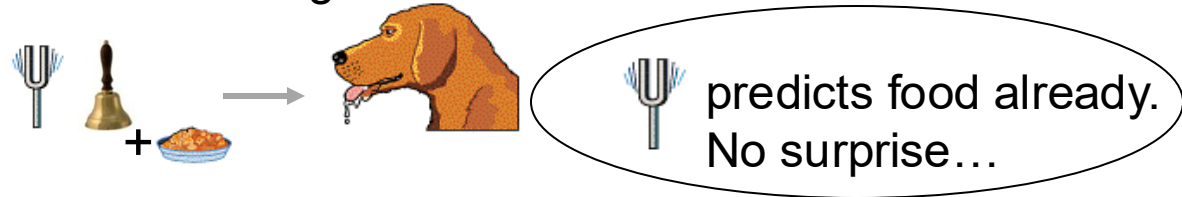
1. Conditioning



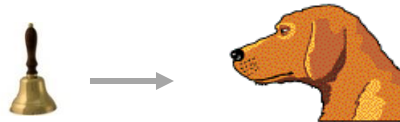
2. After conditioning



3. 2nd conditioning



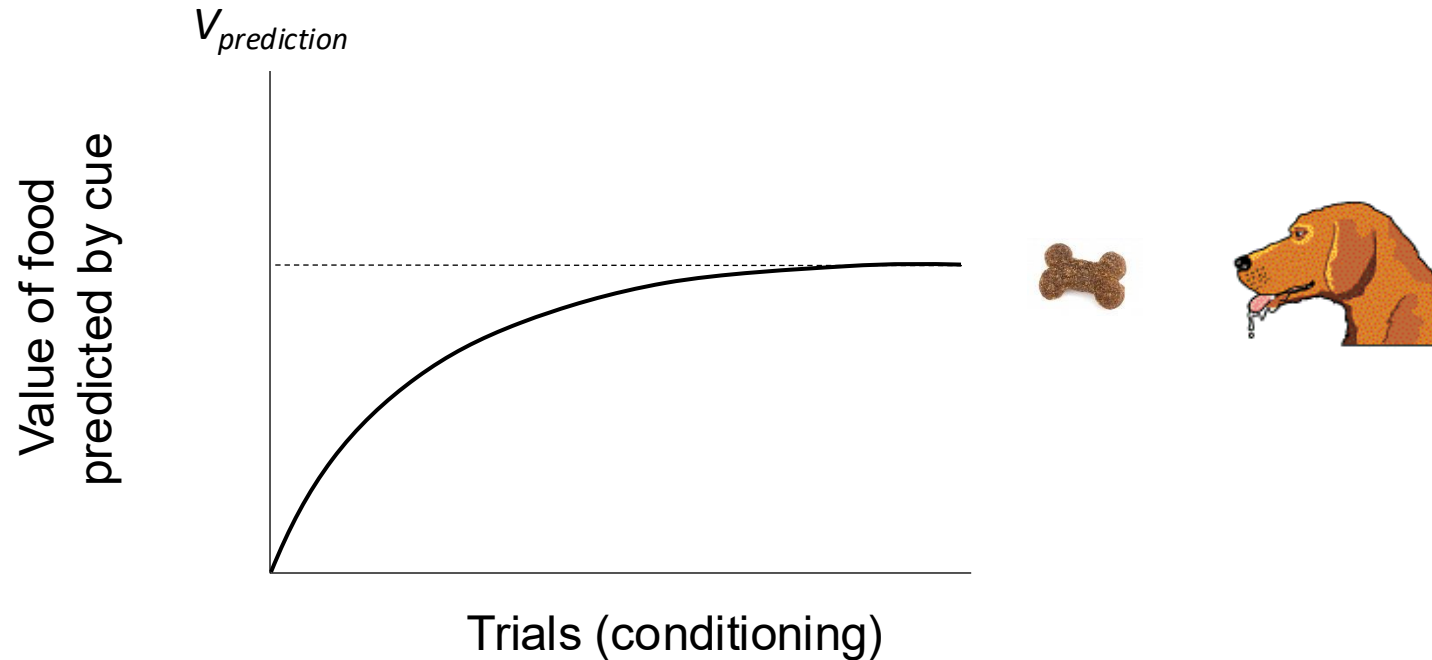
4. Test



Blocking

- Learning occurs only when expectation is violated

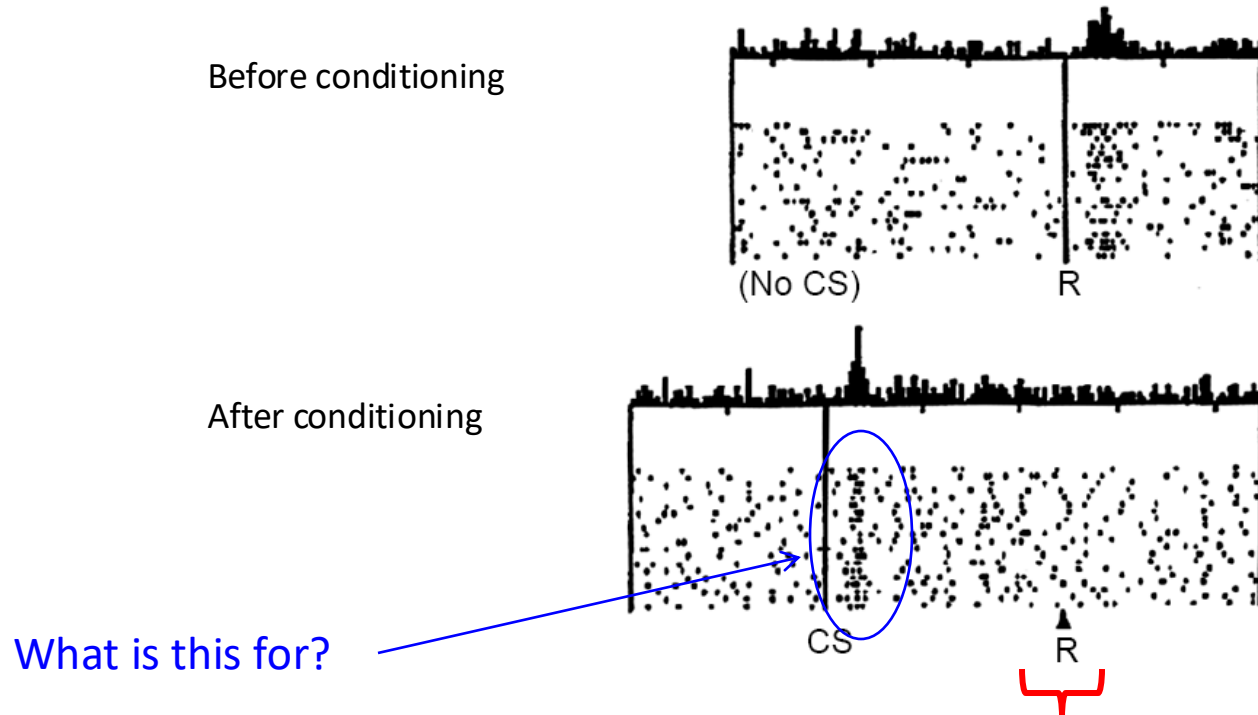
Rescorla, Wagner Rule (1972)



$$\Delta V_{prediction} = \alpha(V_{actual} - V_{prediction})$$

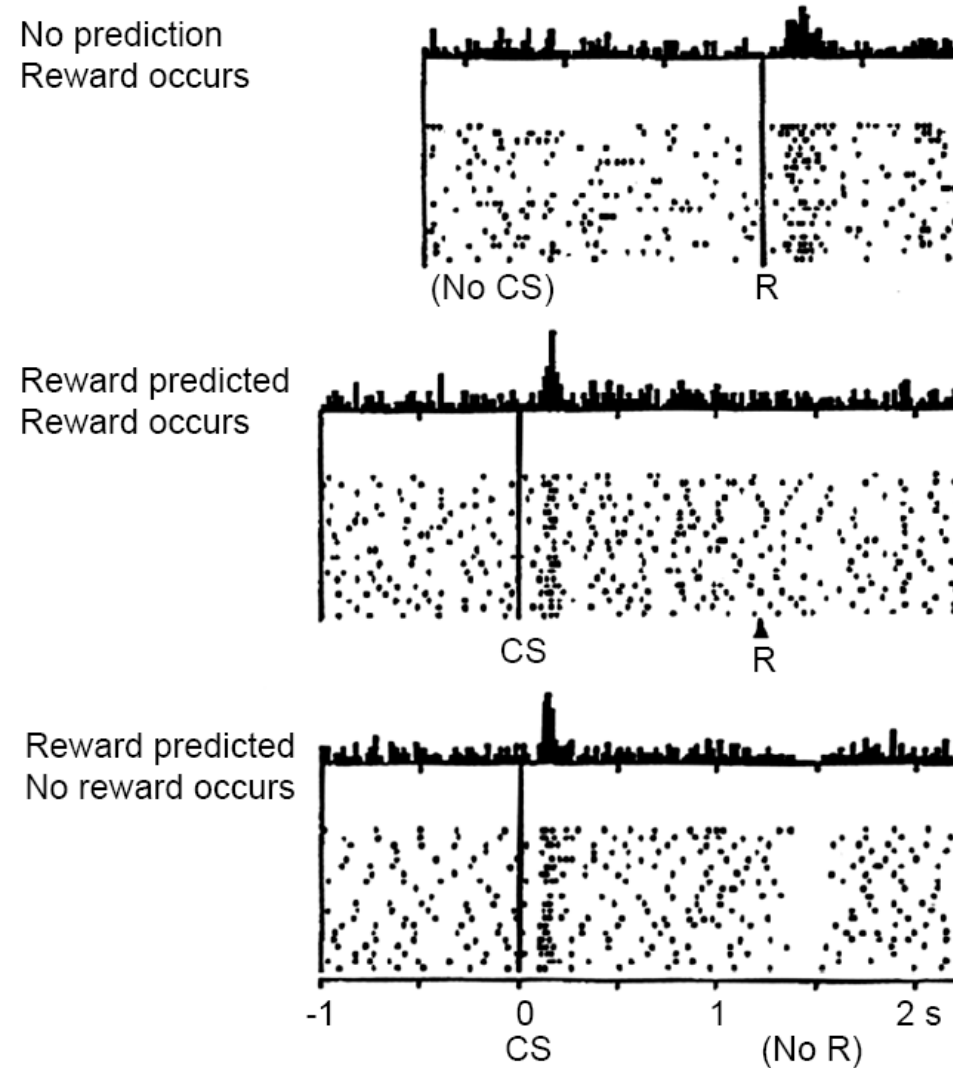
- The leaning rate depends on the difference between **what was predicted** and **what actually happened**.

Dopamine neurons in the ventral tegmental area

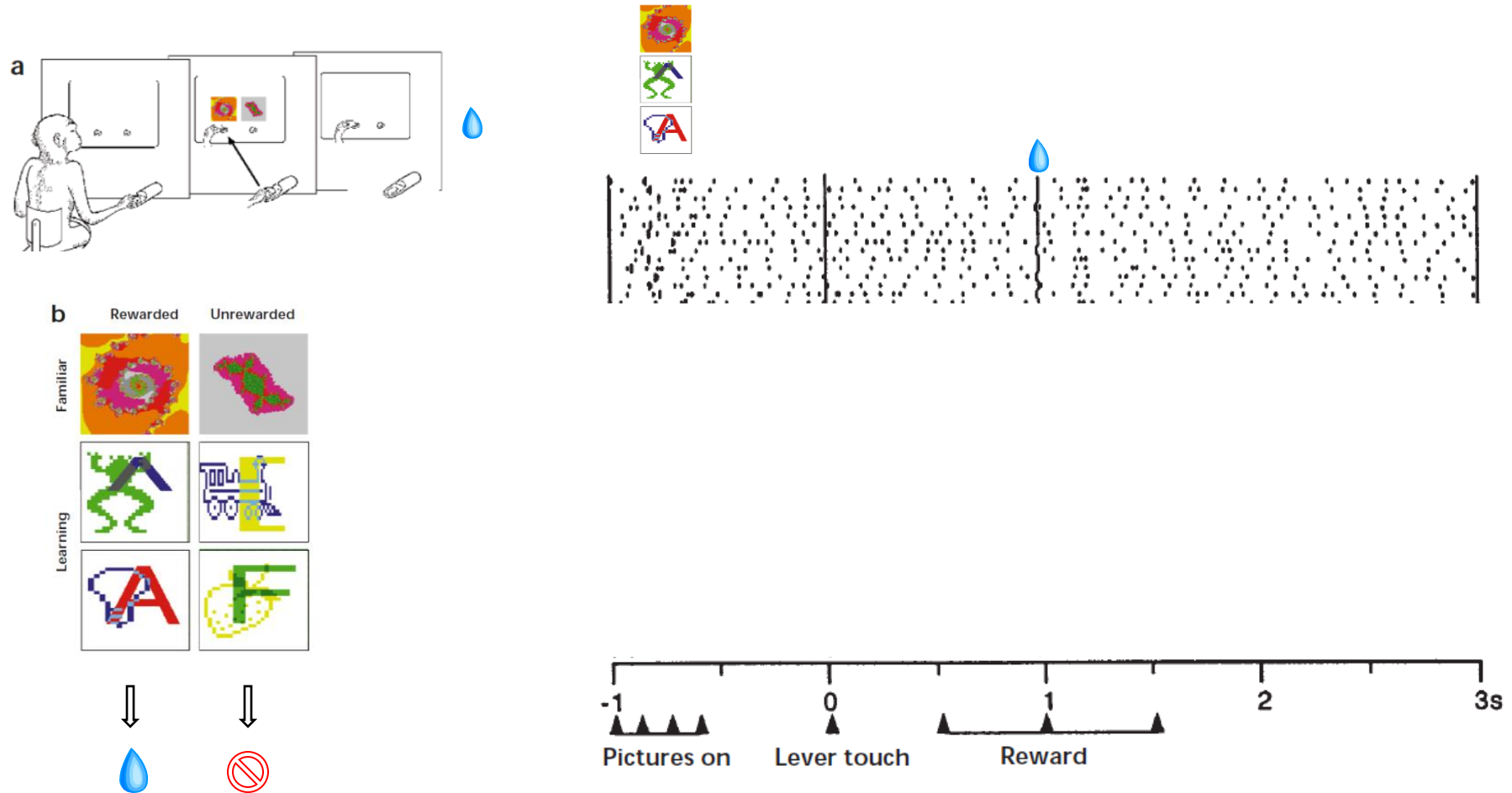


- Lack of reward responses when the reward was fully predicted
 - may explain blocking (new association to X does not occur)
 - Rescorla-Wagner rule

Dopamine as reward temporal difference (TD) error: reward prediction errors!

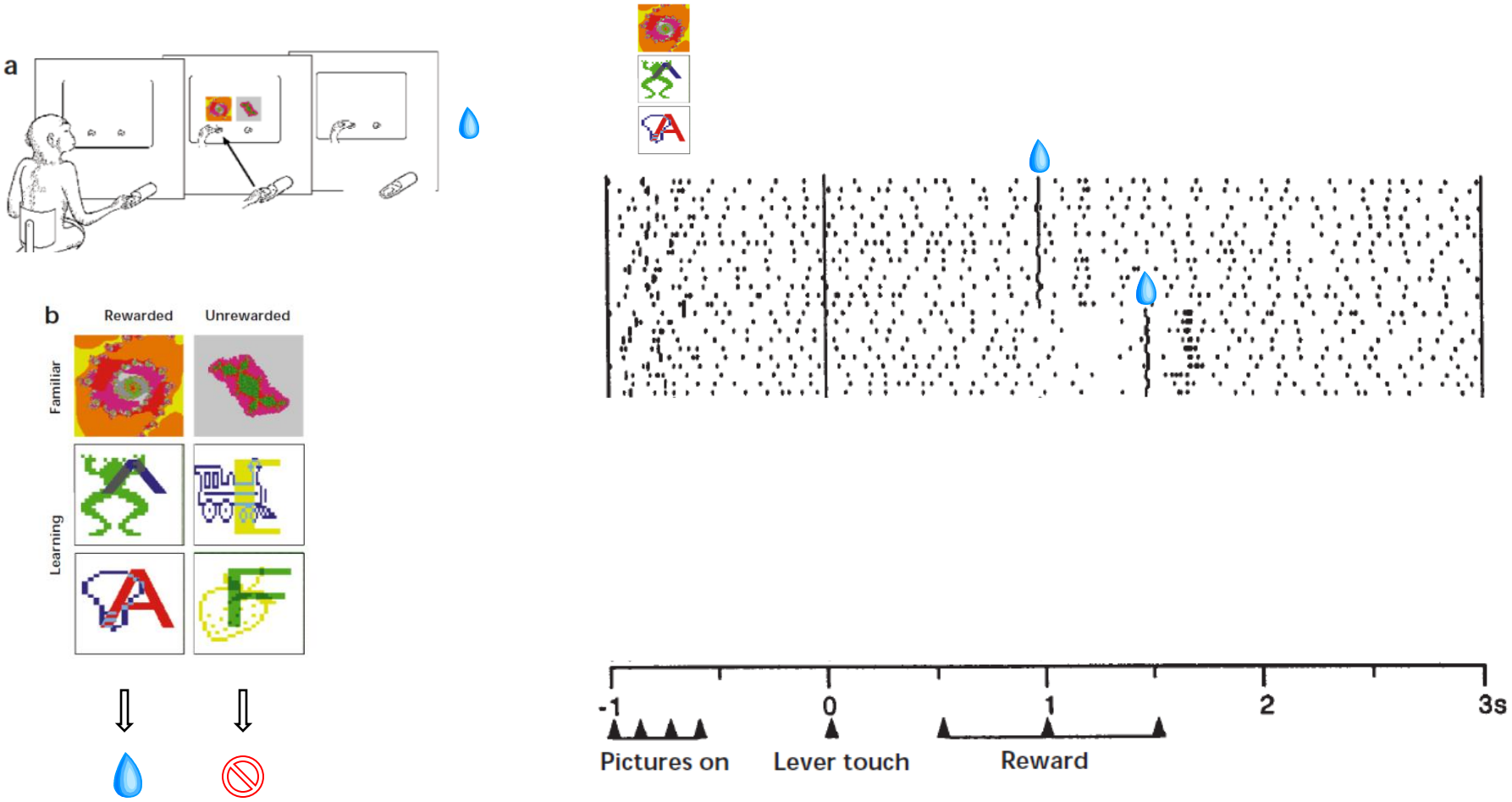


Reward prediction error: test by *temporal prediction*



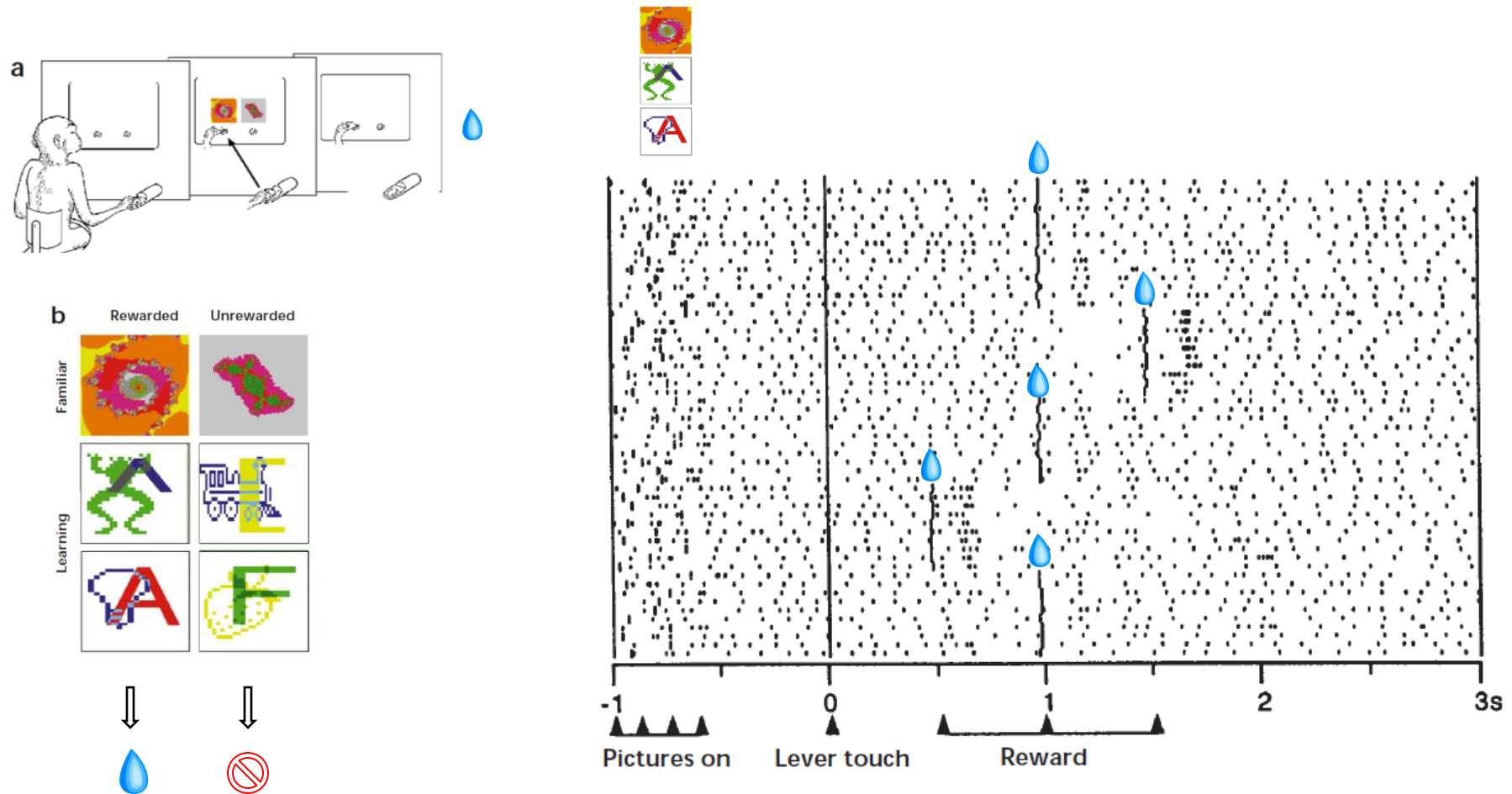
(Hollerman & Schultz, 1998, Dopamine neurons report an error in the temporal prediction of reward during learning)

Reward prediction error: test by *temporal prediction*



(Hollerman & Schultz, 1998, Dopamine neurons report an error in the temporal prediction of reward during learning)

Reward prediction error: test by *temporal prediction*

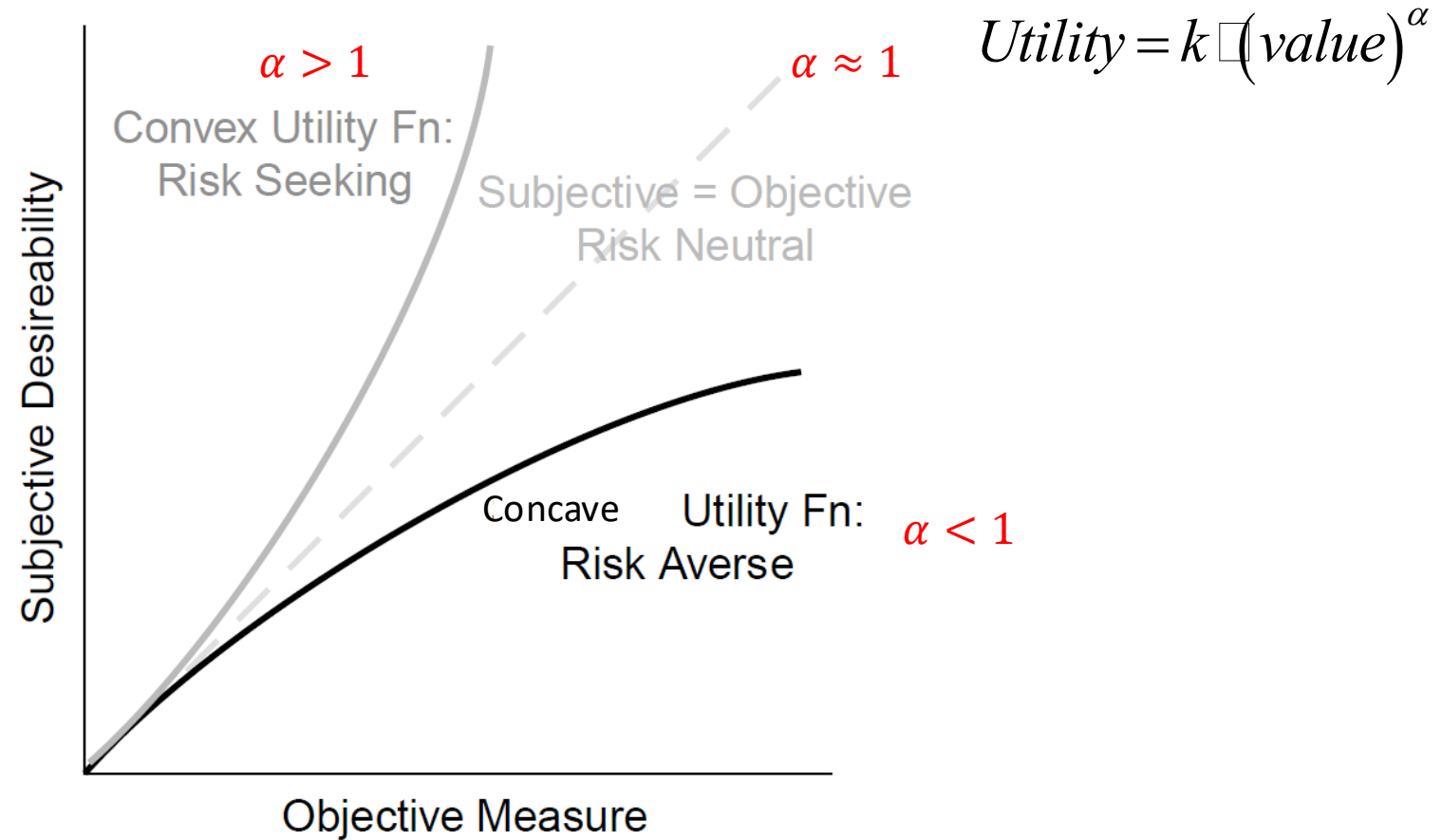


- Response depends on **predicted timing** of reward. (i.e. not simply “values”)

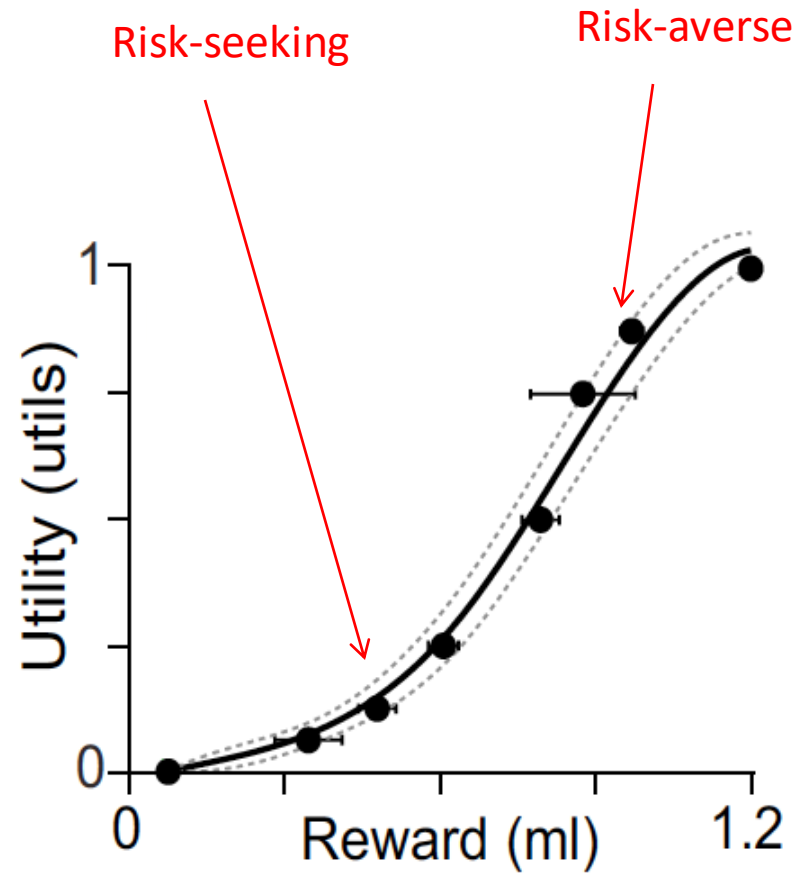
(Hollerman & Schultz, 1998, Dopamine neurons report an error in the temporal prediction of reward during learning)

Is dopamine “utility”?

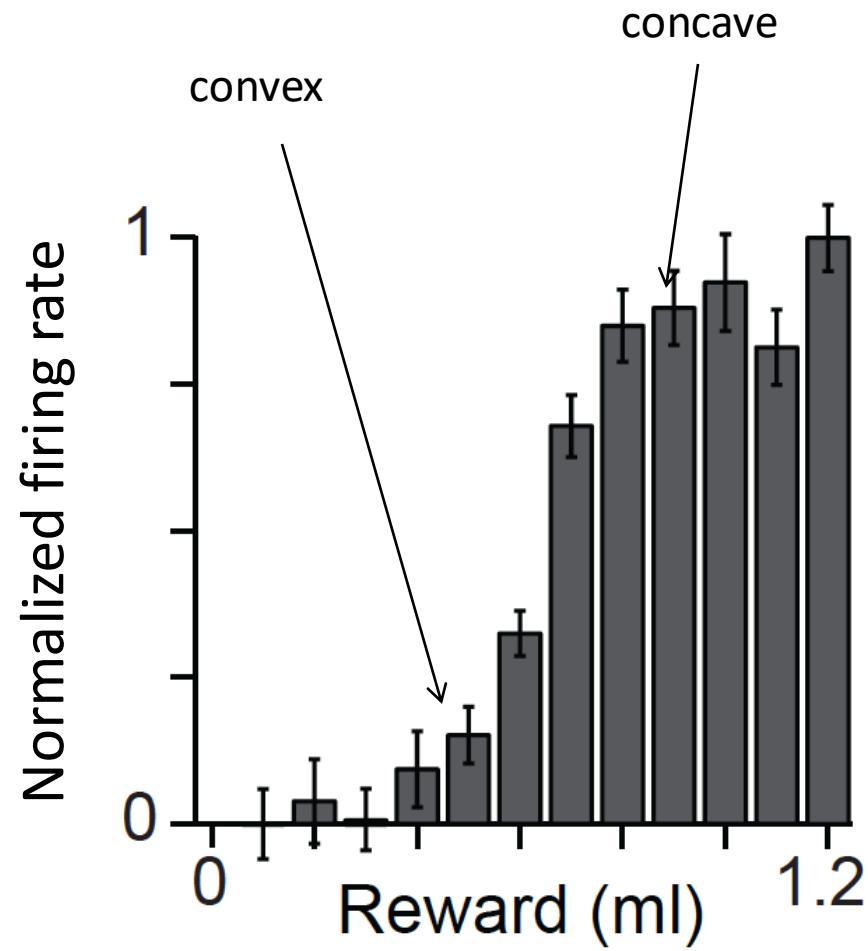
Risk preference and utility functions



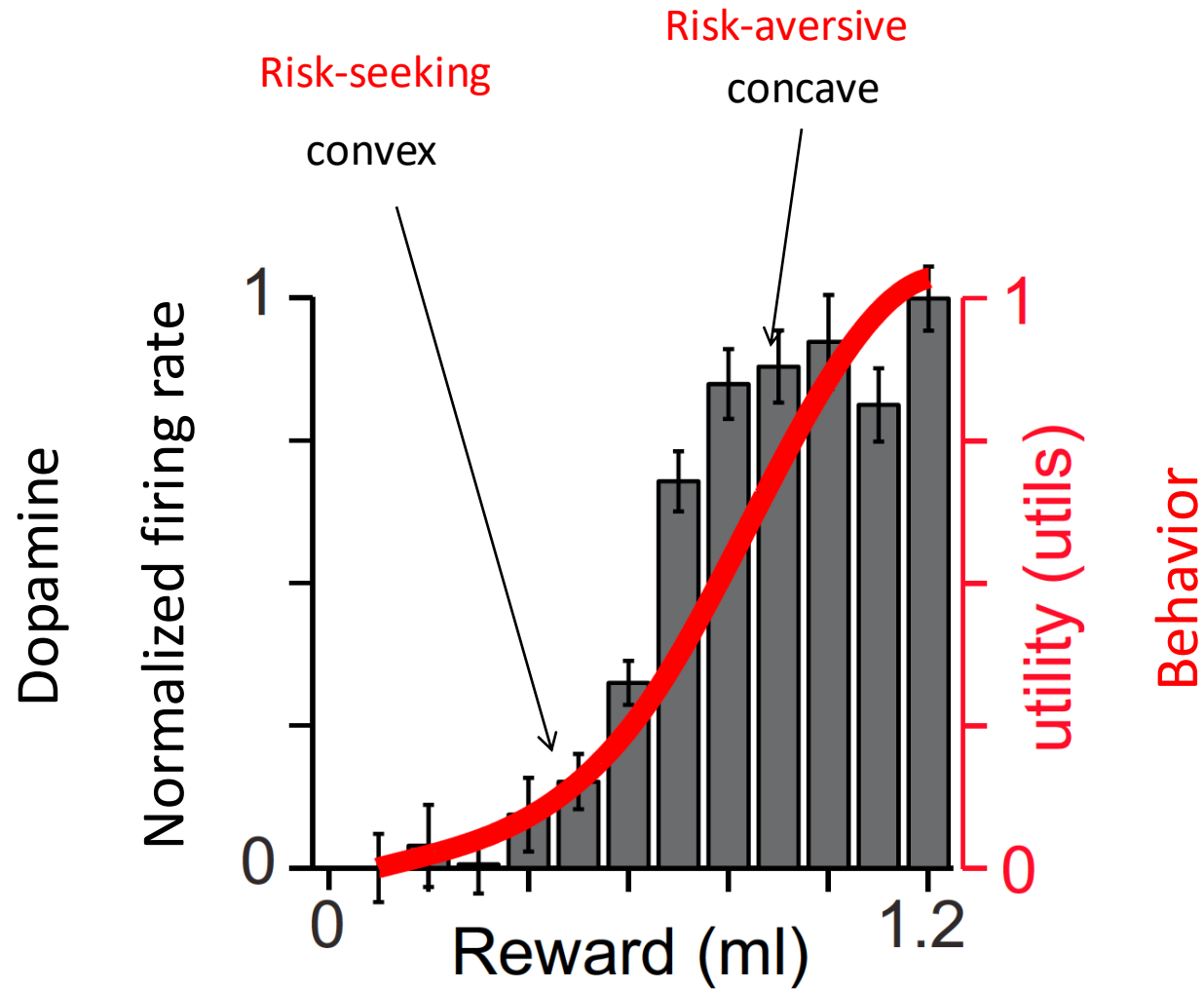
“Utility function” of a monkey



Dopamine neurons' response to different amounts of juice



Dopamine response function matches monkey's risk preference

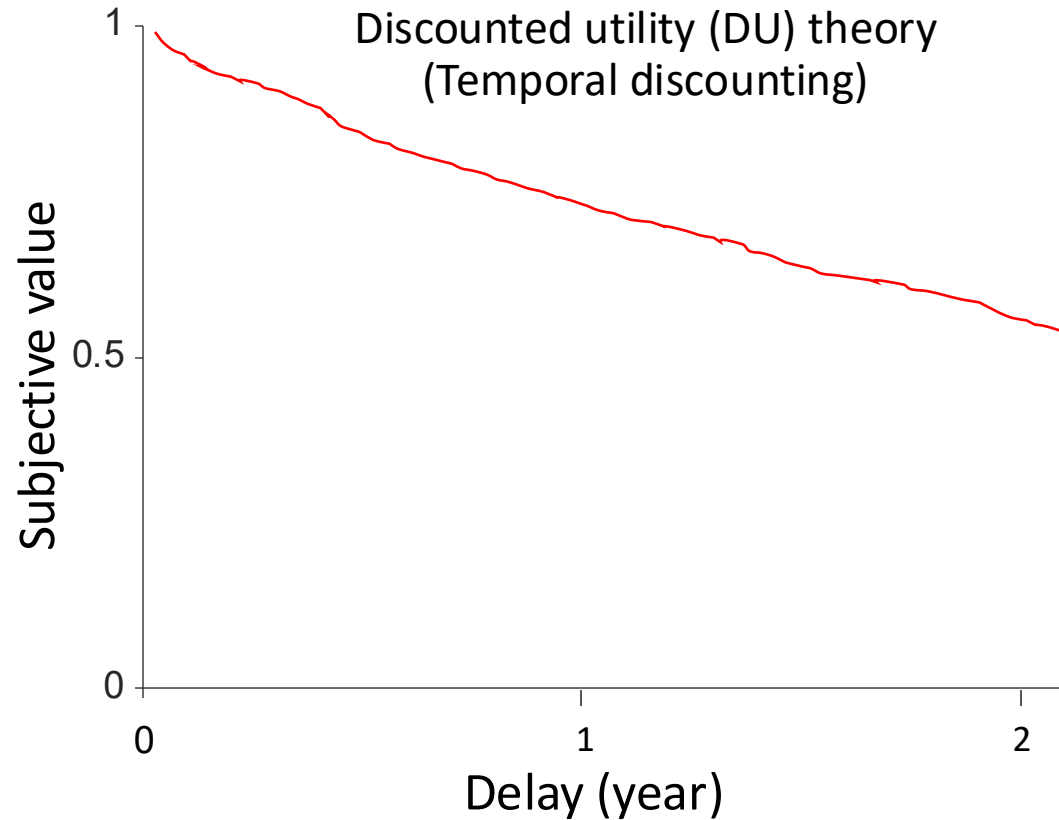


(Stauffer, Lak and Schultz, Current Biology, 2014)

Decision making over longer timescales

- A: 100 CHF now
- B: 110 CHF tomorrow

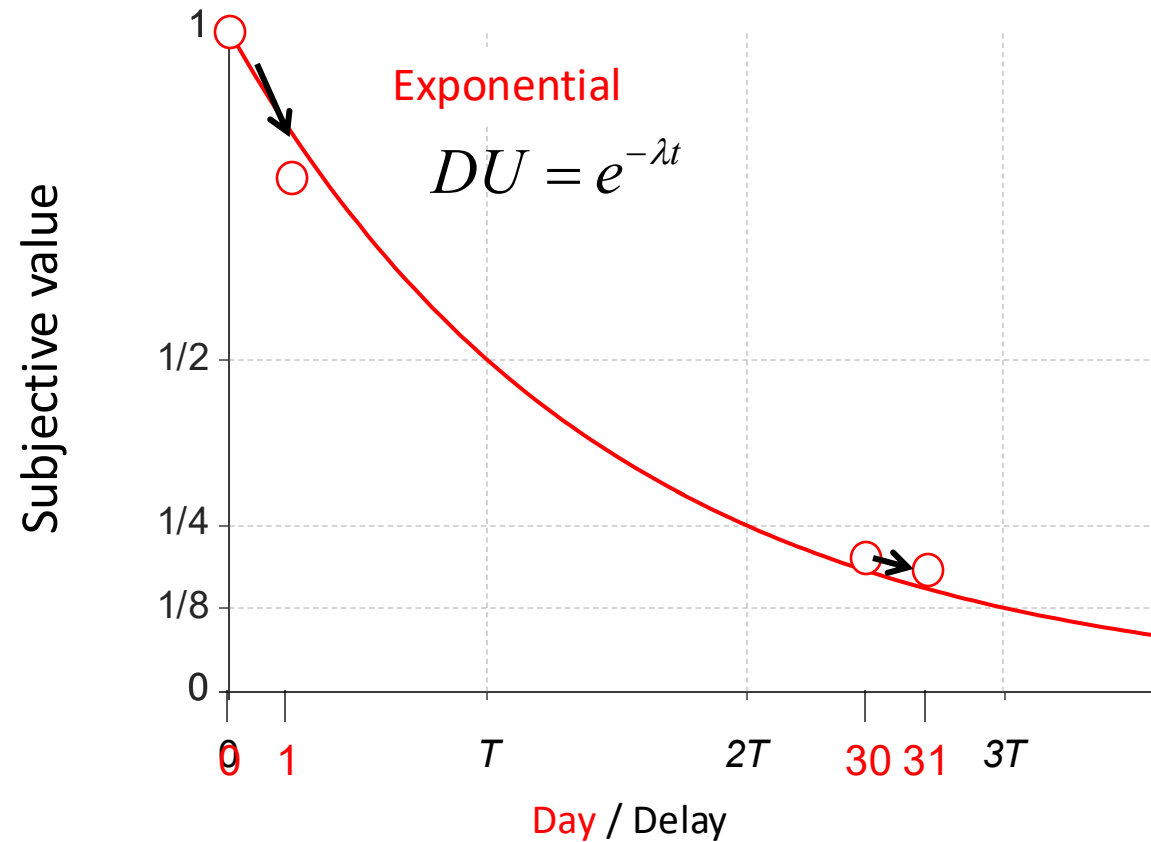
- A: 100 CHF in 30 days
- B: 110 CHF in 31 days



Future rewards are discounted!

Preference reversal – “dynamic inconsistency”

“Normative” temporal discounting



$$\frac{dDU}{dt} = -\lambda DU$$

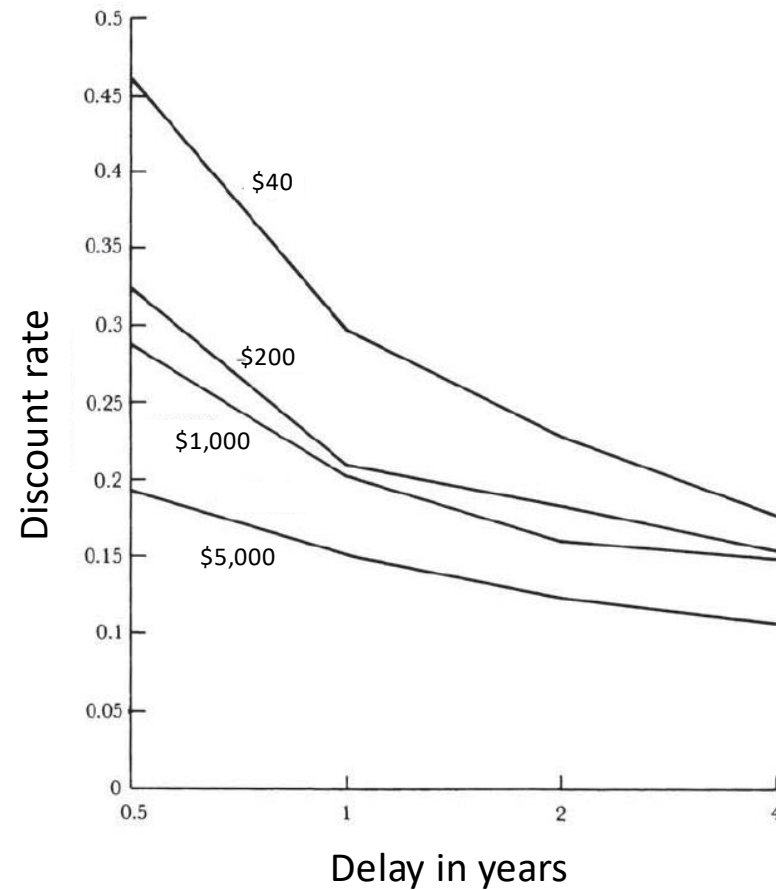
or

$$\frac{DU'}{DU} = -\lambda$$

DU: discounted utility

- The rate of decline is constant (decrementing by a fixed percentage for each time step).
- It treats each time period equivalently.

Thaler (1981); Benzion, Rapoport, Yagil (1989)



- Discount rates declined sharply with the length of time to be waited.
- Discount rates for small amounts were very high, while those for larger amounts were more reasonable.
- *Discount rates for gains were much higher than for losses.*

Ⓐ: 100 CHF now Short

B: 110 CHF *after 30 days* Long

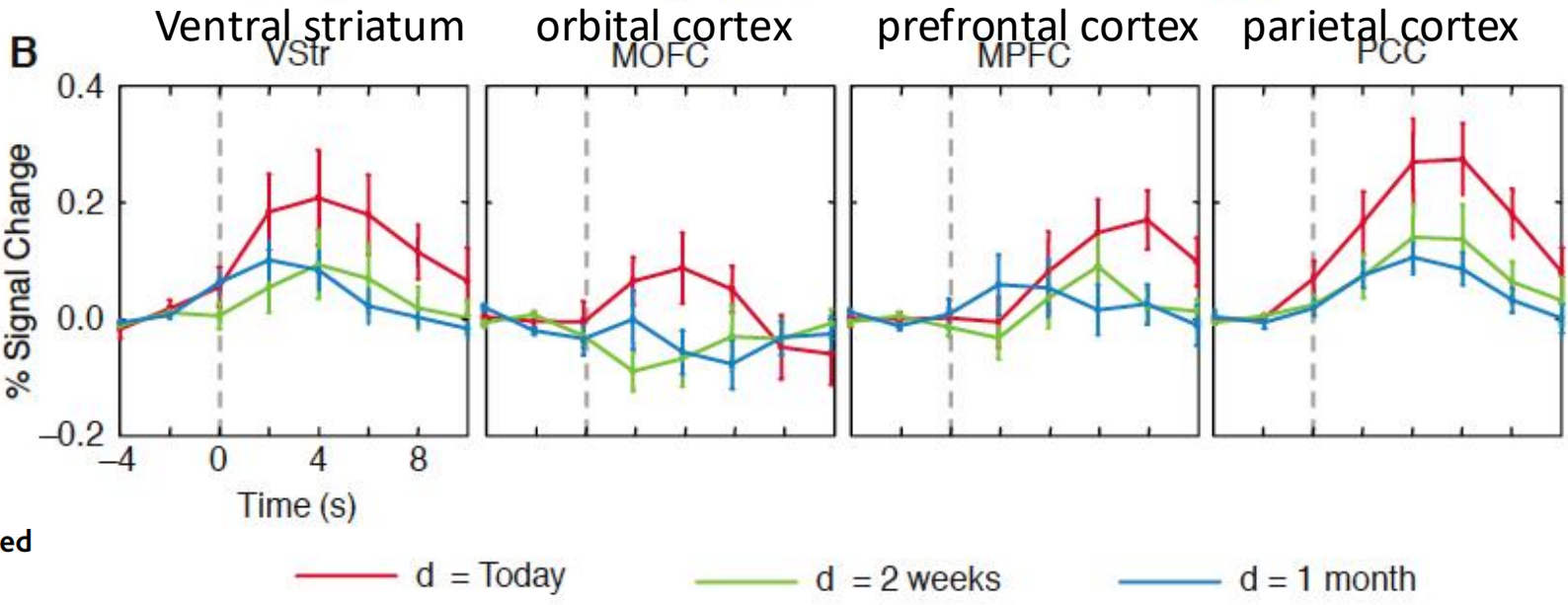
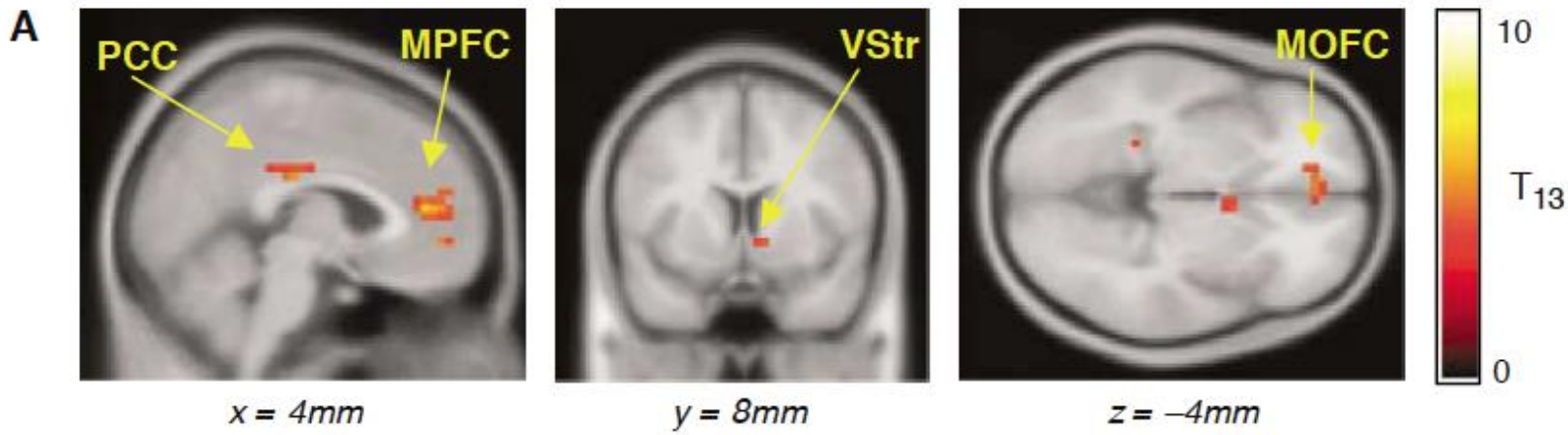


A: 100 CHF after 30 days Long

Ⓑ: 110 CHF after 31 days Long

Hypothesis: Different neural systems value
immediate and delayed rewards

Brain areas that are preferentially activated for choices in which money is available immediately 🔥



Separate Neural Systems
Value Immediate and Delayed
Monetary Rewards

Samuel M. McClure,^{1*} David I. Laibson,² George Loewenstein,³
Jonathan D. Cohen^{1,4}

Separate Neural Systems Value Immediate and Delayed Monetary Rewards

Samuel M. McClure,^{1*} David I. Laibson,² George Loewenstein,³ Jonathan D. Cohen^{1,4}

When humans are offered the choice between rewards available at different points in time, the relative values of the options are discounted according to their expected delays until delivery. Using functional magnetic resonance imaging, we examined the neural correlates of time discounting while subjects made a series of choices between monetary reward options that varied by delay to delivery. We demonstrate that two separate systems are involved in such decisions. Parts of the limbic system associated with the midbrain dopamine system, including paralimbic cortex, are preferentially activated by decisions involving immediately available rewards. In contrast, regions of the lateral prefrontal cortex and posterior parietal cortex are engaged uniformly by intertemporal choices irrespective of delay. Furthermore, the relative engagement of the two systems is directly associated with subjects' choices, with greater relative fronto-parietal activity when subjects choose longer term options.

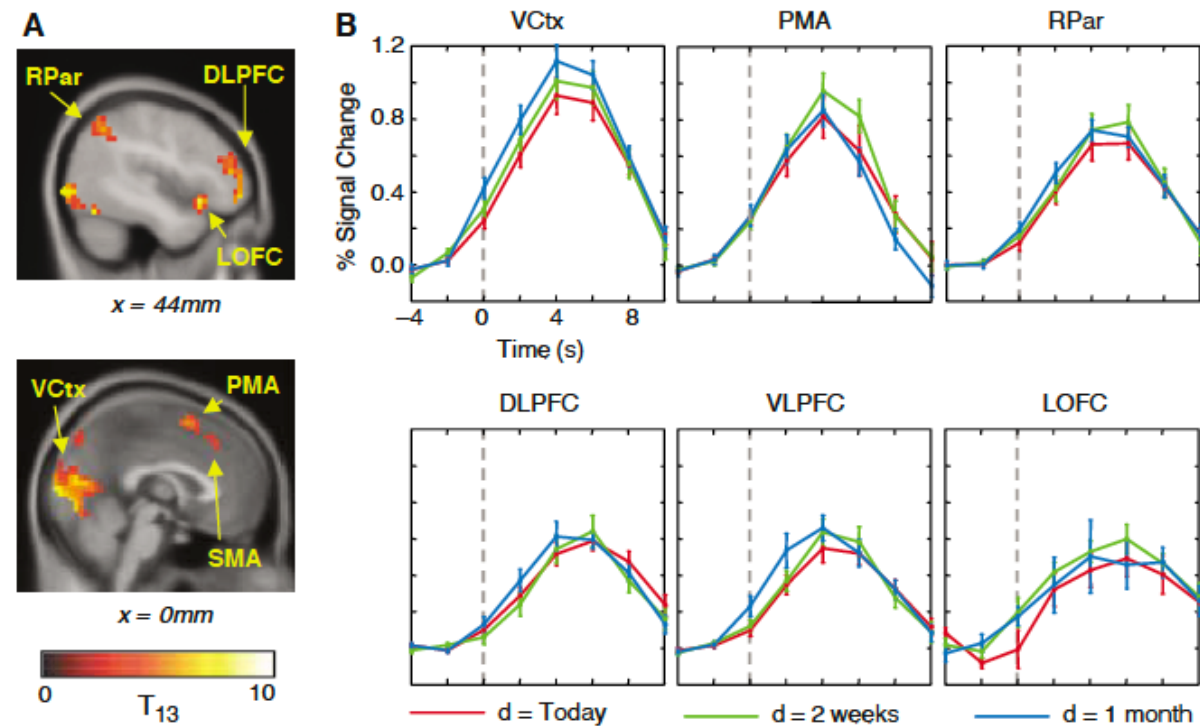


Fig. 2. Brain regions that are active while making choices independent of the delay (d) until the first available reward (δ areas).

Discounting & Addiction

- Discount rates are higher in smokers, alcohol users, stimulant users, opiate users, and pathological gamblers



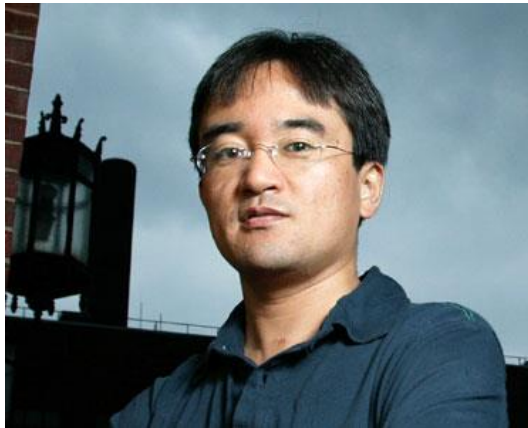
Discounting & Addiction

- Higher discount rates in adolescence predict later smoking & alcohol use (Audrain-McGovern et al., 2009; Fernie et al., 2013)
- Higher discount rates predict smoking cessation treatment failure (Krishnan-Sarin et al, 2007; MacKillop & Kahler, 2009; Sheffer et al., 2012; Yoon et al., 2007)
- Withdrawal increases discount rates (Badger et al., 2007, Field et al., 2006; Giordano et al., 2002; Mitchell, 2004; Yi & Landes, 2012)



Take Homes:

- Illusions allow us to understand how conscious perception shapes “what we see” and how we act
- You should be able to delineate the neural pathways involved; from visual input to actions
- quantitative methods to measure neural responses (encoding, decoding), tuning curves (lower & higher visual areas)
- Consider how we link neurons and perception!
- Drift diffusion models (accumulation of noisy signal) explain the relationships between the speed and accuracy in perceptual decision tasks.
- LIP neurons increase or decrease their firing rates as evidence accrues for or against the direction associated with the choice target in the response field of each neuron.
- Neural decoding can be used to “read out” perception/stimulus
- Economic theories of decision making (normative, descriptive) predict human behavior (risk, gambling)
- We are more sensitive to losses than to gains (concave, convex)
- Framing has a large impact on how neural activity (see amygdala slide), and behavior!
- Dopamine is not reward, its reward prediction errors – influenced by timing, utility 😊
- Discounting of rewards is critical in how we behave: (100 now, or 1000 much later?)



Prof. Naoshige Uchida
Harvard University

*Special thanks to Prof. Uchida
for slides & discussions over many years!*

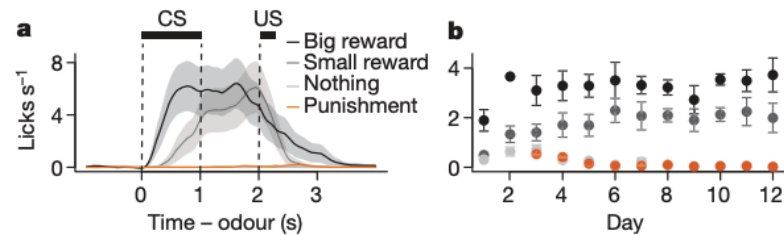
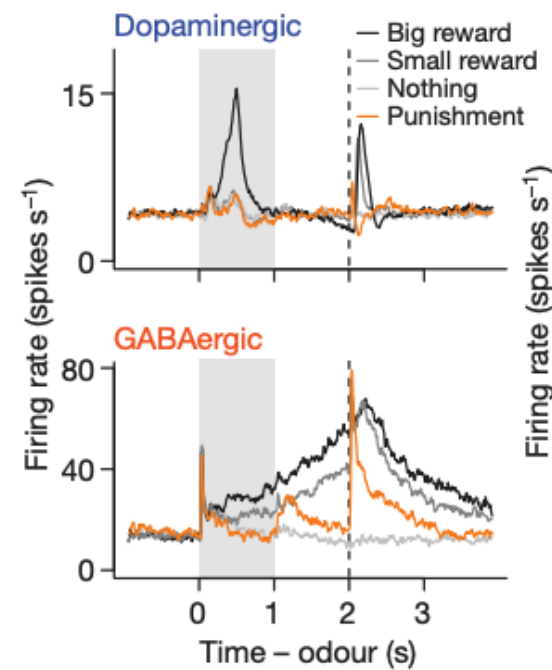


Figure 1 | Odour-outcome association task in mice. **a**, Licking behaviour from a representative experimental session. Black bars indicate CS and US delivery. Shaded regions around lick traces denote standard error of the mean (s.e.m.). **b**, Mean \pm s.e.m. licks during the delay between CS and US as a function of days of the experiment across animals.



Neuron-type-specific signals for reward and punishment in the ventral tegmental area

Jeremiah Y. Cohen^{1*}, Sebastian Haesler^{1*}, Linh Vong², Bradford B. Lowell² & Naoshige Uchida¹

