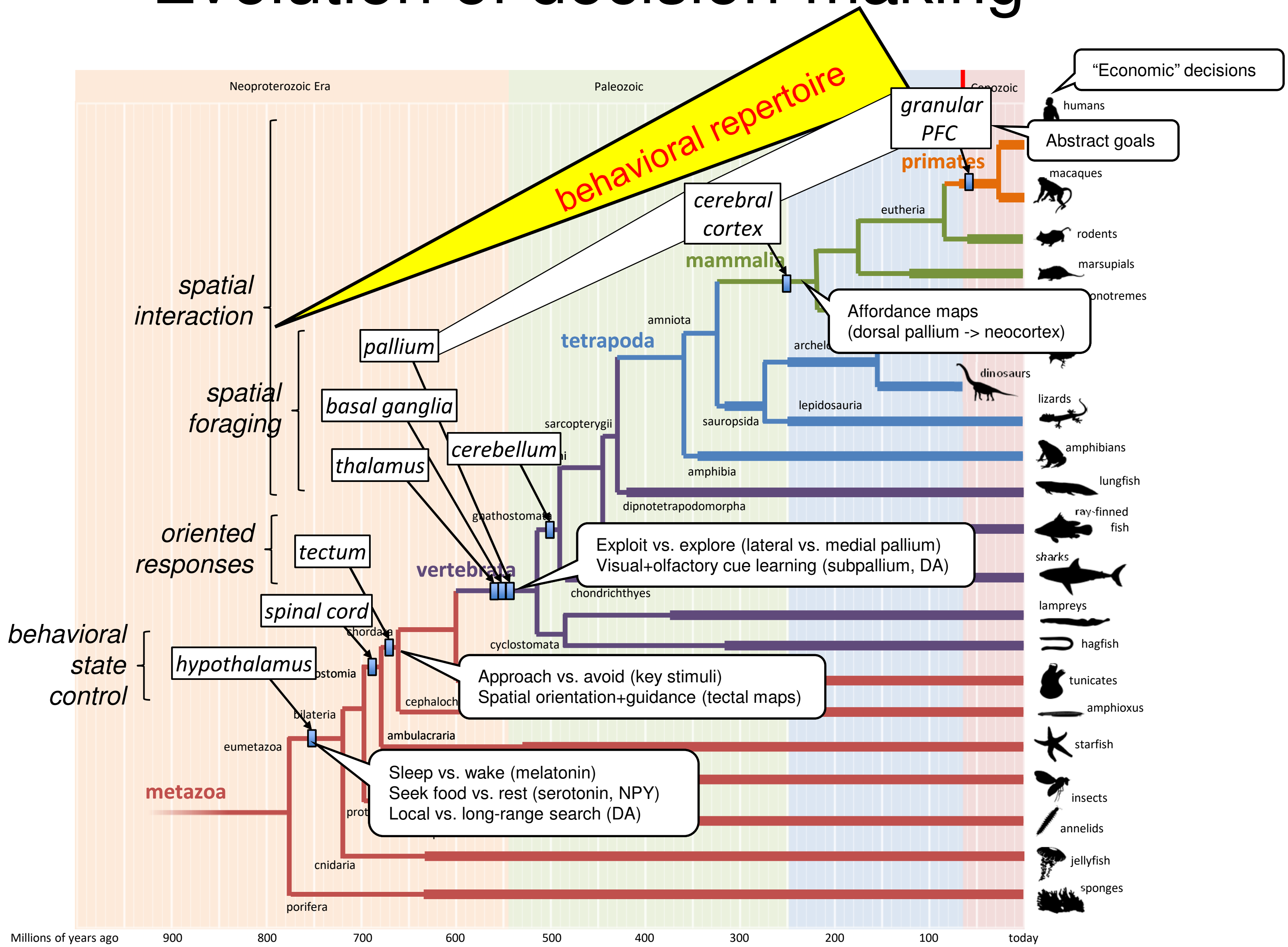
Neur 603
Decision-making

- Types of decisions
- Perceptual decisions
    - Motivated procrastination and race models
    - Optimal accumulation of evidence
    - Neural correlates of accumulation mechanisms
    - Variations of accumulation models
    - Recurrent attractor models
- Lab: Recurrent attractor models

Types of decisions

- Perceptual / categorical
  - What the hell is that thing?
- Economic / value-based
  - Which house should I buy?
- Probabilistic
  - Should I call, raise, or fold?
- Emotional
  - Should I propose? Should I accept?
- Physical
  - Should I run left or right?
- Scientific
  - What kind of decision-making should I study?

Evolution of decision-making



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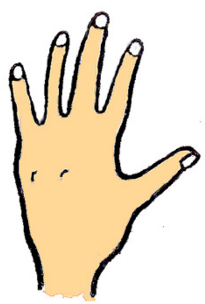
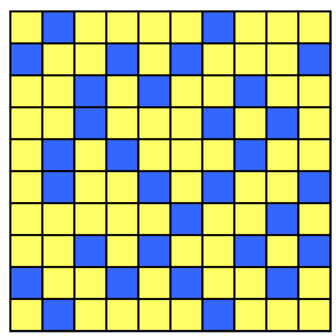
Perceptual decisions

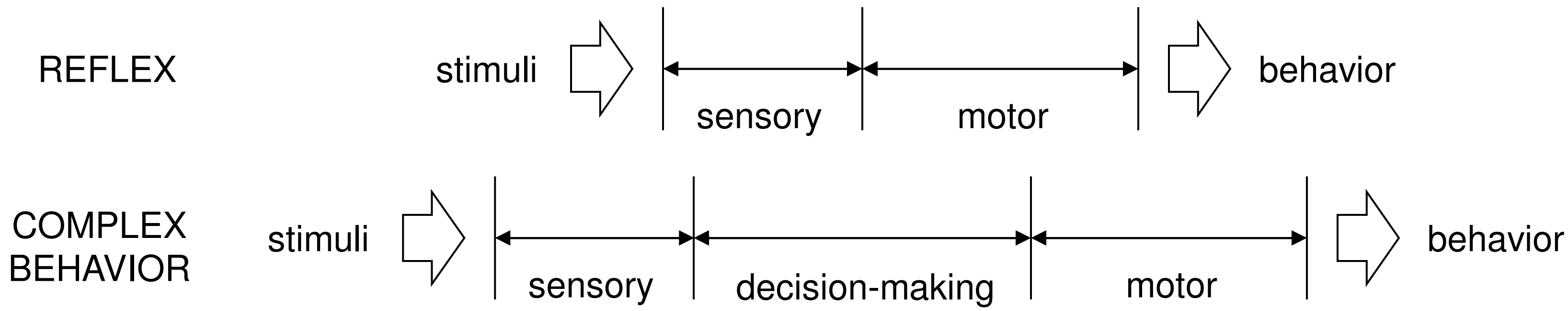
- Question: Are the more blue or yellow squares?
- Response:
  - If more blue, slap your desk with your right hand
  - If more yellow, slap your desk with your left hand





Mental chronometry

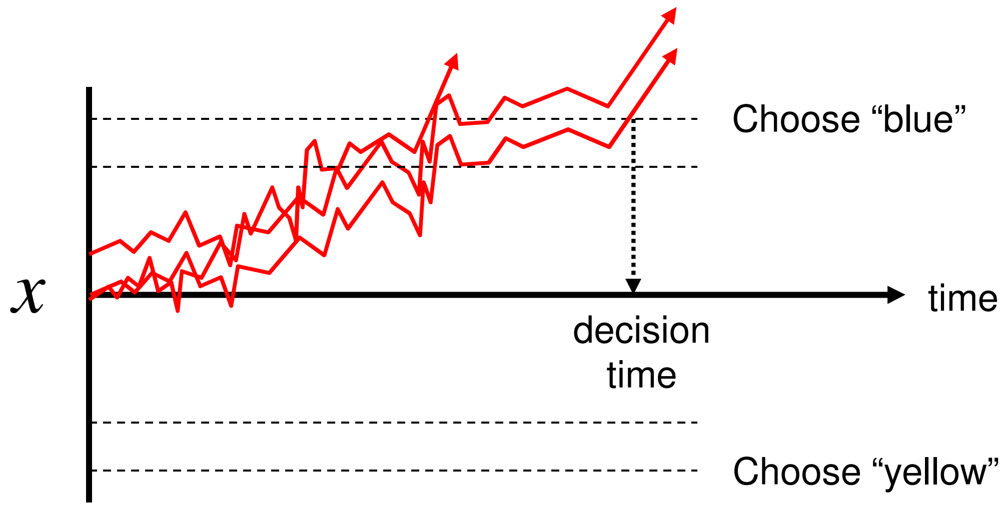
- Can we deduce something about the processes of decision-making by measuring the timing of decisions?



- Some phenomena:
  - Harder choices → slower, more variability
  - More common → faster
  - More choices → slower

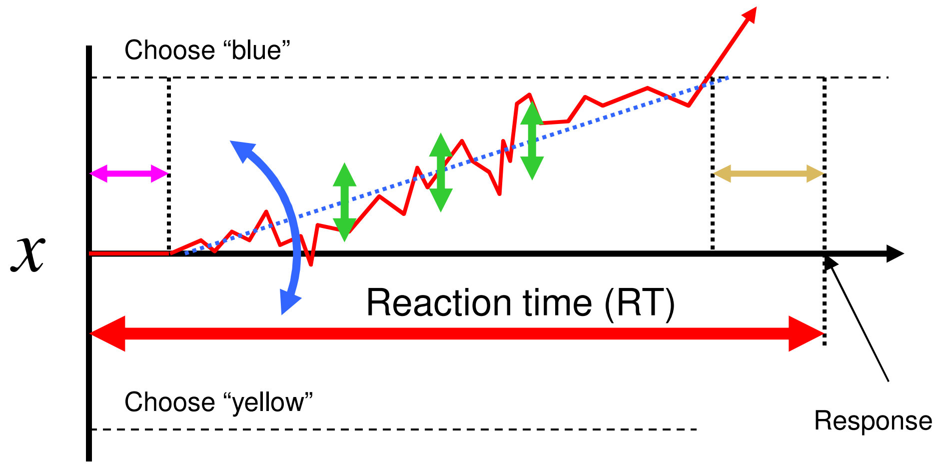
“Diffusion model”

- Hypothesis: Deliberation is similar to a random walk



- Some noisy mental variable (x) is changing in time, biased by sensory information, until it crosses one of two decision thresholds
  - The strength of the evidence determines the rate of drift
  - The desired accuracy determines the threshold
  - Any prior bias determines the starting point

Different kinds of noise



- Variation in non-decision processes
  - Delays in sensory processing
  - Delays in response initiation
- Variation between trials
  - E.g. Changes in arousal / attention
- Variation within a trial
  - E.g. Neural activity fluctuations

Diffusion model

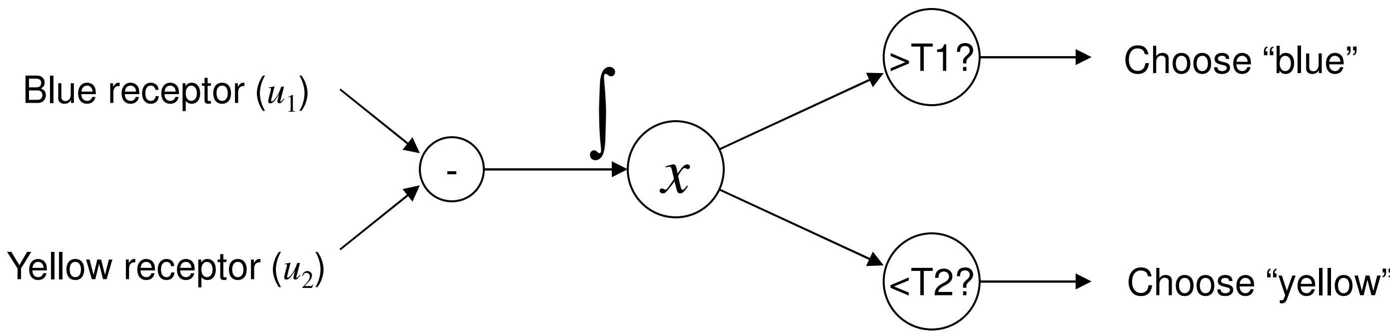
$$\boxed{x(N) = x(0) + \sum_{k=1}^{N} \alpha(u_1(k) - u_2(k)) + noise}$$

- Update your decision variable x as you sample sensory input
- $x(0)$: Initial state
- u_1 : Momentary sensory evidence for choice 1
- u_2 : Momentary sensory evidence for choice 2
- α : Rate of integration
- In a continuous form: $x(t) = x(0) + \int_0^t \left(\alpha(u_1(\tau) - u_2(\tau)) + noise\right) d\tau$

$$\boxed{\frac{dx}{dt} = \alpha(u_1 - u_2) + noise}$$

Integration of differential evidence

- "Diffusion model" (Ratcliff, 1978):



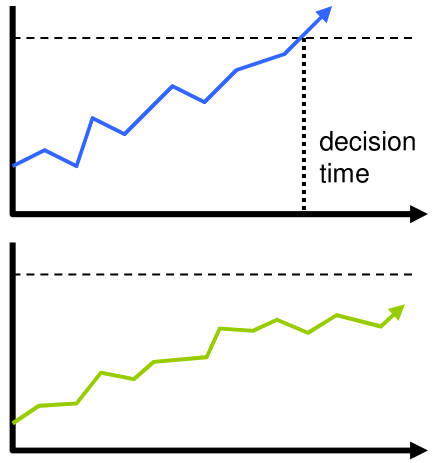
- Integration of the *difference* of evidence and comparison to thresholds

$$\frac{dx}{dt} = \alpha(u_1 - u_2) + noise$$

- Realistic?

Independent integration

- "Race model" (Vickers, 1970)



Choose "blue"

$$\frac{dx_1}{dt} = \alpha u_1 + noise$$

Choose "yellow"

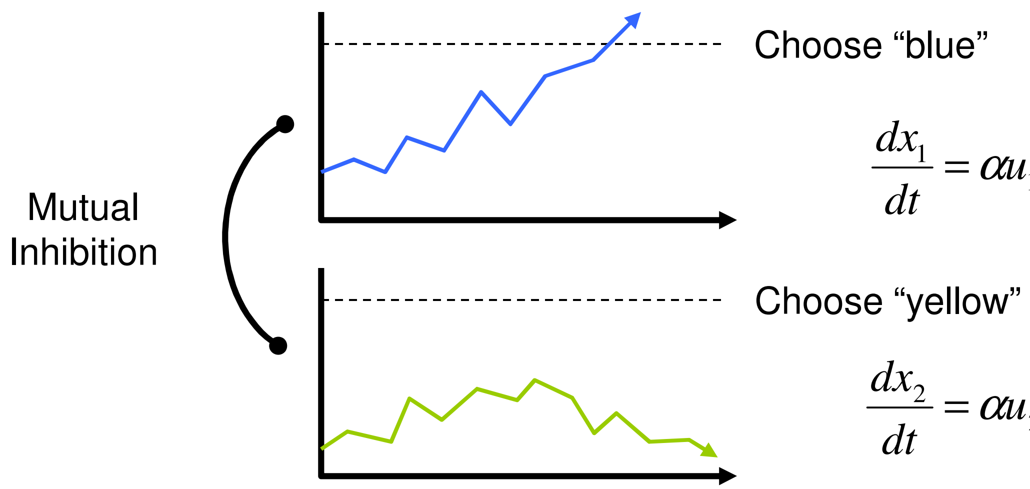
$$\frac{dx_2}{dt} = \alpha u_2 + noise$$

- Independent processes race to their individual thresholds, and whichever arrives first, wins the decision
- Perfect integration vs. leakage

$$\frac{dx_1}{dt} = \alpha u_1 - \beta x_1 + noise \qquad \frac{dx_2}{dt} = \alpha u_2 - \beta x_2 + noise$$

Competing integration

- “Leaky competing accumulator model” (Usher & McClelland, 2001)



$$\frac{dx_1}{dt} = \alpha u_1 - \beta x_1 - \gamma x_2 + noise$$

$$\frac{dx_2}{dt} = \alpha u_2 - \beta x_2 - \gamma x_1 + noise$$

- If $\beta = \gamma$ then it’s equivalent to the diffusion model
- But it can handle multiple options, and is biologically plausible

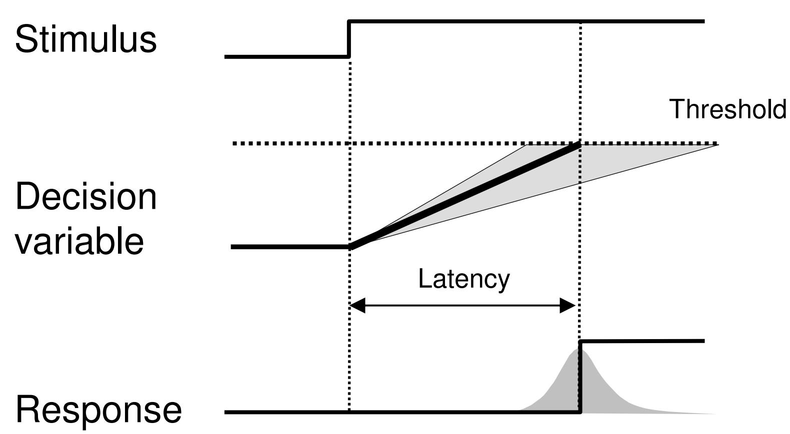
$$x_d = x_1 - x_2$$

$$\frac{dx_d}{dt} = \alpha u_1 - \beta x_1 - \gamma x_2 - \alpha u_2 + \beta x_2 + \gamma x_1 + noise$$

$$= \alpha(u_1 - u_2) + noise$$

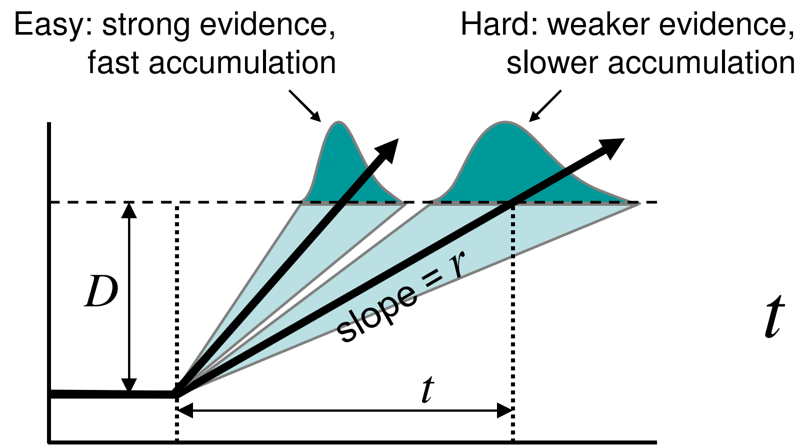
Behavioral predictions

- Accumulator models predict a specific relationship between strength of evidence and reaction times
- Ex: “LATER” model (Carpenter & Williams, 1995)



- Given Gaussian noise, what is the distribution of reaction times?

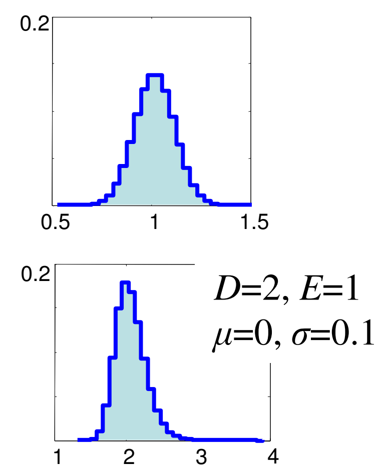
Timing of easy vs. hard choices



$$t = D / r$$

- As a decision gets harder, the reaction time distribution gets later and broader
- If rate is subject to Gaussian noise $r = E + G(\mu, \sigma)$
- Then the distribution of RTs is a skewed Gaussian

$$t = \frac{D}{E + G(\mu, \sigma)}$$



Reciprobit plot

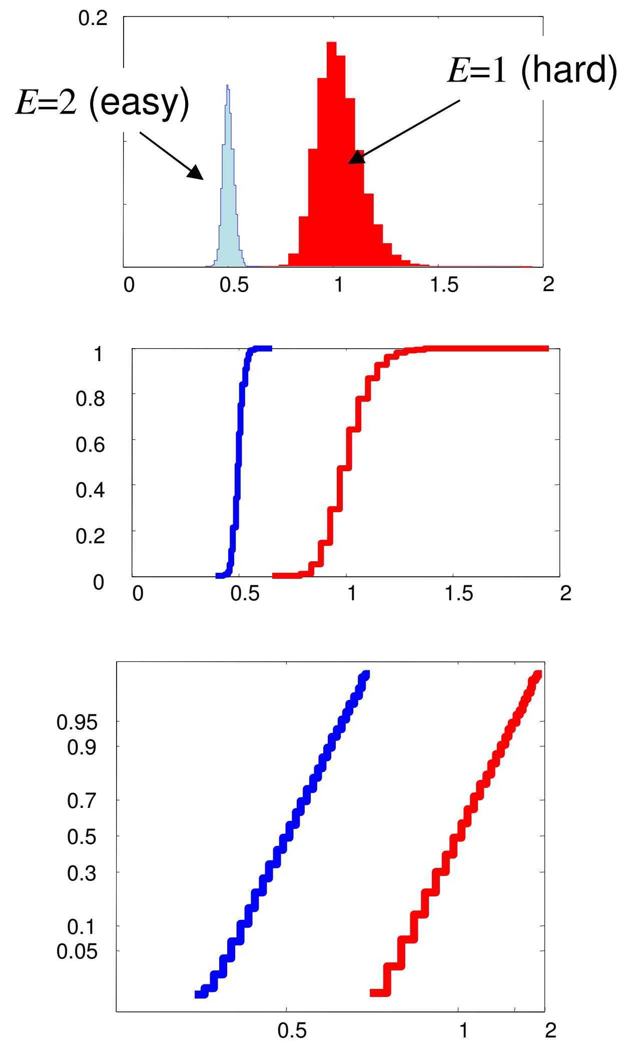
- Suppose we have some distributions of reaction times

$$t = \frac{D}{E + G(\mu,\sigma)}$$

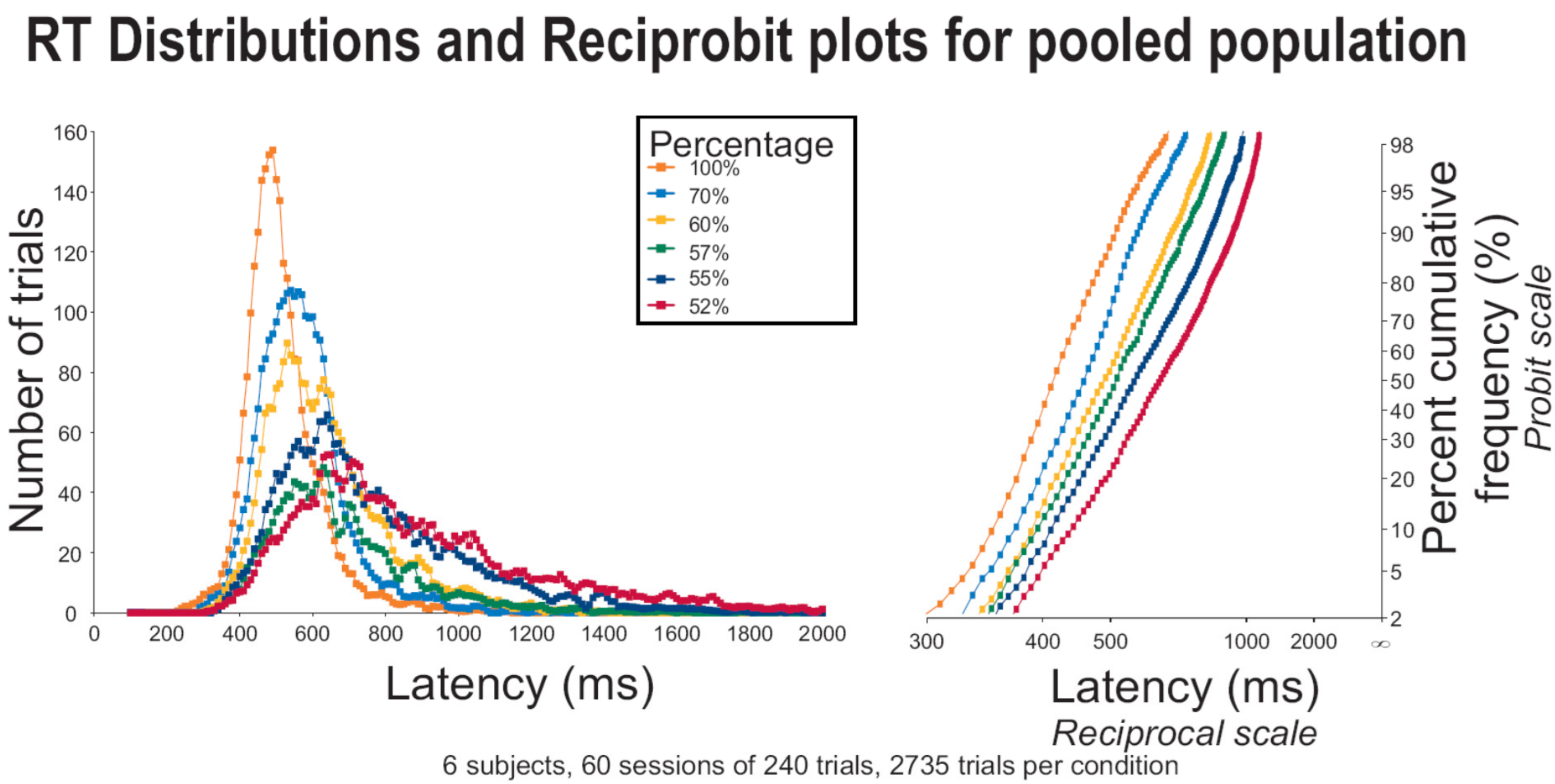
- We can plot these as cumulative RT distributions

- And replot on a "reciprobit" scale
  - Reciprocal x-axis
  - Inverse gaussian y-axis

- Different rates of accumulation produce different parallel lines



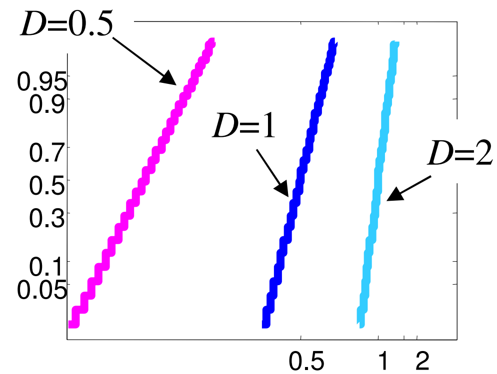
Change difficulty → Parallel lines



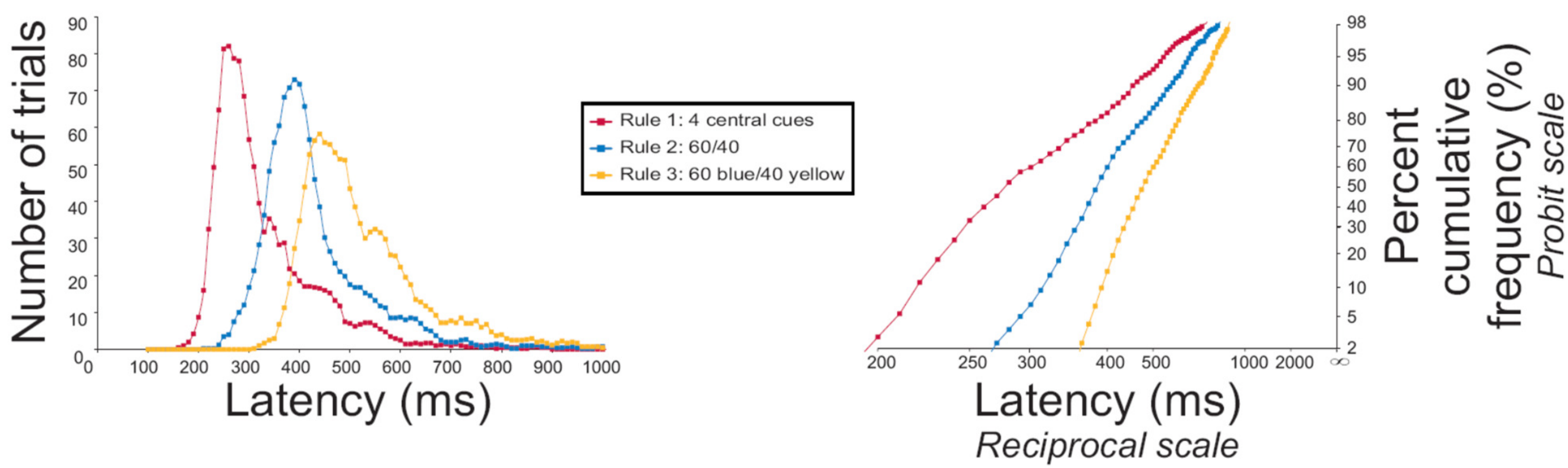
E. Coallier & J. Kalaska

Change threshold → Covergent lines

- Changing the threshold D changes the slopes of the lines so that they converge
- EX: Changing the number of possible conditions



RT Distributions and Reciprobit plots for pooled



4 subjects, 24 sessions of 200 trials, 1150 trials per condition

Why accumulation is a good idea

- Good way to control tradeoff between speed and accuracy
  - If you're getting reliable information, accumulate faster, reach threshold sooner
  - If you're getting weak information, accumulate slower, let more information come in with time…
  - In a situation of urgency, lower the threshold
  - In a situating requiring high accuracy, raise the threshold

- Accumulation maximizes the expected value of choices
  - Expected value

$$EV = p(V)V$$

  - The payoff value V multiplied by its probability $p(V)$

How to maximize expected value?

- Suppose you have to guess between two mutually-exclusive hypotheses, h1 and h2, exactly one of which is correct
  - The consequences of being right or wrong
    - If you assume h1 and are correct, you win W1
    - If you assume h1 but are wrong, you win L1 (“loss”: it’s negative)
    - If you assume h2 and are correct, you win W2
    - If you assume h2 and are wrong, you win L2
- So the expected values are:
  - EV for assuming h1: $p(h_1)W_1 + p(h_2)L_1$
  - EV for assuming h2: $p(h_2)W_2 + p(h_1)L_2$
- Therefore, you should choose h1 when $EV_1 > EV_2$, or when

$$p(h_1)W_1 + p(h_2)L_1 > p(h_2)W_2 + p(h_1)L_2$$

$$p(h_1)(W_1 - L_2) > p(h_2)(W_2 - L_1)$$

$$\frac{p(h_1)(W_1 - L_2)}{p(h_2)(W_2 - L_1)} > 1$$

Add an accuracy criterion

- Assuming no evidence for or against either hypothesis, you'll be correct 50% of the time
- Suppose you want to have an accuracy of C, (where C=0.95, for example)
- Replace right hand side with $C/(1 - C)$

$$\frac{p(h_1)(W_1 - L_2)}{p(h_2)(W_2 - L_1)} > \frac{C}{1 - C}$$

- Now, if this criterion is not met, wait until you have more information to make a better choice

Taking evidence into account

- We start with

$$\frac{p(h_1)(W_1 - L_2)}{p(h_2)(W_2 - L_1)} > \frac{C}{1-C}$$

The probability of h_1 given e

- Suppose we receive new evidence e

$$\frac{p(h_1)(W_1 - L_2)}{p(h_2)(W_2 - L_1)} > \frac{C}{1-C} \quad \Rightarrow \quad \frac{p(h_1 \mid e)(W_1 - L_2)}{p(h_2 \mid e)(W_2 - L_1)} > \frac{C}{1-C}$$

- How do we calculate this?

Bayes' rule

- The probability of A: $p(A)$
- The probability of B: $p(B)$
- What is the probability of both A and B?

$$p(A \cap B) = p(A \mid B)\, p(B) = p(B \mid A)\, p(A)$$

posterior probability

likelihood

prior probability

$$\boxed{p(A \mid B) = \frac{p(B \mid A)\, p(A)}{p(B)}}$$

normalizing factor

Taking evidence into account

- We have $$\frac{p(h_1 \mid e)(W_1 - L_2)}{p(h_2 \mid e)(W_2 - L_1)} > \frac{C}{1-C}$$

- From Bayes' Rule we know that $$p(h_1 \mid e) = \frac{p(e \mid h_1)\,p(h_1)}{p(e)}$$

- So $$\frac{\dfrac{p(e \mid h_1)\,p(h_1)}{\cancel{p(e)}}(W_1 - L_2)}{\dfrac{p(e \mid h_2)\,p(h_2)}{\cancel{p(e)}}(W_2 - L_1)} > \frac{C}{1-C}$$ $$\frac{p(e \mid h_1)\,p(h_1)(W_1 - L_2)}{p(e \mid h_2)\,p(h_2)(W_2 - L_1)} > \frac{C}{1-C}$$

Taking evidence into account

$$\frac{p(e \mid h_1)\, p(h_1)(W_1 - L_2)}{p(e \mid h_2)\, p(h_2)(W_2 - L_1)} > \frac{C}{1-C}$$

- Take the logarithm

$$\log\frac{p(h_1)}{p(h_2)} + \log\frac{p(e \mid h_1)}{p(e \mid h_2)} + \log\frac{(W_1 - L_2)}{(W_2 - L_1)} > T \qquad T = \log\frac{C}{1-C}$$

- Add more evidence, e_1, e_2, etc.

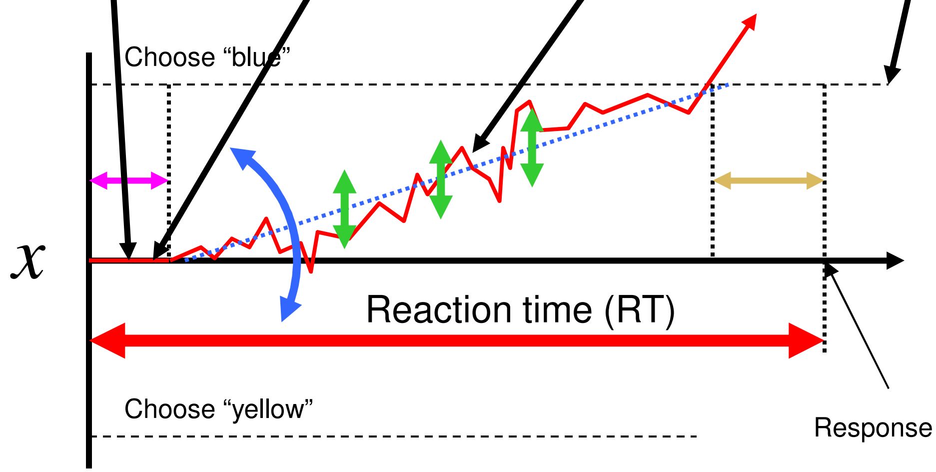
$$\log\frac{p(h_1)}{p(h_2)} + \log\frac{p(e_1 \mid h_1)}{p(e_1 \mid h_2)} + \log\frac{p(e_2 \mid h_1)}{p(e_2 \mid h_2)} + \log\frac{(W_1 - L_2)}{(W_2 - L_1)} > T$$

The result

prior knowledge value sum of evidence criterion of accuracy

$$\log\frac{p(h_1)}{p(h_2)}+\log\frac{(W_1-L_2)}{(W_2-L_1)}+\sum_{k=1}^{N}\log\frac{p(e_k\mid h_1)}{p(e_k\mid h_2)}>T$$

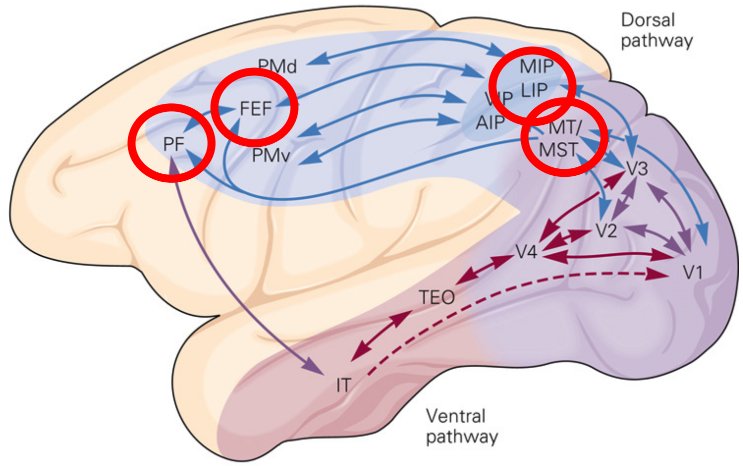
- Similar to the diffusion model



- Start at a level related to priors and payoffs, add evidence (log likelihood ratio) until the sum exceeds a threshold
  – SPRT: sequential probability ratio test

A simple decision: Where to look?

Figure 27–2 Cortical areas involved with intermediate-level visual processing. Many cortical areas in the macaque monkey, including V1, V2, V3, V4, and middle temporal area (**MT**), are involved with integrating local cues to construct contours and surfaces and segregating foreground from background. The shaded areas extend into the frontal and temporal lobes because cognitive output from these areas, including attention, expectation, and perceptual task, contribute to the process of scene segmentation. (**AIP**, anterior intraparietal cortex; **FEF**, frontal eye fields; **IT**, inferior temporal cortex; **LIP**, lateral intraparietal cortex; **MIP**, medial intraparietal cortex; **MST**, medial superior temporal cortex; **MT**, middle temporal cortex; **PF**, prefrontal cortex; **PMd**, dorsal premotor cortex; **PMv**, ventral premotor cortex; **TEO**, occipitotemporal cortex; **VIP**, ventral intraparietal cortex; **V1**, **V2**, **V3**, **V4**, primary, secondary, third, and fourth visual areas.)



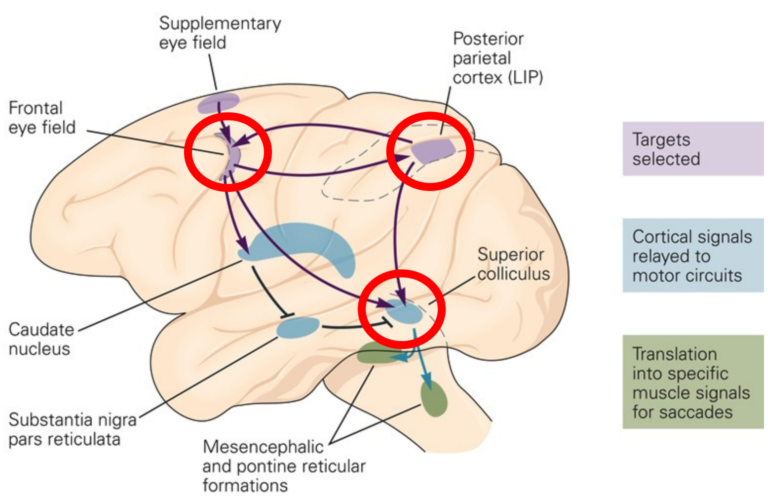
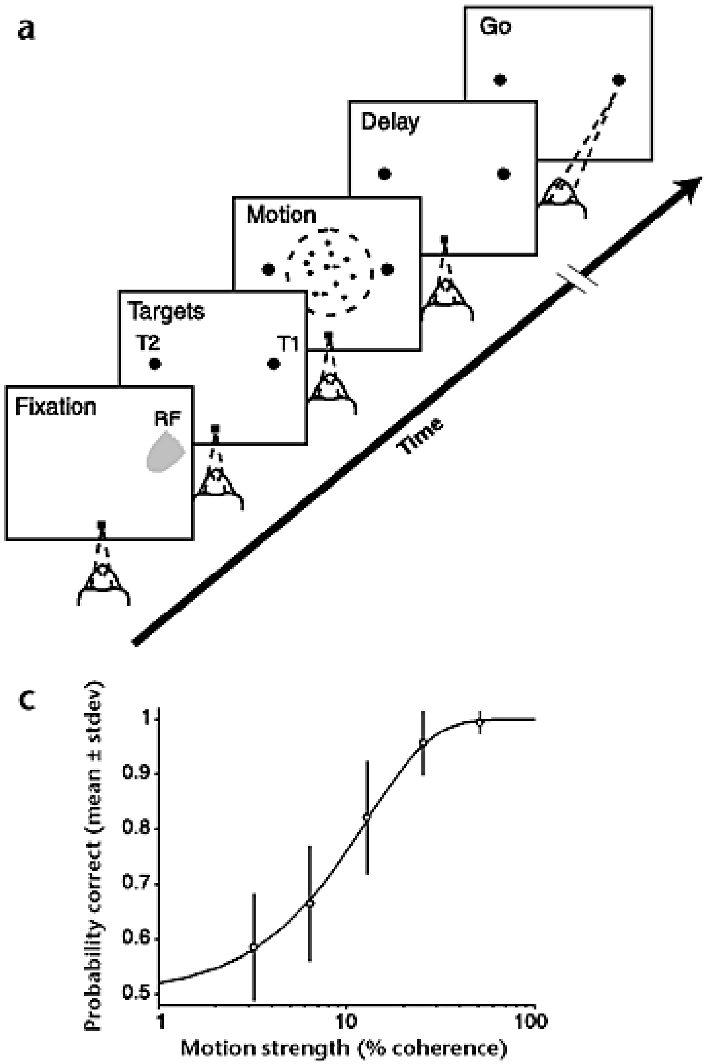
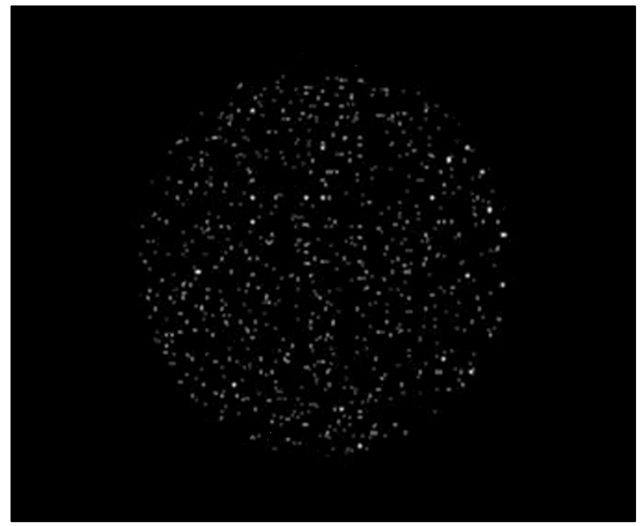


Figure 39–10 Cortical pathways for saccades. **A.** In the monkey the saccade generator in the brain stem receives a command from the superior colliculus. The colliculus receives direct excitatory projections from the frontal eye fields and the lateral intraparietal area (**LIP**) and an inhibitory projection from the substantia nigra. The substantia nigra is suppressed by the caudate nucleus, which in turn is excited by the frontal eye fields. Thus the frontal eye fields directly excite the colliculus and indirectly release it from suppression by the substantia nigra by exciting the caudate nucleus, which inhibits the substantia nigra. (Reproduced, with permission, from R. J. Krausliz.)

Coherent motion discrimination task

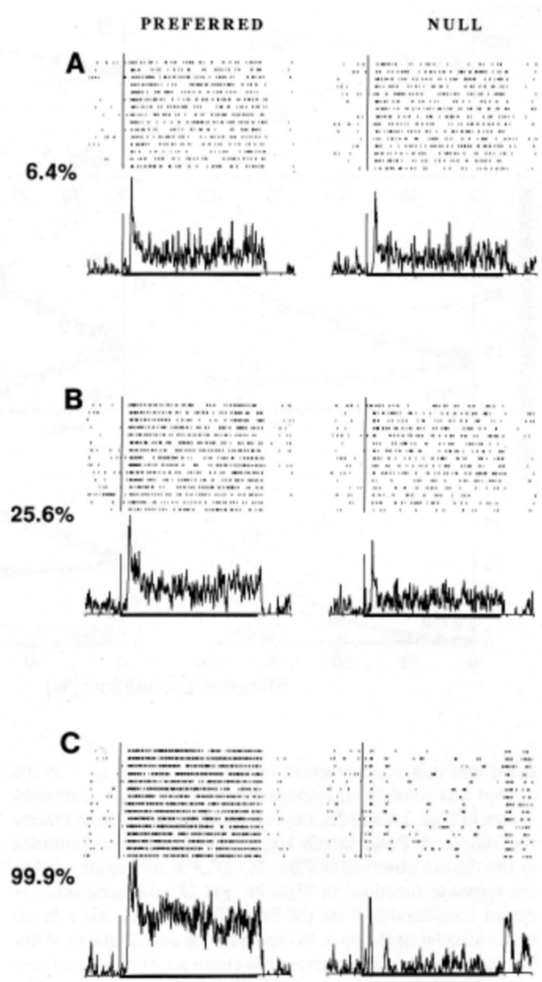


- Monkey trained to discriminate the direction of motion



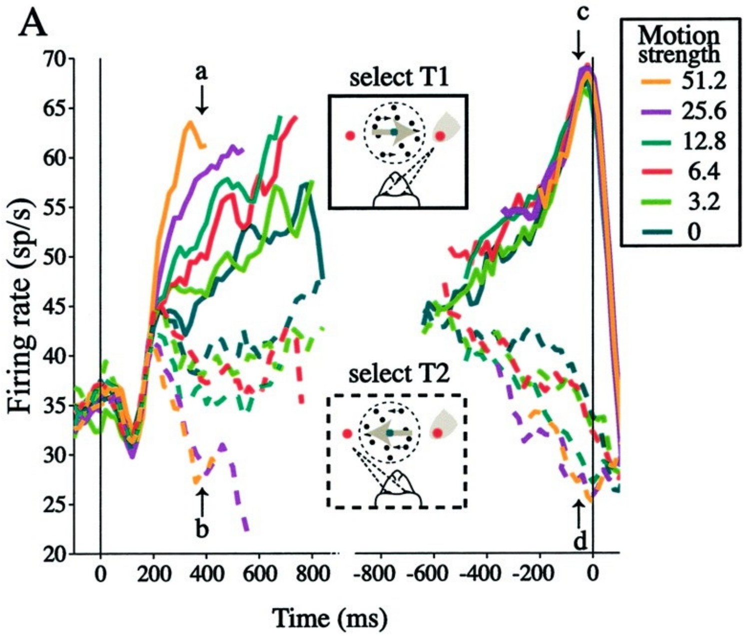
- Perceptual report made by a saccade to a target in the direction of the motion
- Two versions
  - Fixed Duration
  - Reaction Time

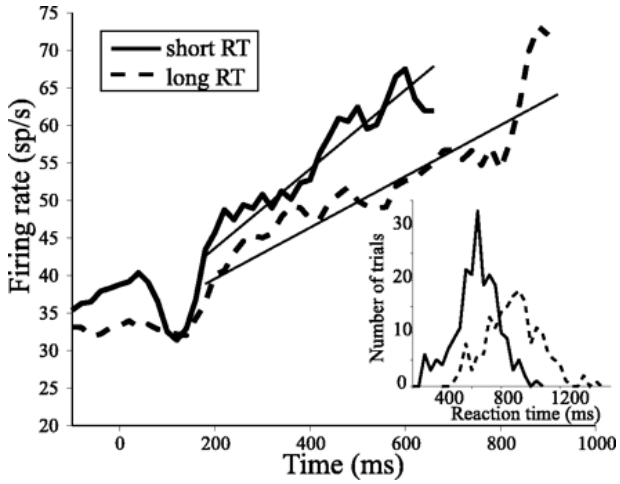
Activity in medial temporal area (MT)



- Britten, Shadlen, Newsome, & Movshon (1993) *Visual Neuroscience*
- Neurons in area MT are sensitive to the direction of visual motion signals
- During coherent motion viewing, the response of these neurons depends upon the coherence of the motion stimulus

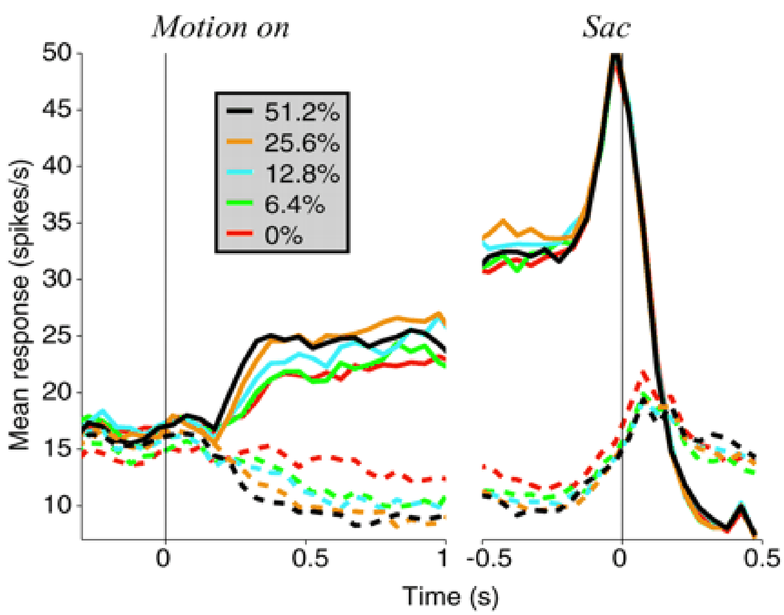
Activity in LIP (reaction time task)

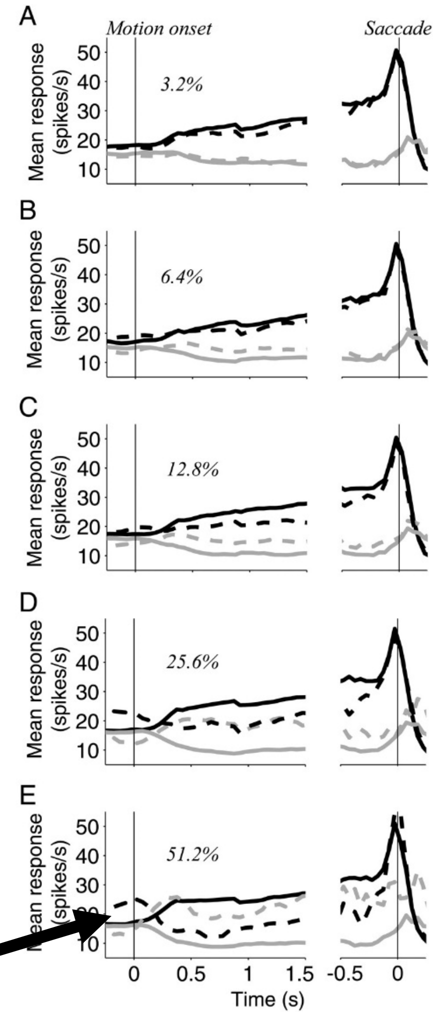




- Roitman & Shadlen (2002) *J. Neurosci*
- Neural activity in LIP grows at a rate related to the coherence of the motion stimulus
- Rate of activity growth predicts the reaction time

Activity in LIP (fixed duration task)

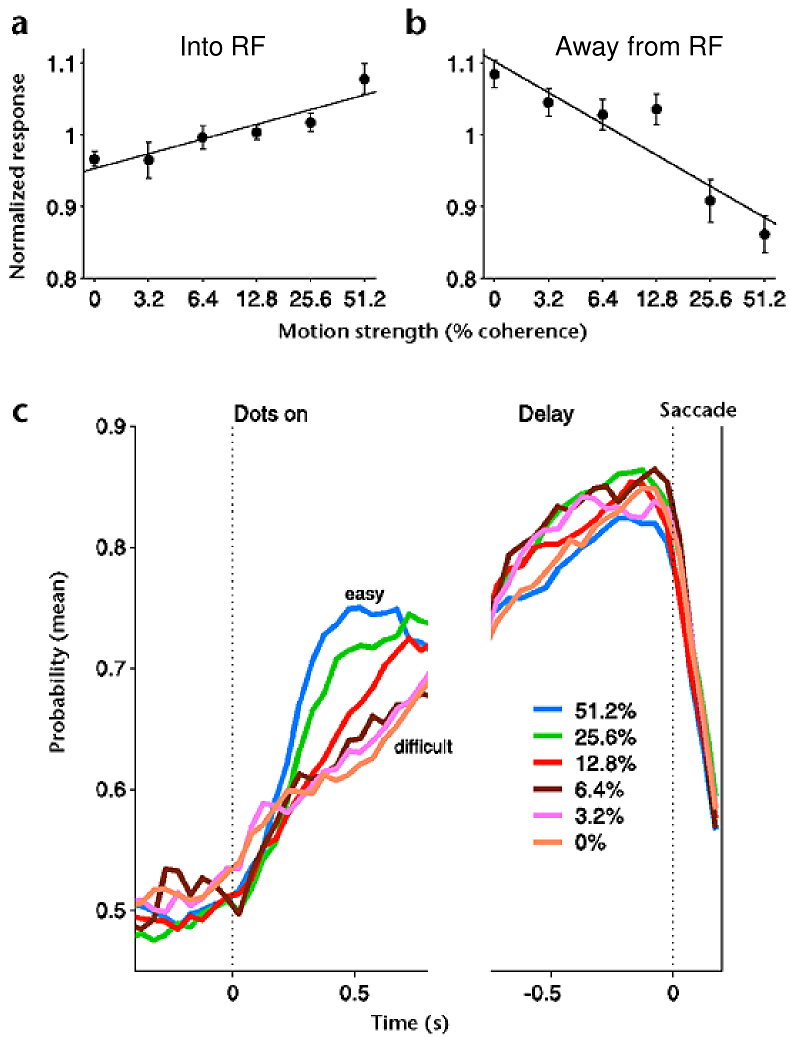




- Shadlen & Newsome (2001) *J. Neurophysiol*
- Neural activity in area LIP predicts the choice that the monkey will make, and reflects the strength of the motion signal

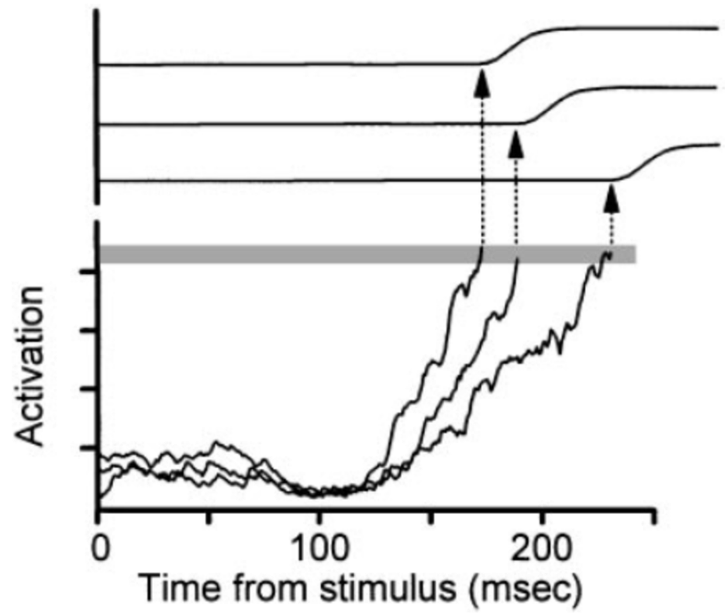
Note the bias!

Activity in dorsolateral prefrontal cortex



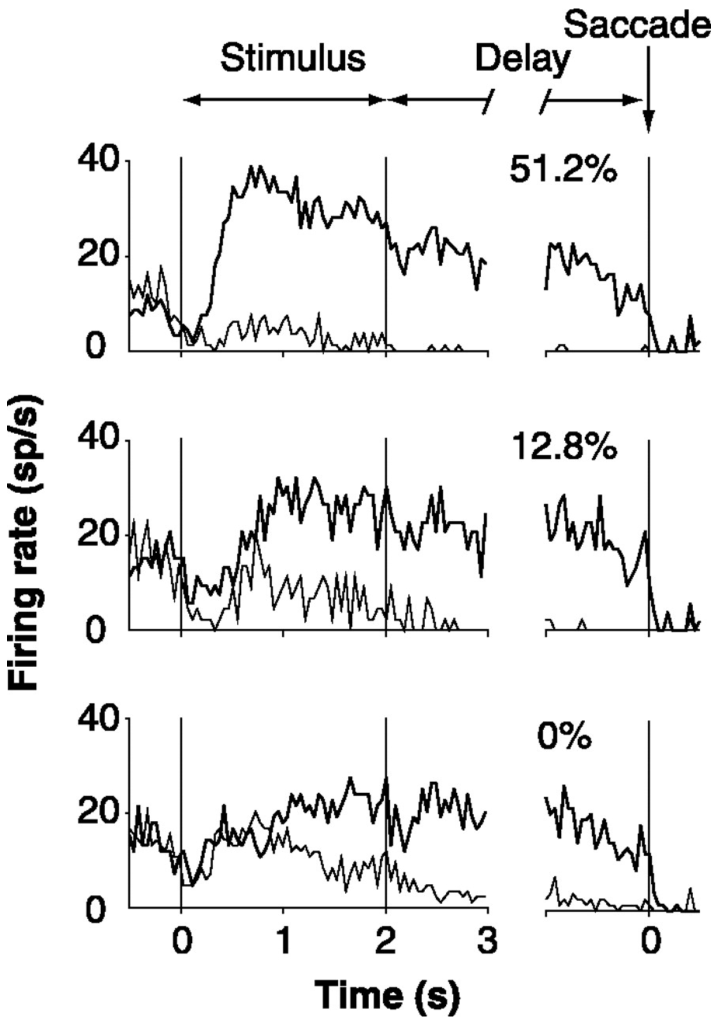
- Kim & Shadlen (1999) *Nature Neuroscience*
- dlPFC activity is proportional to the coherence
- Probability of predicting the monkey's choice on the basis of neural activity grows as a function of coherence.

Initiation threshold in FEF



- Schall & Thompson (1999) *Annual Review of Neuroscience*
- FEF activity (of movement-related neuron) predicts the time of a saccade

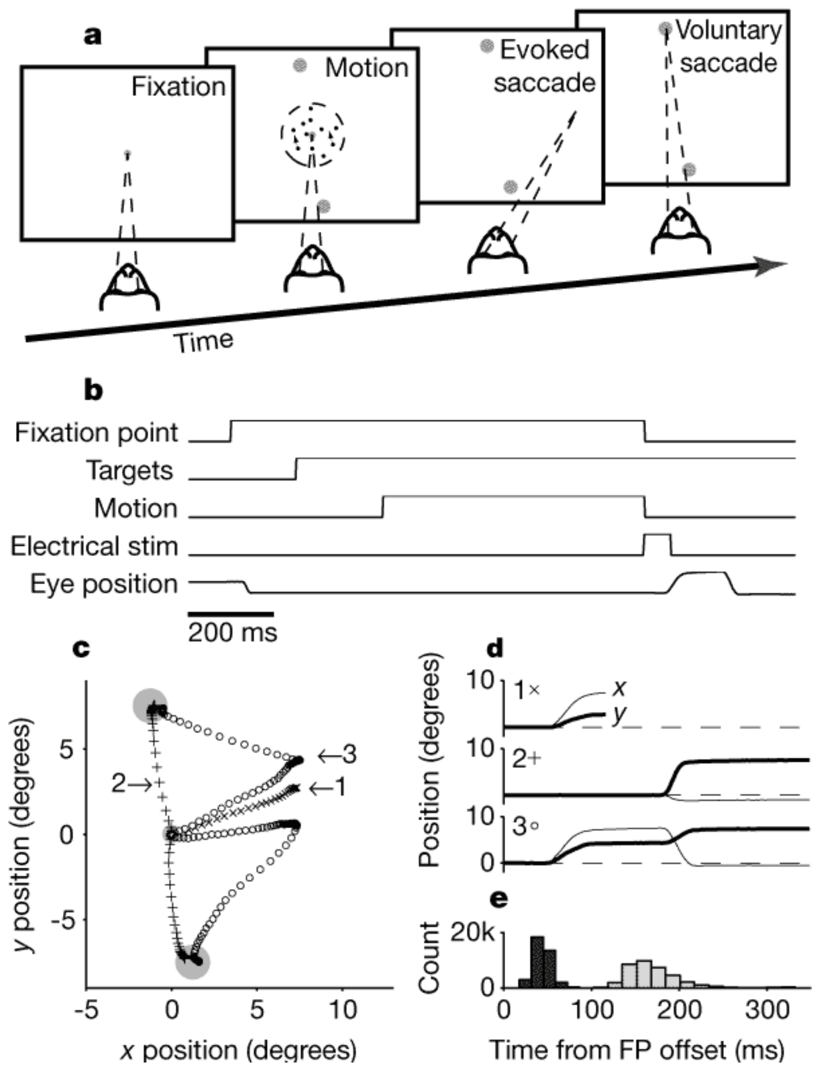
Activity in the superior colliculus



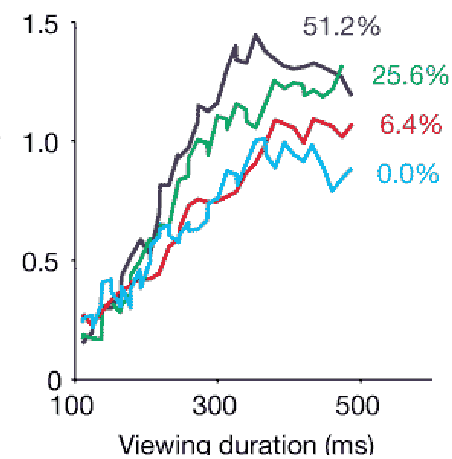
- Horwitz and Newsome (1999) *Science*
- Neural activity predicts the monkey's choice, even when the stimulus coherence is 0%
- Early activity dependent on coherence
- Late activity simply predicts the movement

- The same cells change from "representing stimulus information" to "representing the chosen action"

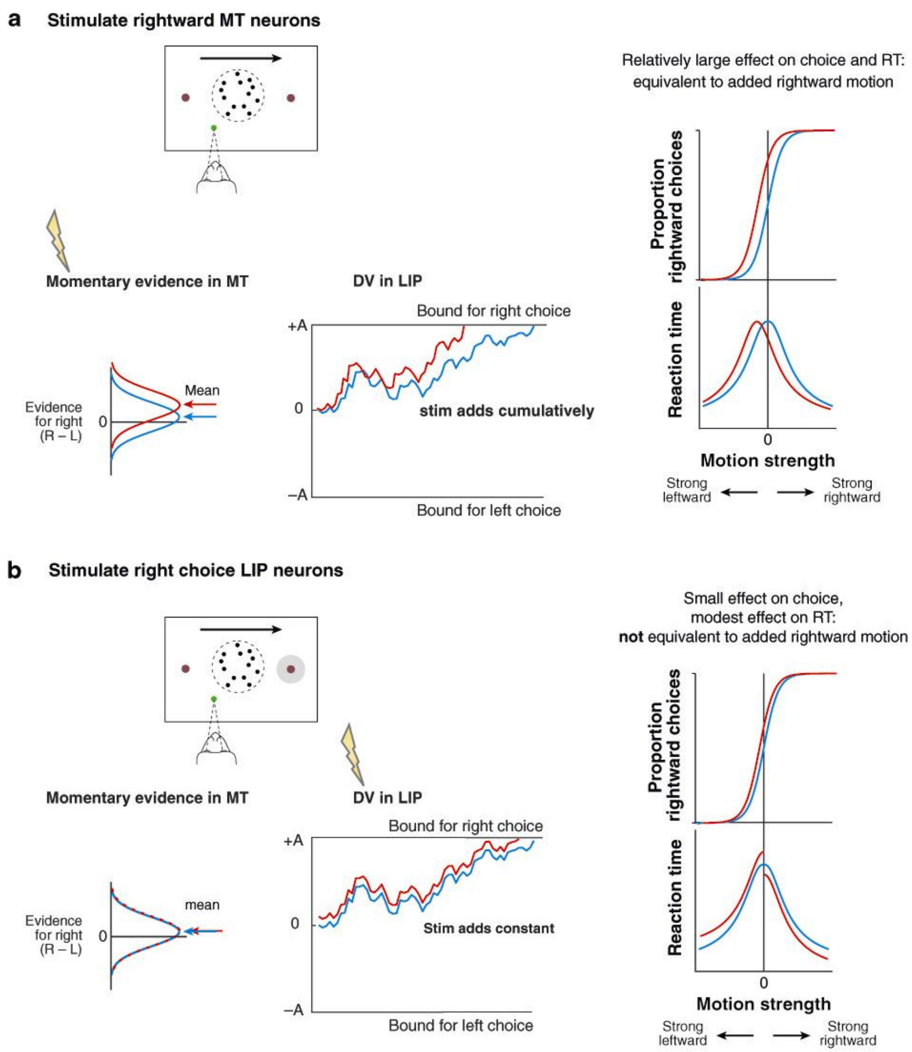
Decisions spilling into commands



- Gold & Shadlen (2000) *Nature*
- Microstimulation in frontal eye fields produces saccades
- If microstimulation occurs while the monkey is in the process of deciding between stimulus motion, the saccade is deviated in the direction of the developing motor command
- A function of coherence and viewing duration



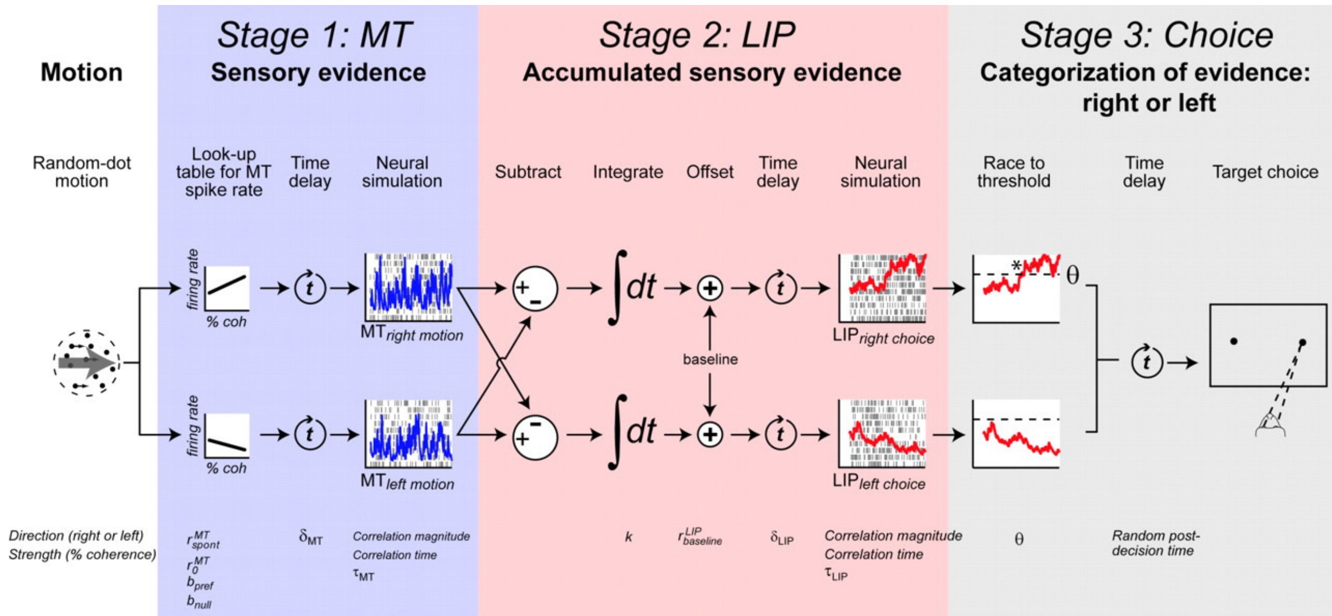
Changing the mind



Gold JI, Shadlen MN. 2007. Annu. Rev. Neurosci. 30:535–74

- Intracortical microstimulation
  - By stimulating rightward preferring cells we can bias the decision toward the right, and modify the RT
- Stimulation in MT
  - Shifts decision and timing
  - Acts like a change in the strength of rightward motion
- Stimulation in LIP
  - Small shift in decision, speed up rightward RT, slow down leftward RT
  - Acts like a change in the threshold

A neural model

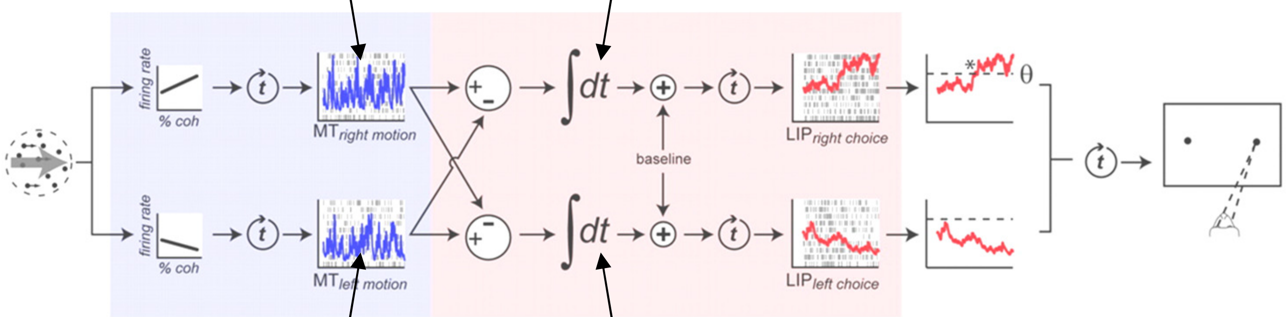


- Mazurek, Roitman, Ditterich, & Shadlen (2003) *Cerebral Cortex*
- Three stages:
  1. Detection of sensory evidence (area MT)
  2. Accumulation of sensory evidence for a given choice (LIP / PFC / FEF)
  3. Categorization of evidence (?)

A neural model

$$r_{right}^{MT}$$

$$r_{right}^{LIP}(T) = r_{baseline}^{LIP} + k \int_{\delta_{MT}}^{T-\delta_{LIP}} r_{right}^{MT}(t) - r_{left}^{MT}(t)\,dt$$



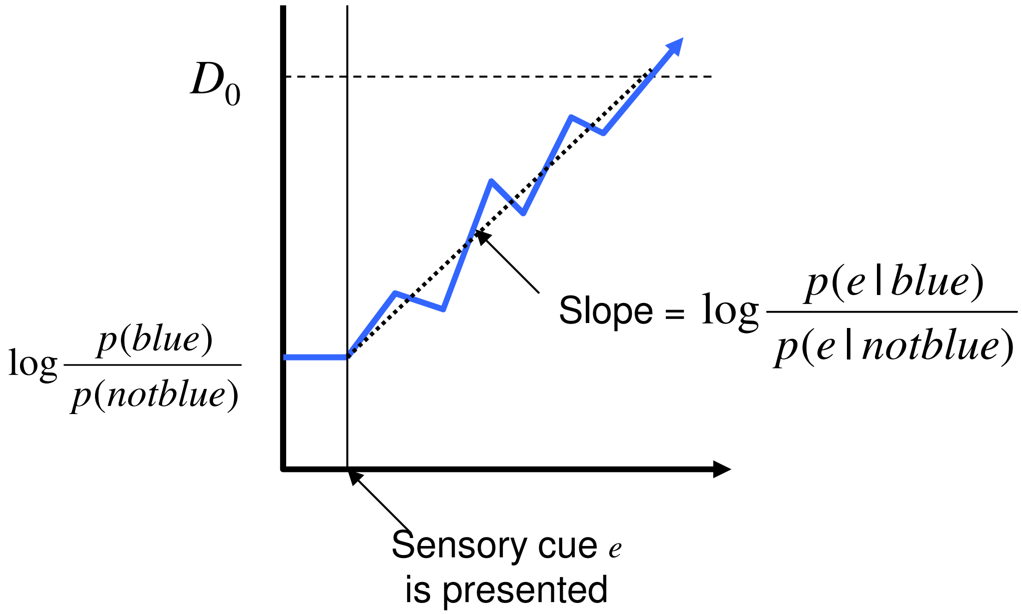
$$r_{left}^{MT}$$

$$r_{left}^{LIP}(T) = r_{baseline}^{LIP} + k \int_{\delta_{MT}}^{T-\delta_{LIP}} r_{left}^{MT}(t) - r_{right}^{MT}(t)\,dt$$

- Note: This is equivalent to the diffusion model

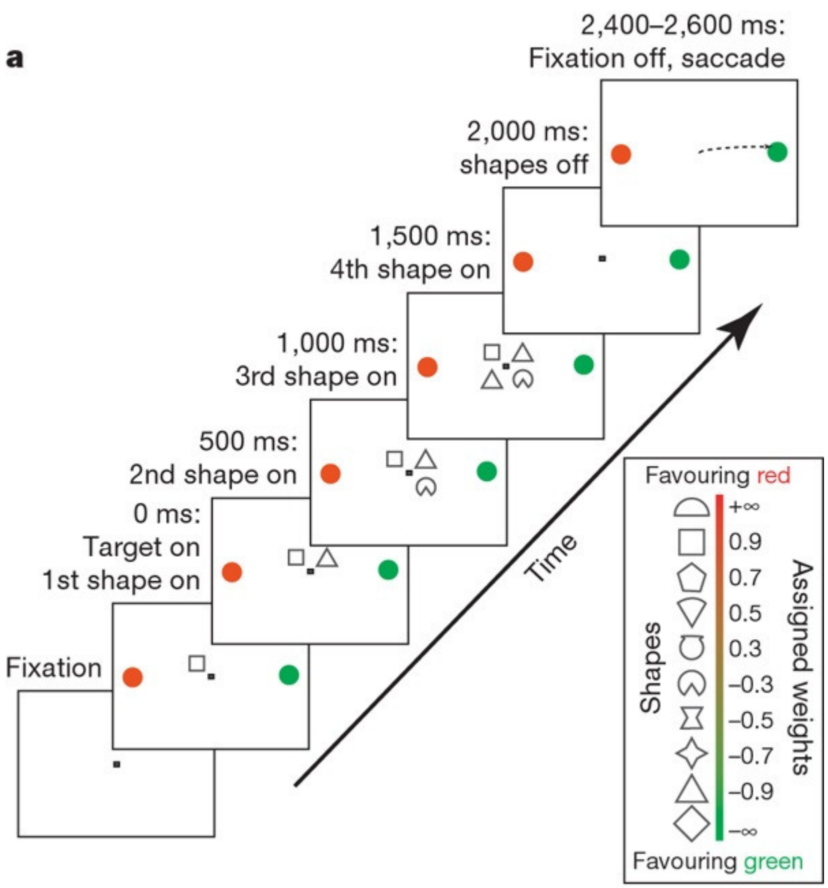
$$x(N) = x(0) + \sum_{k=1}^{N} \alpha(u_1(k) - u_2(k)) + noise$$

What's the best way to accumulate?



- Recall
  - Want to initialize at a level proportional to log of the prior probability ratios
  - Each time a new stimulus appears, want to increase activity by the **log likelihood ratio**
  - Is that what is being accumulated in area LIP?

Probabilistic inference

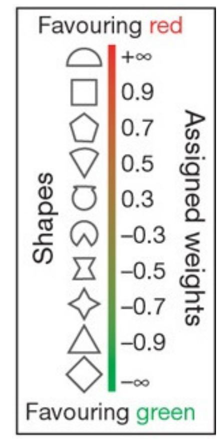


- Yang & Shadlen (2007) *Nature*
- Probabilistic categorization task
  1. Fixate
  2. Two targets (red and green) appear, and a symbol in the center
     - Each shape has a meaning: it favors either the red target or the green target
  3. After 500ms, another shape appears
  4. And another
  5. And another
  6. Now, move to the target which has more evidence
  7. If guessed correctly, receive reward

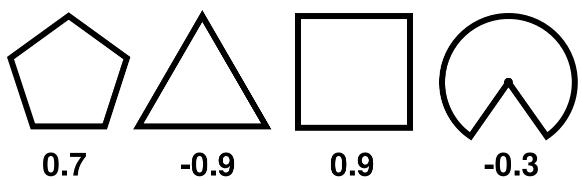
Weight of evidence

- At the end of the trial, the total evidence from all of the shapes is computed, and the rewarded target assigned by the rule

$$p(R \mid s_1, s_2, s_3, s_4) = \frac{10^S}{1+10^S} \qquad S = \sum_{i=1}^{4} w_i$$



- Example:



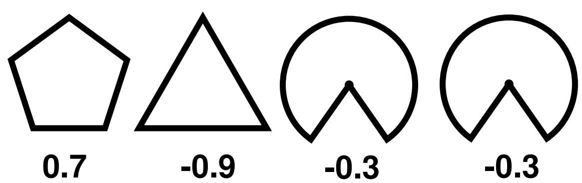
$$S = 0.4 \qquad p(R \mid s_1, s_2, s_3, s_4) = \frac{10^{0.4}}{1+10^{0.4}} = \frac{2.51}{3.51} = 0.71$$

- The monkey should guess "red"

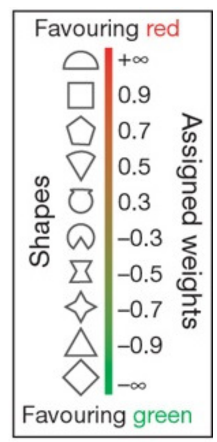
What's the right way to accumulate the evidence?

$$\log \frac{p(red)}{p(green)} + \sum_{i=1}^{N} \left(\log \frac{p(s_i \mid red)}{p(s_i \mid green)} \right) > T$$

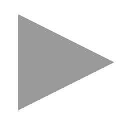
- Start at a level determined by priors (since they are equal, start unbiased)
- Add up the log likelihood ratios each time a symbol appears
- Example:



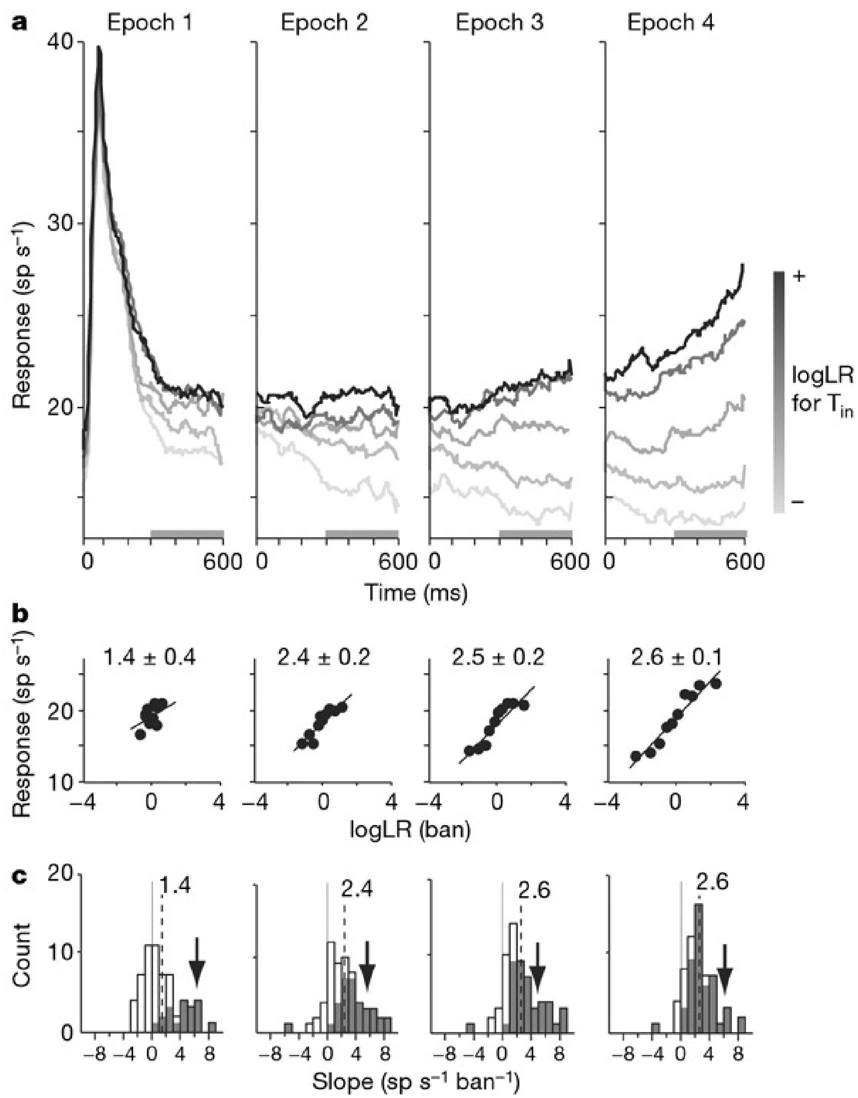
  – First favor red, then choose green



A cell which prefers lower right (red)



Log likelihood ratio in LIP



- Each time a symbol appears, neural activity in LIP changes.
- The magnitude of the change is a function of the log likelihood ratio conveyed by each symbol
  - Not quite a linear function, but pretty good
  - Slope ≈ 2.5 spikes/sec/ban
    - (1 ban = 10:1, 2 bans = 100:1)
- Neural activity reflects the subjective weight of evidence that the monkeys use to make their decisions

$$FR \approx b + \sum_{k=1}^{N} \left(\log \frac{p(s_k \mid red)}{p(s_k \mid green)} \right)$$

Summary

- The diffusion model is widely accepted as the explanation for decision-making during perceptual discrimination tasks
  - Makes good mathematical sense
  - Explains behavioral data on reaction time distributions
  - Explains the build-up of neural activity

However

- 3 questions:

1. What if the world changes?
   – Need to be sensitive to changes

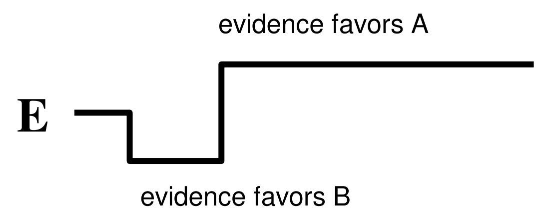
2. What kind of optimality do we want?
   – Animals care about reward rate

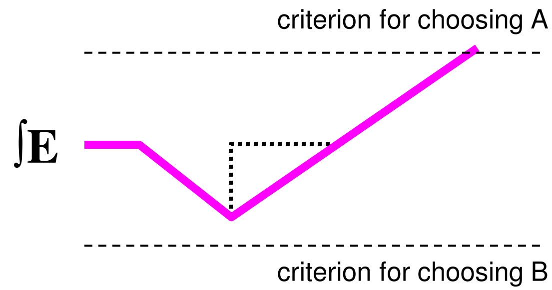
3. What if the samples are not completely independent?
   – Need to take redundancy into account

   – (Ex: Buying 2 newspapers)

Q1: What if the world changes?

- During natural behavior, the world is always changing
- Any integrator will be sluggish in its response to such changes
- Need to be able to quickly respond to changes
  - Reset?
  - Sudden increase in gain?
  - Some other mechanism?





?

Q2: What should we optimize?

- If you're doing statistics then what you care about is ***accuracy***
  - The criterion of desired accuracy is determined by convention
    - $p<0.05$ = 95% confidence in your result
    - $p<0.01$ = 99% confidence in your result
  - So the SPRT is optimal in that it minimizes the time required to reach that level of accuracy
    - (If results not significant, get more data, even if it takes you another year to finish your thesis…)

- But what if you're an animal in the wild?
  - Suppose you've reached 93% confidence
    - Do you wait to reach 95%?
      - What if it would take another thirty minutes?
      - What if it would take a year?
  - Time is running out, opportunities are lost, predators come and eat you!
  - You want to optimize ***reward rate***

Reward rate

- Reward Rate $$RR = \frac{p(t)\cdot U - C}{t + m + d}$$
- where
  - $p(t)$ is the probability of achieving a favorable outcome
  - t is the time spent deciding and planning
  - U is the subjective utility of that outcome
  - C is the subjective cost of trying (including "opportunity cost")
  - m is the time spent moving
  - d is the delay before you can try again
- "Time-discounted expected value"
- Similar form as "harvest intake" in foraging (Charnov, 1976)

How to optimize reward rate?

$$RR = \frac{p(t) \cdot U - C}{t + m + d}$$

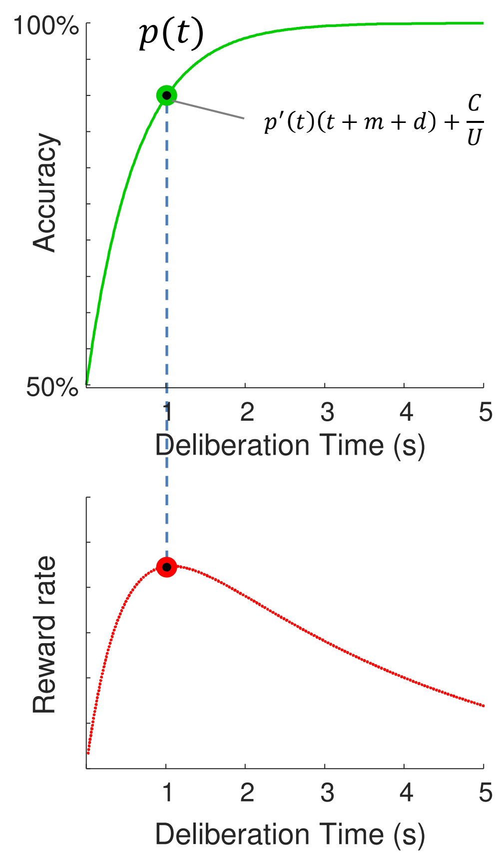
1. The probability of achieving a favorable outcome improves with time
2. But with diminishing returns

Therefore, the expected reward rate has a peak

– The peak of reward rate occurs when $RR'(t) = 0$, or when

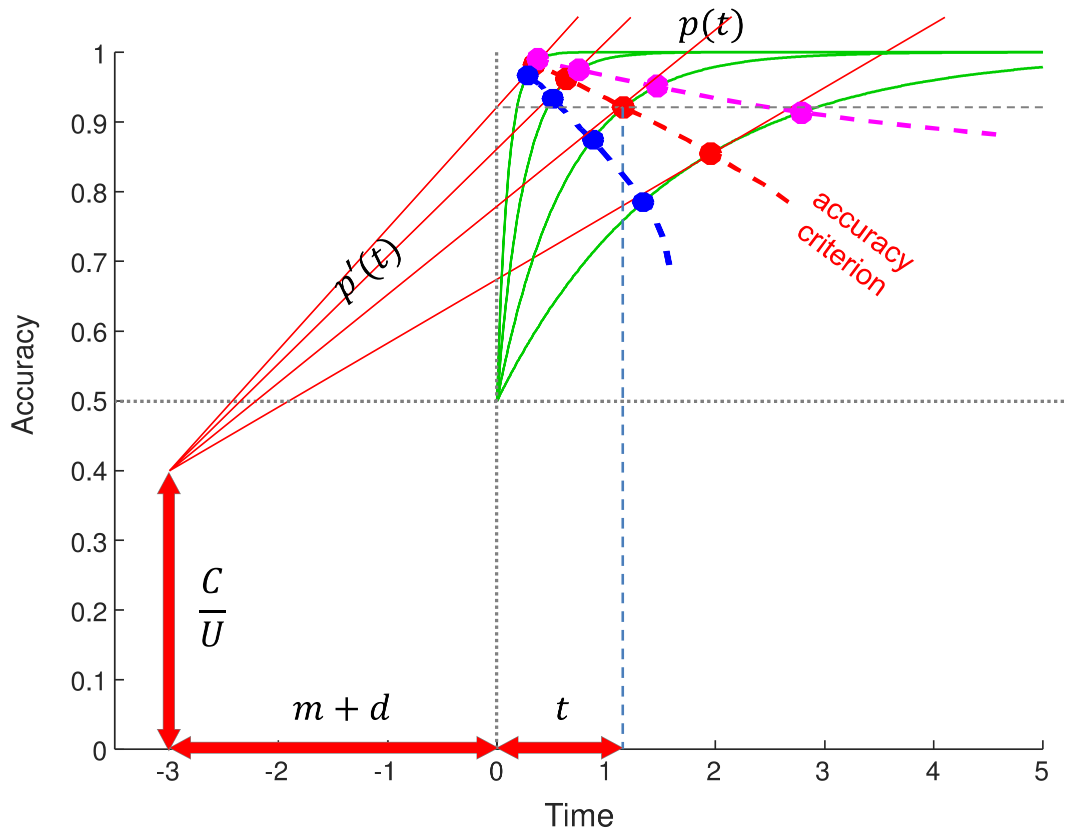
$$p(t) = p'(t)(t + m + d) + \frac{C}{U}$$

- This is the best time to commit

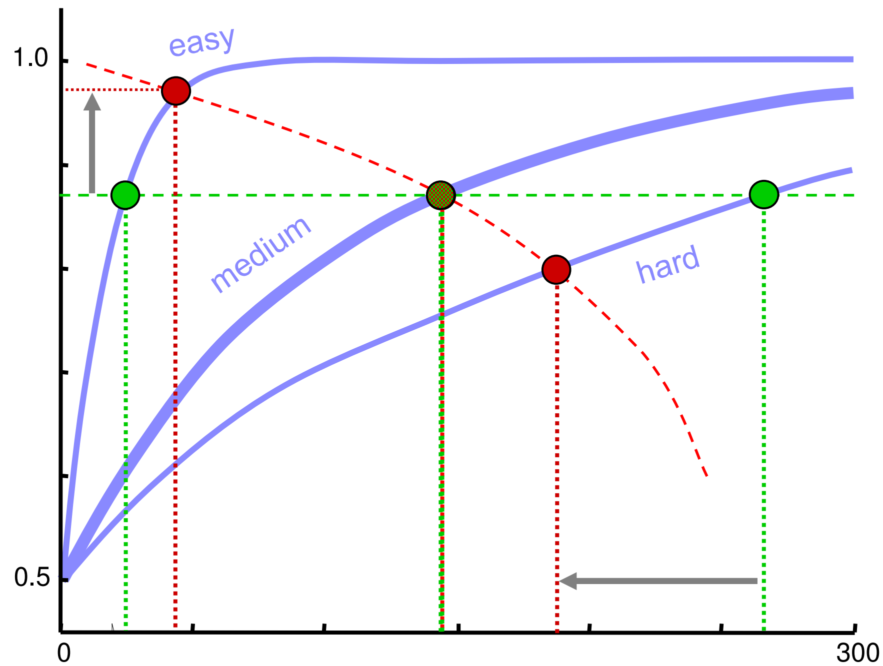


Geometric interpretation

$$p(t) = p'(t)(t + m + d) + \frac{C}{U}$$



This is the best that you can do



There is no setting of a constant accuracy criterion that will do as well as a dropping criterion in conditions where individual trials vary

Q3: What should we accumulate?

Extended Bayes' Rule for three variables

$$\boxed{p(a \mid b,c) = \frac{p(a)\,p(b \mid a)\,p(c \mid a,b)}{p(b)\,p(c \mid b)}}$$

$$x_R(n) = \log \frac{p(R \mid e_1 \ldots e_n)}{p(L \mid e_1 \ldots e_n)}$$

$$x_R(1) = \log \frac{p(R)}{p(L)} + \log \frac{p(e_1 \mid R)}{p(e_1 \mid L)}$$

$$x_R(2) = \log \frac{p(R \mid e_1, e_2)}{p(L \mid e_1, e_2)} = \log \frac{\dfrac{p(R)\,p(e_1 \mid R)\,p(e_2 \mid e_1, R)}{\cancel{p(e_1)\,p(e_2 \mid e_1)}}}{\dfrac{p(L)\,p(e_1 \mid L)\,p(e_2 \mid e_1, L)}{\cancel{p(e_1)\,p(e_2 \mid e_1)}}}$$

Q3: What should we accumulate?

$$x_R(n) = \log \frac{p(R \mid e_1 \ldots e_n)}{p(L \mid e_1 \ldots e_n)}$$

Extended Bayes' Rule for three variables

$$\boxed{p(a \mid b, c) = \frac{p(a)\,p(b \mid a)\,p(c \mid a, b)}{p(b)\,p(c \mid b)}}$$

$$x_R(2) = \log \frac{p(R)}{p(L)} + \log \frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log \frac{p(e_2 \mid e_1, R)}{p(e_2 \mid e_1, L)}$$

$$\left(\text{NOTE: Not } x_R(2) = \log \frac{p(R)}{p(L)} + \log \frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log \frac{p(e_2 \mid R)}{p(e_2 \mid L)} \right)$$

$$p(e_2 \mid e_1, R) = p(e_2 \mid R) \left(\frac{p(e_1, e_2 \mid R)}{p(e_1 \mid R)\,p(e_2 \mid R)} \right)$$

Q3: What should we accumulate?

$$x_R(n) = \log \frac{p(R \mid e_1 \ldots e_n)}{p(L \mid e_1 \ldots e_n)}$$

Extended Bayes' Rule for three variables

$$\boxed{p(a \mid b, c) = \frac{p(a)\, p(b \mid a)\, p(c \mid a, b)}{p(b)\, p(c \mid b)}}$$

$$x_R(2) = \log \frac{p(R)}{p(L)} + \log \frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log \frac{p(e_2 \mid e_1, R)}{p(e_2 \mid e_1, L)}$$

$$\boxed{x_R(2) = \log \frac{p(R)}{p(L)} + \log \frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log \left(\frac{\dfrac{p(e_1, e_2 \mid R)}{p(e_1 \mid R)\, p(e_2 \mid R)}}{\dfrac{p(e_1, e_2 \mid L)}{p(e_1 \mid L)\, p(e_2 \mid L)}} \times \frac{p(e_2 \mid R)}{p(e_2 \mid L)} \right)}$$

Now let's examine two cases…

SPRT with independent samples

$$x_R(2) = \log\frac{p(R)}{p(L)} + \log\frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log\left(\frac{\underbrace{\cancel{\dfrac{p(e_1, e_2 \mid R)}{p(e_1 \mid R)\, p(e_2 \mid R)}}}_{=1}}{\underbrace{\cancel{\dfrac{p(e_1, e_2 \mid L)}{p(e_1 \mid L)\, p(e_2 \mid L)}}}_{=1}} \times \frac{p(e_2 \mid R)}{p(e_2 \mid L)} \right)$$

If samples are truly independent

$$p(e_1, e_2 \mid X) = p(e_1 \mid X)\, p(e_2 \mid X)$$

$$x_R(2) = \log\frac{p(R)}{p(L)} + \log\frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log\left(\frac{1}{1} \times \frac{p(e_2 \mid R)}{p(e_2 \mid L)} \right)$$

$$\boxed{x_R(n) = \log\frac{p(R)}{p(L)} + \sum_{i=1}^{n} \log\frac{p(e_i \mid R)}{p(e_i \mid L)}}$$

So we should sum pieces of evidence when they are independent

SPRT with dependent samples

$$x_R(2) = \log\frac{p(R)}{p(L)} + \log\frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \log\left(\frac{\dfrac{\cancel{p(e_1, e_2 \mid R)}}{\cancel{p(e_1 \mid R)}\, p(e_2 \mid R)}}{\dfrac{\cancel{p(e_1, e_2 \mid L)}}{\cancel{p(e_1 \mid L)}\, p(e_2 \mid L)}} \times \frac{p(e_2 \mid R)}{p(e_2 \mid L)} \right)$$

If sample 2 is completely dependent on sample 1

$$p(e_1, e_2 \mid X) = p(e_1 \mid X)$$

$$x_R(2) = \log\frac{p(R)}{p(L)} + \log\frac{p(e_1 \mid R)}{p(e_1 \mid L)} + \cancel{\log\left(\underbrace{\frac{\dfrac{1}{p(e_2 \mid R)}}{\dfrac{1}{p(e_2 \mid L)}} \times \frac{p(e_2 \mid R)}{p(e_2 \mid L)}}_{=1} \right)}$$

So we ***should ignore*** redundant samples

So what should we accumulate?

Should we accumulate ***all*** evidence?

$$\boxed{x_R(n) = \log\frac{p(R)}{p(L)} + \sum_{i=1}^{n}\log\left(\frac{I_{i|R}}{I_{i|L}} \times \frac{p(e_i \mid R)}{p(e_i \mid L)}\right)}$$

$$I_{i|X} = \frac{p(e_1,\ldots e_{i-1}, e_i \mid X)}{p(e_1,\ldots e_{i-1} \mid X)\,p(e_i \mid X)}$$

related to the mutual information between sample i and previous ones

- Conclusion: We should only accumulate evidence to the extent that it is ***novel***
- i.e. In order to properly implement the SPRT, we should take statistical dependence between samples into account
- (don't buy that 2nd newspaper)

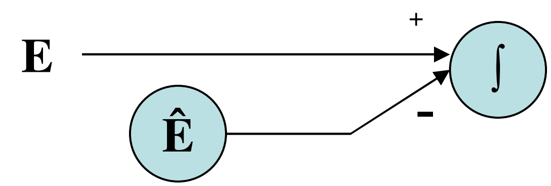
What’s optimal vs. possible vs. reasonable?

- <u>Ideal mechanism</u>:
  Compute the degree to which each sample contributes novel information

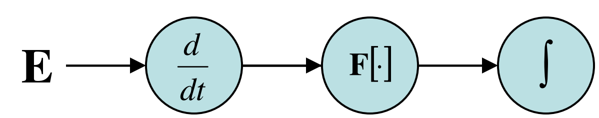
$$x_R(n) = \log\frac{p(A)}{p(B)} + \log\frac{p(s_1 \mid A)}{p(s_1 \mid B)} + \log\left(\frac{\dfrac{p(s_1,s_2 \mid A)}{p(s_1 \mid A)\,p(s_2 \mid A)}}{\dfrac{p(s_1,s_2 \mid B)}{p(s_1 \mid B)\,p(s_2 \mid B)}} \times \frac{p(s_2 \mid A)}{p(s_2 \mid B)}\right)$$

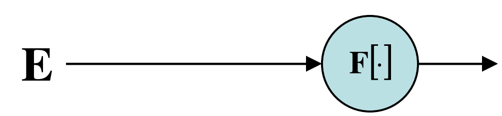
$$+\log\left(\frac{\dfrac{p(s_1,s_2,s_3 \mid A)}{p(s_1,s_2 \mid A)\,p(s_3 \mid A)}}{\dfrac{p(s_1,s_2,s_3 \mid B)}{p(s_1,s_2 \mid B)\,p(s_3 \mid B)}} \times \frac{p(s_3 \mid A)}{p(s_3 \mid B)}\right) + \log\left(\frac{\dfrac{p(s_1,s_2,s_3,s_4 \mid A)}{p(s_1,s_2,s_3 \mid A)\,p(s_4 \mid A)}}{\dfrac{p(s_1,s_2,s_3,s_4 \mid B)}{p(s_1,s_2,s_3 \mid B)\,p(s_4 \mid B)}} \times \frac{p(s_4 \mid A)}{p(s_4 \mid B)}\right) + \ldots$$

- <u>Another approach</u>:
  Try predicting the next sample and accumulate that which you can’t predict

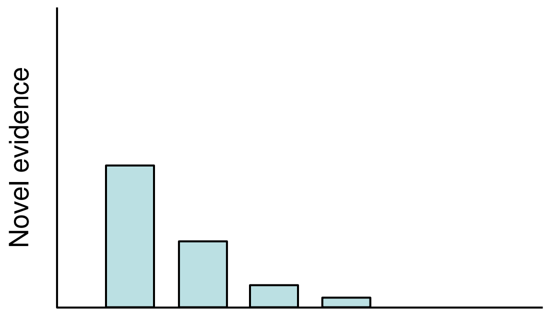


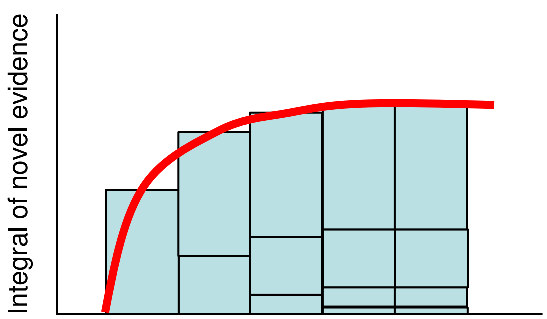
- <u>Simple 0th-order approximation</u>:
  - Novelty = change from previous sample
  - Assume fluctuations above a certain frequency are just noise
  - Low-pass filter





In a noisy task





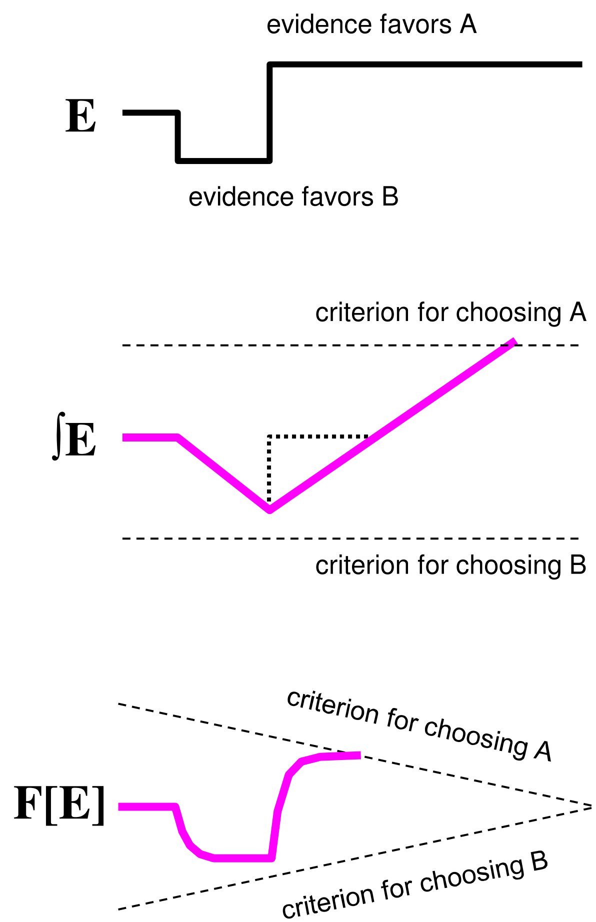
- First sample is independent
- Second gives some uncorrelated novel evidence
- Third sample gives less
- Etc.

- The integral…

  …looks like a low-pass filter

What if the world changes?

- During natural behavior, the world is always changing
- Any integrator will be sluggish in its response to such changes
- Need to be able to quickly respond to changes
  - Reset?
  - Sudden increase in gain?
  - Some other mechanism?



A low-pass filter has a short time constant – it responds to changes quickly

Summary

- 3 questions:

1. What if the world changes?
   - Need to be sensitive to changes
   - <u>Conclusion</u>: Need a short “time constant”

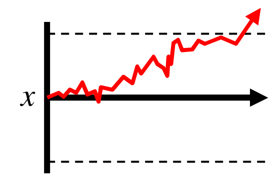
2. What kind of optimality do we want?
   - Animals care about reward rate
   - <u>Conclusion</u>: Want a criterion of confidence that ***drops*** over time

3. What if the samples are not completely independent?
   - Need to take redundancy into account
   - <u>Conclusion</u>: Want to sum only ***novel*** evidence

Summary

- Classic "diffusion" model

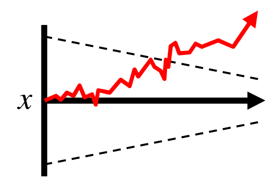
$$x(t) = \alpha \int_0^t E(\tau) d\tau \qquad -T < x(t) < T$$



  – Accumulate ***all*** evidence: $E(t)=u_1(t)- u_2(t)$
  – Compare to a ***constant*** threshold / accuracy criterion

- Our alternative
  – Accumulate only the ***novel*** evidence: ≈ $dE(t)/dt$
  – Compare to a ***dropping*** accuracy criterion

$$x(t) = \alpha \int_0^t \mathrm{F}\left[\frac{dE(\tau)}{d\tau}\right] d\tau \qquad -K(t) < x(t) < K(t)$$



Urgency-gating model

$$x(t) = \alpha \int_0^t \mathrm{F}\left[\tfrac{dE(\tau)}{d\tau}\right] d\tau \qquad\qquad -K(t) < x(t) < K(t)$$

- Let's define $K(t) = \dfrac{T}{u(t)}$ where, for example $u(t) = t$

- and define a new variable

$$\boxed{y(t) = x(t) \cdot u(t) = \left(\alpha \underbrace{\int_0^t \mathrm{F}\left[\tfrac{dE(\tau)}{d\tau}\right] d\tau}_{\text{Sum of novel info}} \right) \cdot u(t)} \qquad\qquad -T < y(t) < T$$

- We compare this variable to a constant threshold T, yielding the ~optimal behaviour described earlier

Urgency-gating model

$$\boxed{y(t) = \left(\alpha \int_0^t \mathrm{F}\left[\frac{dE(\tau)}{d\tau}\right] d\tau \right) \cdot u(t)} \qquad -T < y(t) < T$$

$$y(t) = \alpha\,\mathrm{F}\left[E(t)\right] \cdot u(t)$$

- Noise?
  - Evidence is low-pass-filtered $$y(t) = \alpha\,\mathrm{F}\left[E(t)\right] \cdot u(t)$$

- But what about all of the data explained by the diffusion model???
  - Behavioural data on RT distributions
  - Neural data on activity in LIP, FEF, PFC, etc.

Constant-evidence tasks

- Nearly all experiments have used constant-evidence tasks

$$E(t) = E$$

- In those conditions
  - Diffusion model:

$$x(t) = \alpha \int_0^t E(\tau) d\tau \qquad -T < x(t) < T$$

$$x(t) = \alpha \int_0^t E d\tau = \alpha E \int_0^t d\tau$$

$$x(t) = \alpha E t$$

  - Urgency-gating:

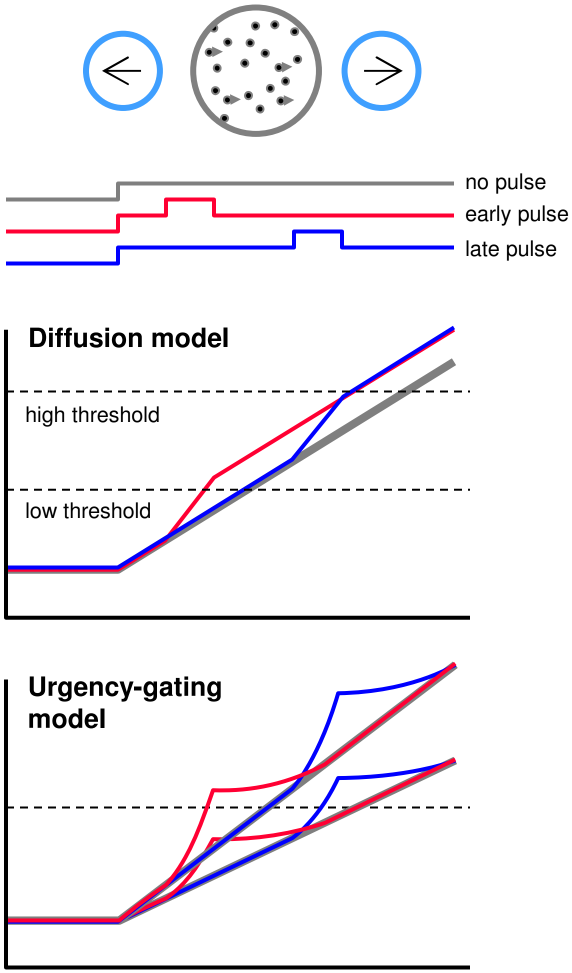
$$y(t) = \alpha \, \mathrm{F}\left[E(t)\right] \cdot u(t) \qquad -T < y(t) < T$$

$$y(t) = \alpha E t$$

  - The models make the same predictions at the behavioral and neural level
  - So what can we do to tell them apart?

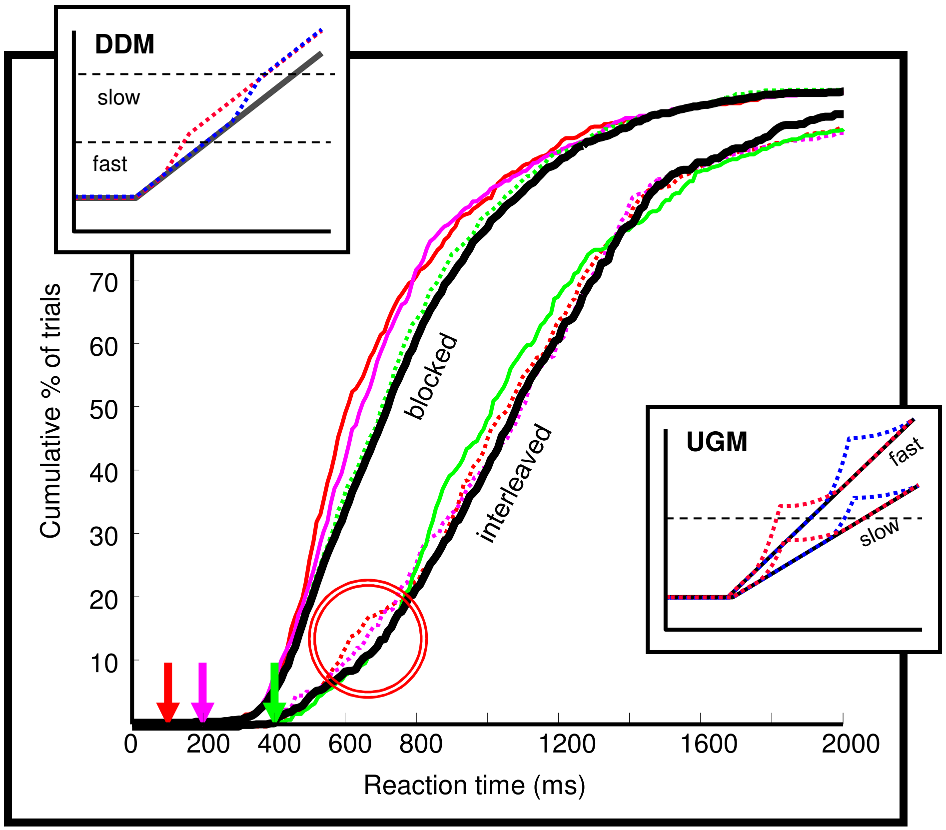
Noisy motion with pulses

Carland, Marcos, Thura, & Cisek (2016) *Journal of Neurophysiology*



- Random dot motion discrimination task
  - Reaction time version
  - Low stimulus coherence (3%)
  - We add brief pulses of extra motion at different times during the trial
- Diffusion model predictions
  - Fast (low threshold): early pulses have an effect but late pulses are too late
  - Slow (high threshold): all pulses have effect
- Urgency-gating model predictions
  - Fast (high urgency): early pulses have an effect but late pulses are too late
  - Slow (low urgency): late pulses have an effect but early pulses “leak out”
- Test subjects in fast and slow conditions

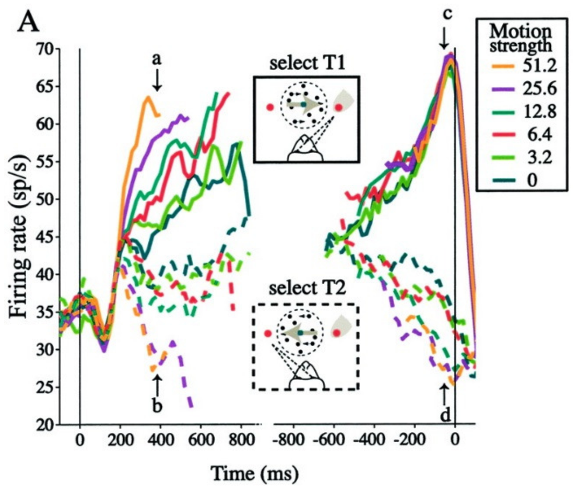
Results: Subject "JM"



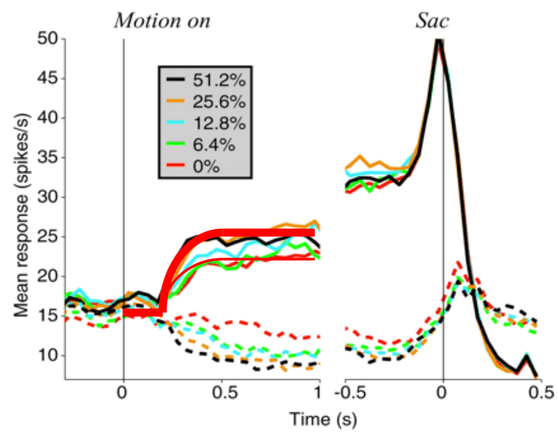
- Blocked (fast) condition
  - Pulses at 100 and 200ms have a significant effect
  - Pulse at 400ms does not
  - Consistent with both models
  - Consistent with previous studies of motion pulses (Huk & Shadlen 2005; Kiani et al. 2008)
- Interleaved (slow) condition
  - Pulse at 400ms has a significant effect
  - Pulses at 100 and 200ms ***do not*** have an effect
  - Suggests strong leak
    Time constant of 100-250ms

What about the neural level?

“Reaction-time”

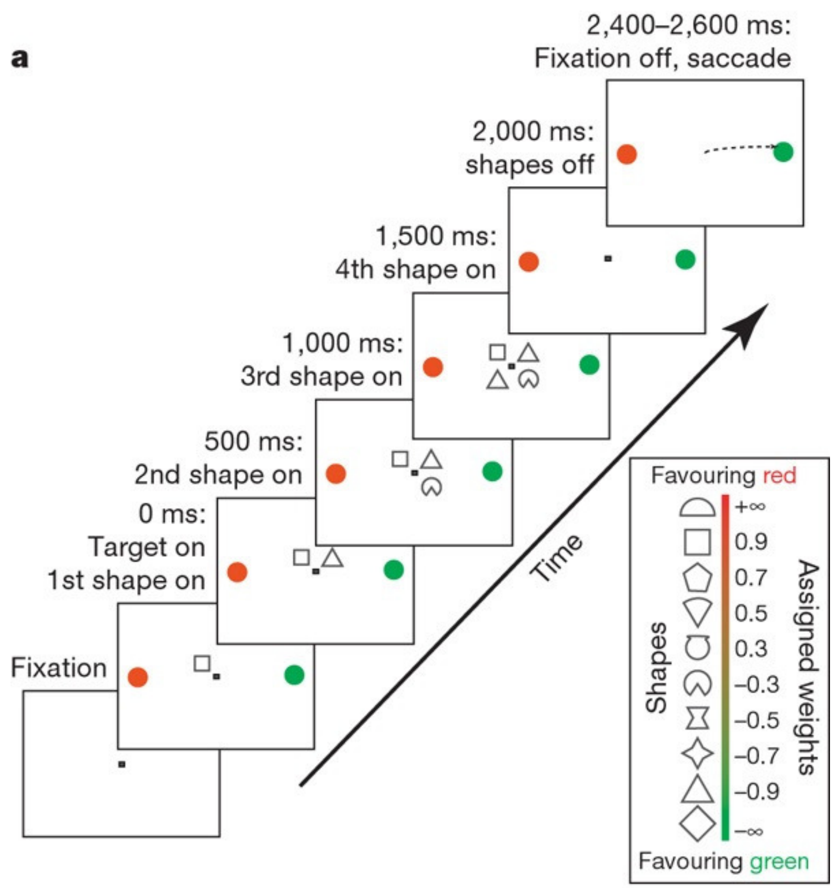


“Fixed-duration”



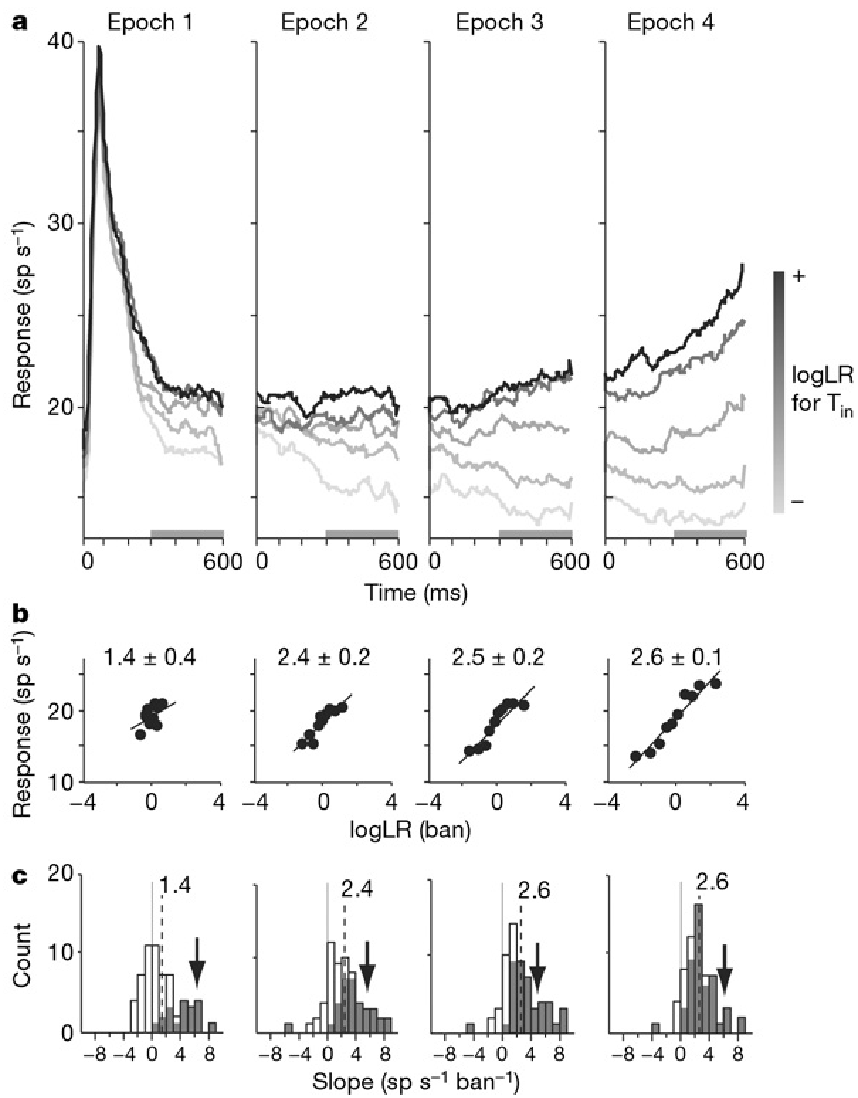
- Build-up is present in the reaction-time version of the task
  – To maximize reward rates, need a growing urgency signal
- Much reduced in the fixed-duration task
  – Urgency must be kept low until the GO signal
  – Result looks like a low-pass filter

Probabilistic inference



- Yang & Shadlen (2007) *Nature*
- Probabilistic categorization task
  1. Fixate
  2. Two targets (red and green) appear, and a symbol in the center
     - Each shape has a meaning: it favors either the red target or the green target
  3. After 500ms, another shape appears
  4. And another
  5. And another
  6. Now, move to the target which has more evidence
  7. If guessed correctly, receive reward

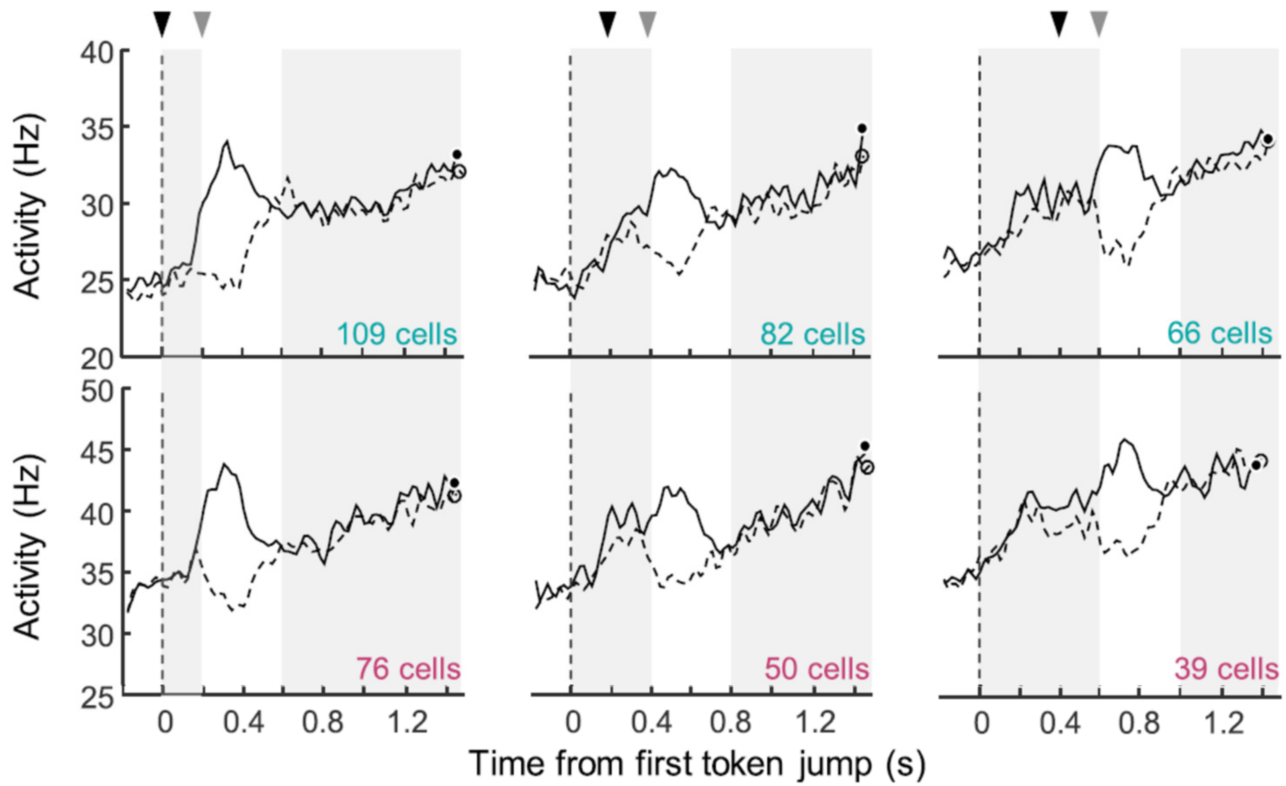
Log likelihood ratio in LIP



- Each time a symbol appears, neural activity in LIP changes.
- The magnitude of the change is a function of the log likelihood ratio conveyed by each symbol
  - Not quite a linear function, but pretty good
  - Slope ≈ 2.5 spikes/sec/ban
    - (1 ban = 10:1, 2 bans = 100:1)
- Neural activity reflects the subjective weight of evidence that the monkeys use to make their decisions

$$FR \approx b + \sum_{k=1}^{N} \left(\log \frac{p(s_k \mid red)}{p(s_k \mid green)} \right)$$

Is evidence integrated?

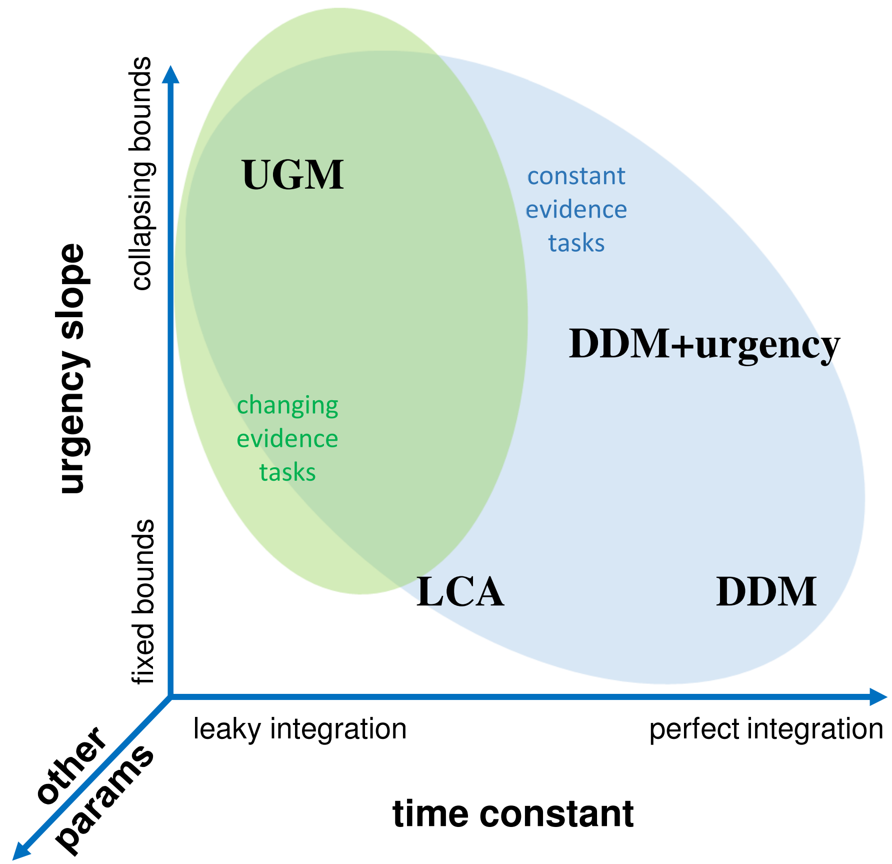


Thura & Cisek, 2017

Summary

- Basic model
  - Deliberation: use sensory information to sequentially update an internal decision variable
  - Commitment: the decision variable reaches some criterion
- Two variations
  - Drift-diffusion model:
    - Update is done by integrating ***all*** samples
    - Criterion is ***constant***
  - Urgency-gating model:
    - Update is done by integrating ***novel*** samples
    - Criterion is ***dropping*** (due to rising urgency)
  - Not really so different, but propose different explanation for the build-up of neural activity observed during deliberation

A space of models

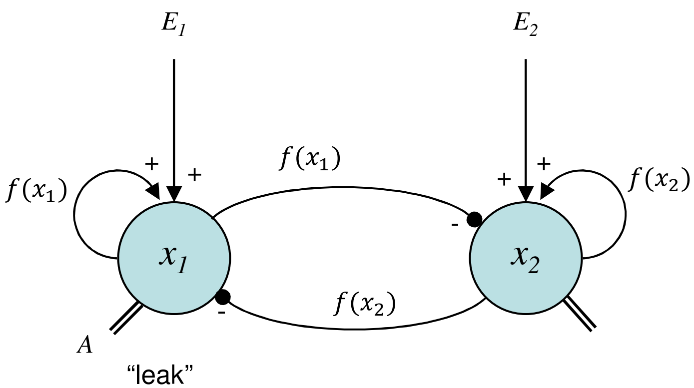


How is it implemented?

- Does the brain explicitly compute and compare it to a threshold? $$y(t) = \alpha\,\mathrm{F}\big[E(t)\big] \cdot u(t)$$

- Alternative approach: “attractor models”
  - Imagine two (or more) competing cells, each related to a choice
  - Each cell receives information in favor of that choice
    - This is “deliberation” about the choices
  - When one cell suppresses the other(s), it wins the competition
    - This is “commitment” to a choice

A recurrent attractor model



x_1 represents the activity of cell 1

x_2 represents the activity of cell 2

$$\frac{dx_1}{dt} = E_1$$

$$\frac{dx_1}{dt} = (M - x_1)E_1$$

$$\frac{dx_1}{dt} = (M - x_1)E_1 - x_1 A$$

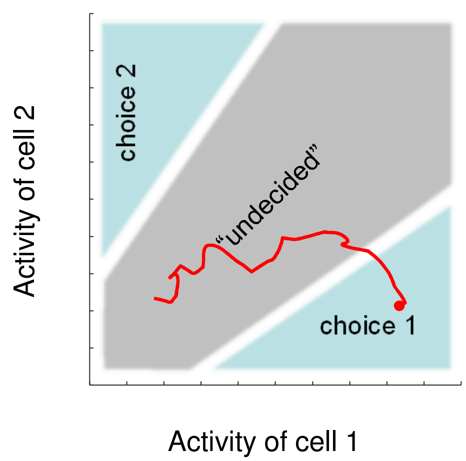
$$\frac{dx_2}{dt} = (M - x_2)E_2 - x_2 A$$

$$\frac{dx_1}{dt} = (M - x_1)E_1 - x_1\big(A + f(x_2)\big)$$

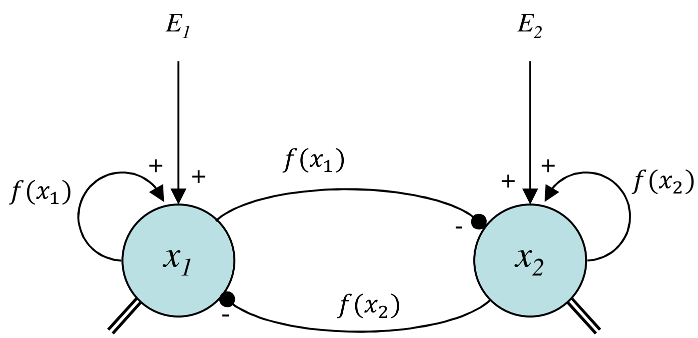
$$\frac{dx_2}{dt} = (M - x_2)E_2 - x_2\big(A + f(x_1)\big)$$

$$\frac{dx_1}{dt} = (M - x_1)(E_1 + f(x_1)) - x_1\big(A + f(x_2)\big)$$

$$\frac{dx_2}{dt} = (M - x_2)(E_2 + f(x_2)) - x_2\big(A + f(x_1)\big)$$



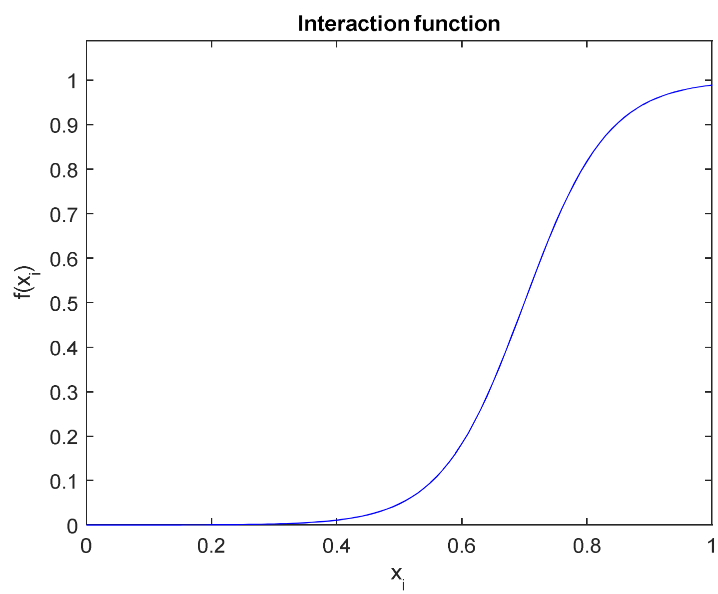
A recurrent attractor model



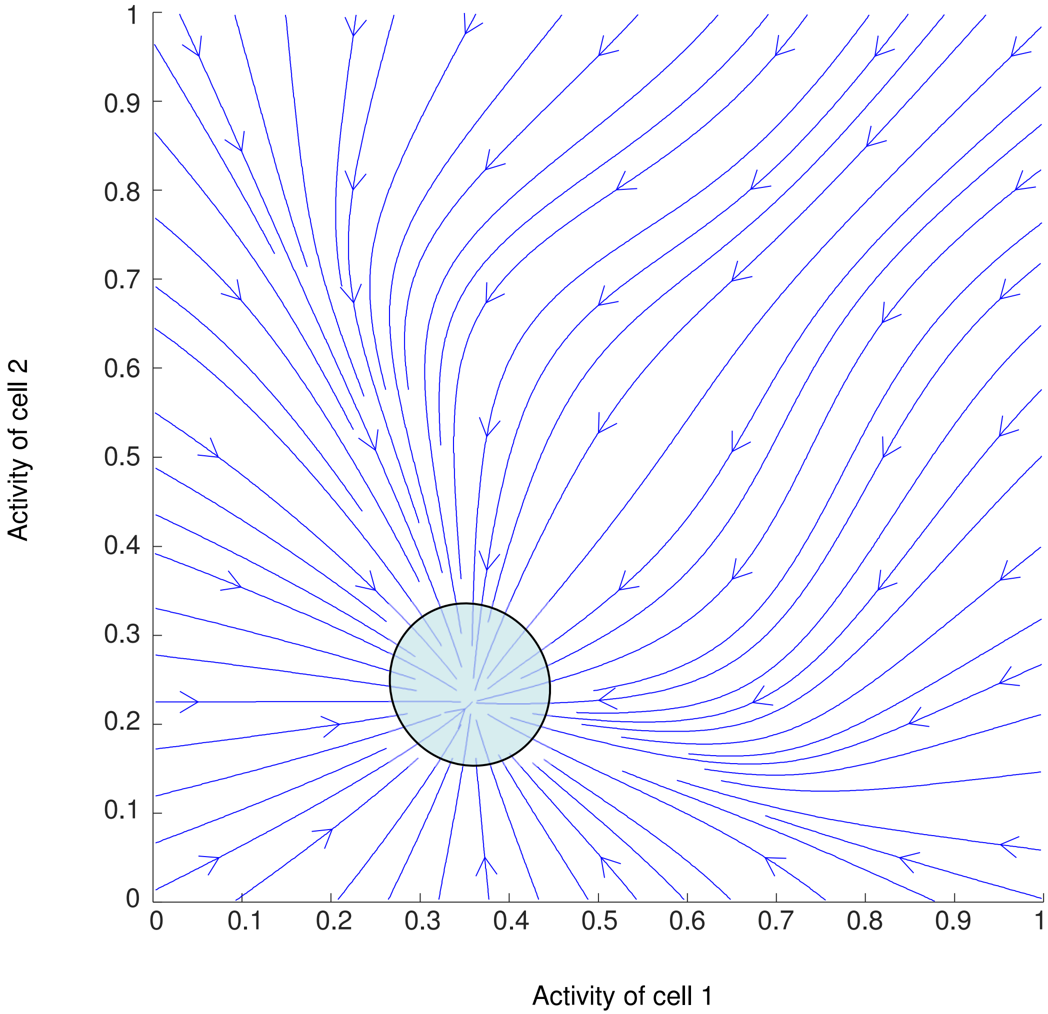
$$\frac{dx_1}{dt} = (M - x_1)(E_1 + f(x_1)) - x_1\big(A + f(x_2)\big)$$
$$\frac{dx_2}{dt} = (M - x_2)(E_2 + f(x_2)) - x_2\big(A + f(x_1)\big)$$

What is *f(x)*?

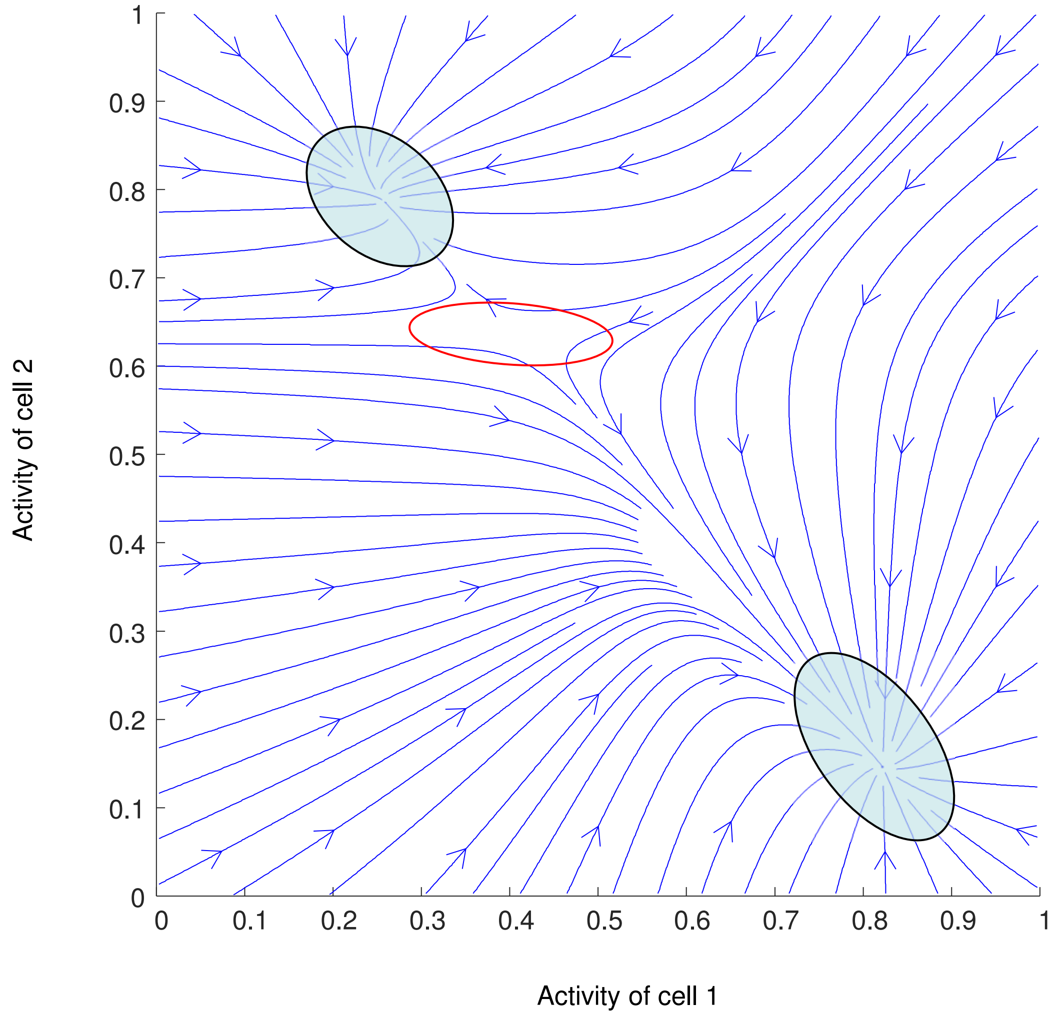
S. Grossberg (1973) *Studies in Applied Math.*



Flow field with an “attractor”

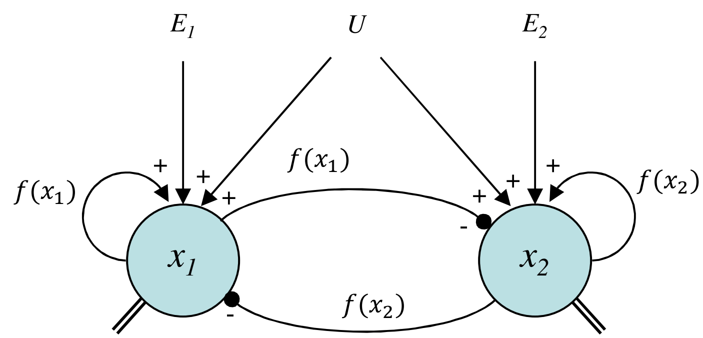


Flow field with two “attractors”



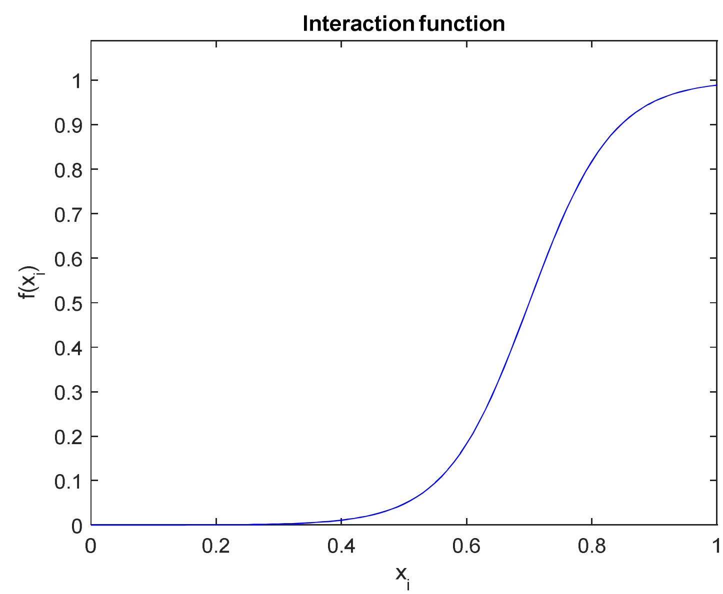
MATLAB demo

A recurrent attractor model with urgency

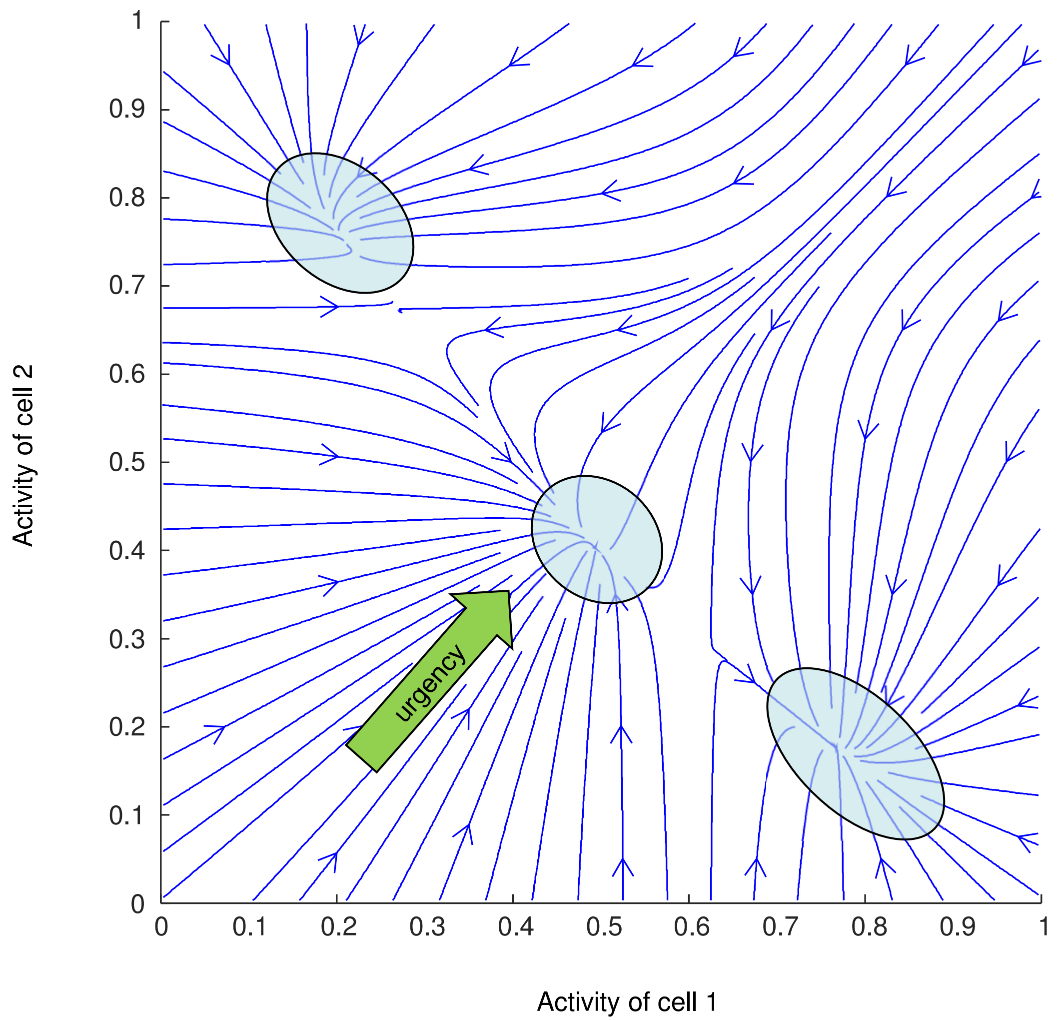


$$\frac{dx_1}{dt} = (M - x_1)(E_1 + f(x_1)) - x_1\big(A + f(x_2)\big)$$
$$\frac{dx_2}{dt} = (M - x_2)(E_2 + f(x_2)) - x_2\big(A + f(x_1)\big)$$

$$\frac{dx_1}{dt} = (M - x_1)(E_1 + f(x_1) + U) - x_1\big(A + f(x_2)\big)$$
$$\frac{dx_2}{dt} = (M - x_2)(E_2 + f(x_2) + U) - x_2\big(A + f(x_1)\big)$$



Flow field of attractor model with urgency



Summary

- Attractor models
  - Cells compete against each other
    - Competition is biased by evidence
    - by expected value, or by anything relevant for the choice
  - Commitment is made when one cell wins and suppresses the other(s)
    - The system falls into an “attractor” corresponding to a choice
      - “Basins of attraction”, “saddle points”
    - This will look like a “threshold”, but isn’t
  - Urgency can push the network to commit
    - It shifts the basins of attraction and saddle points, forcing a decision even if there’s no evidence for one choice versus another
- Lots of ways for making a model of decision-making