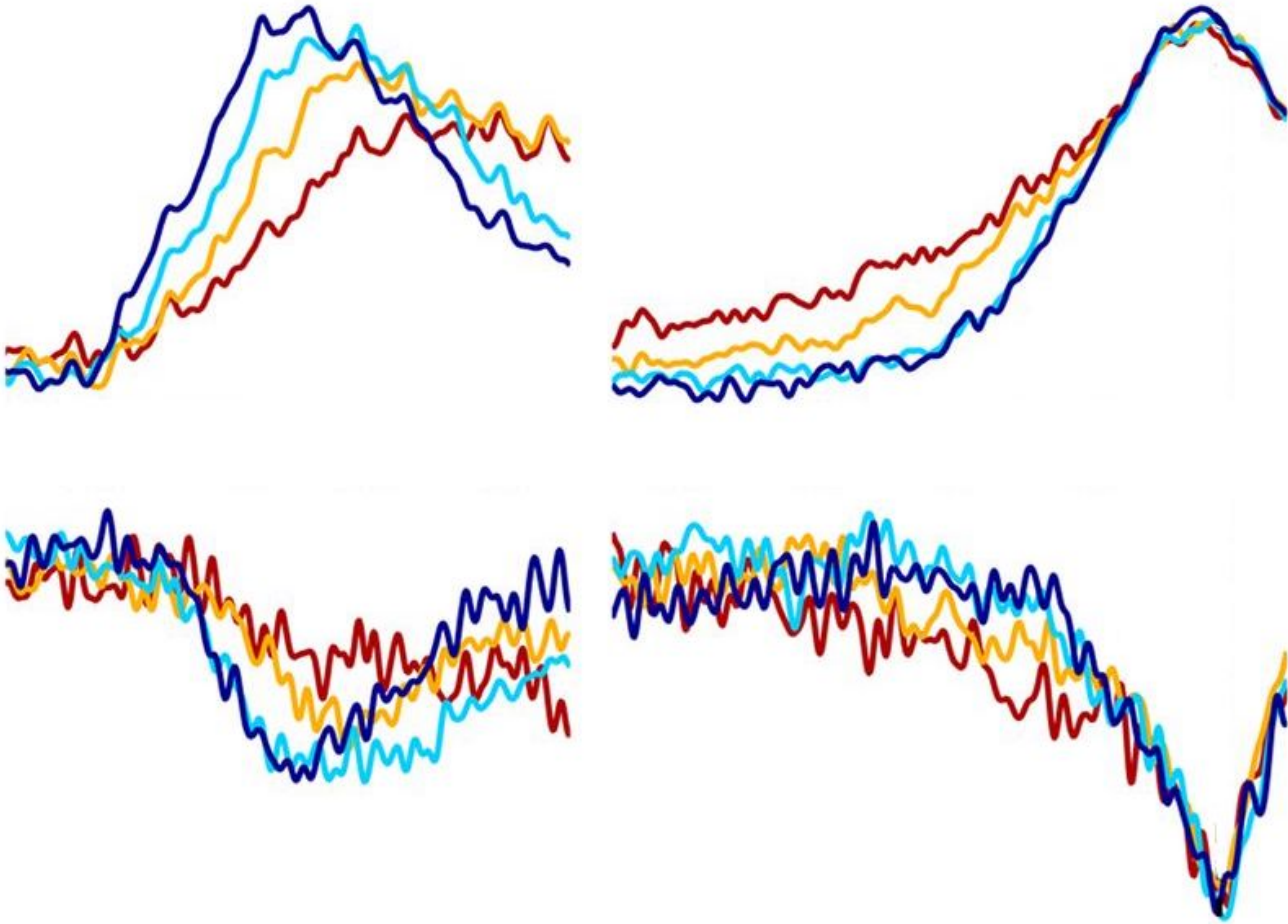
The Neuroscience of Decision Making

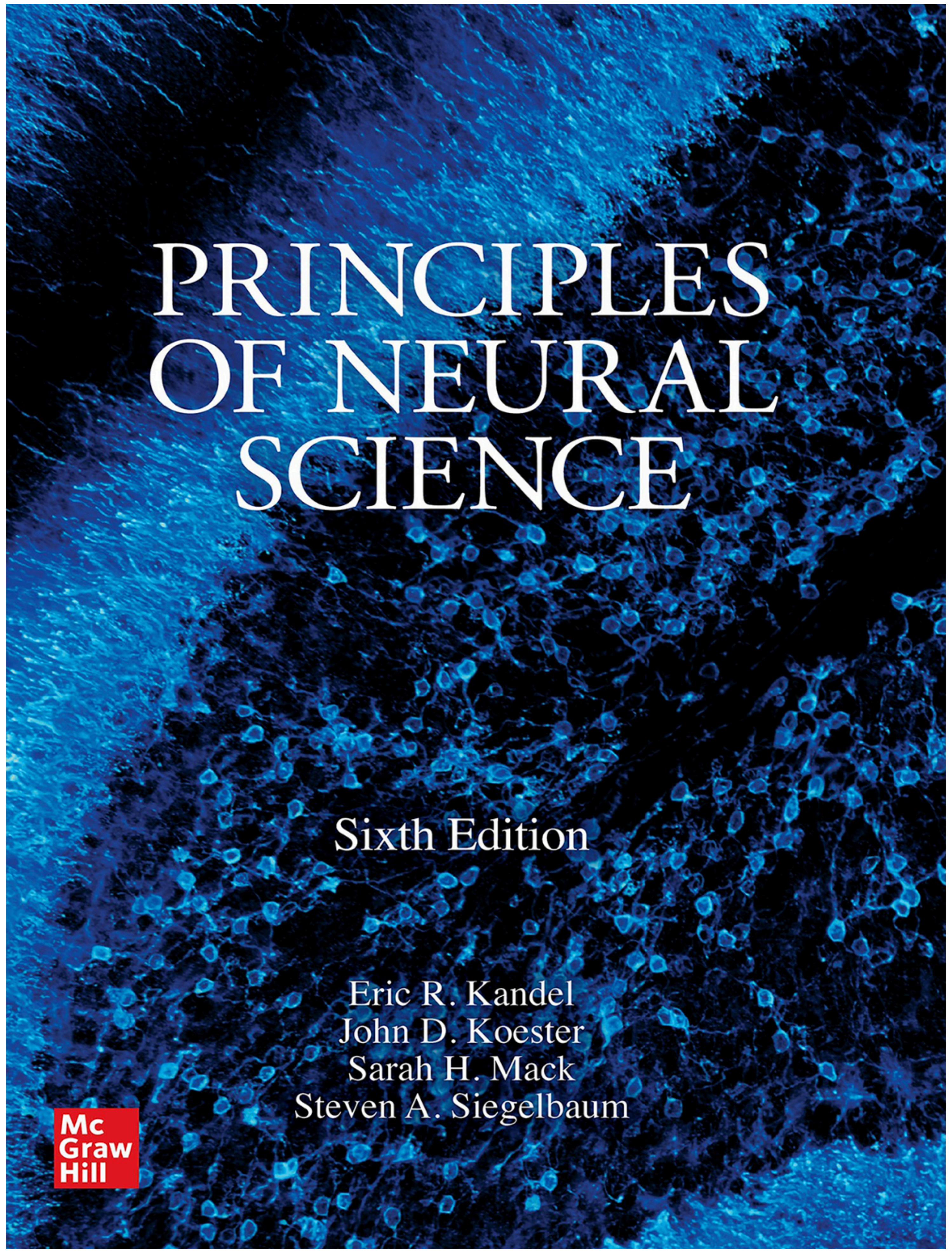
for the 26th IrBO Summer Camp



Nikan Amirkhani, 22 July 2023

Reference

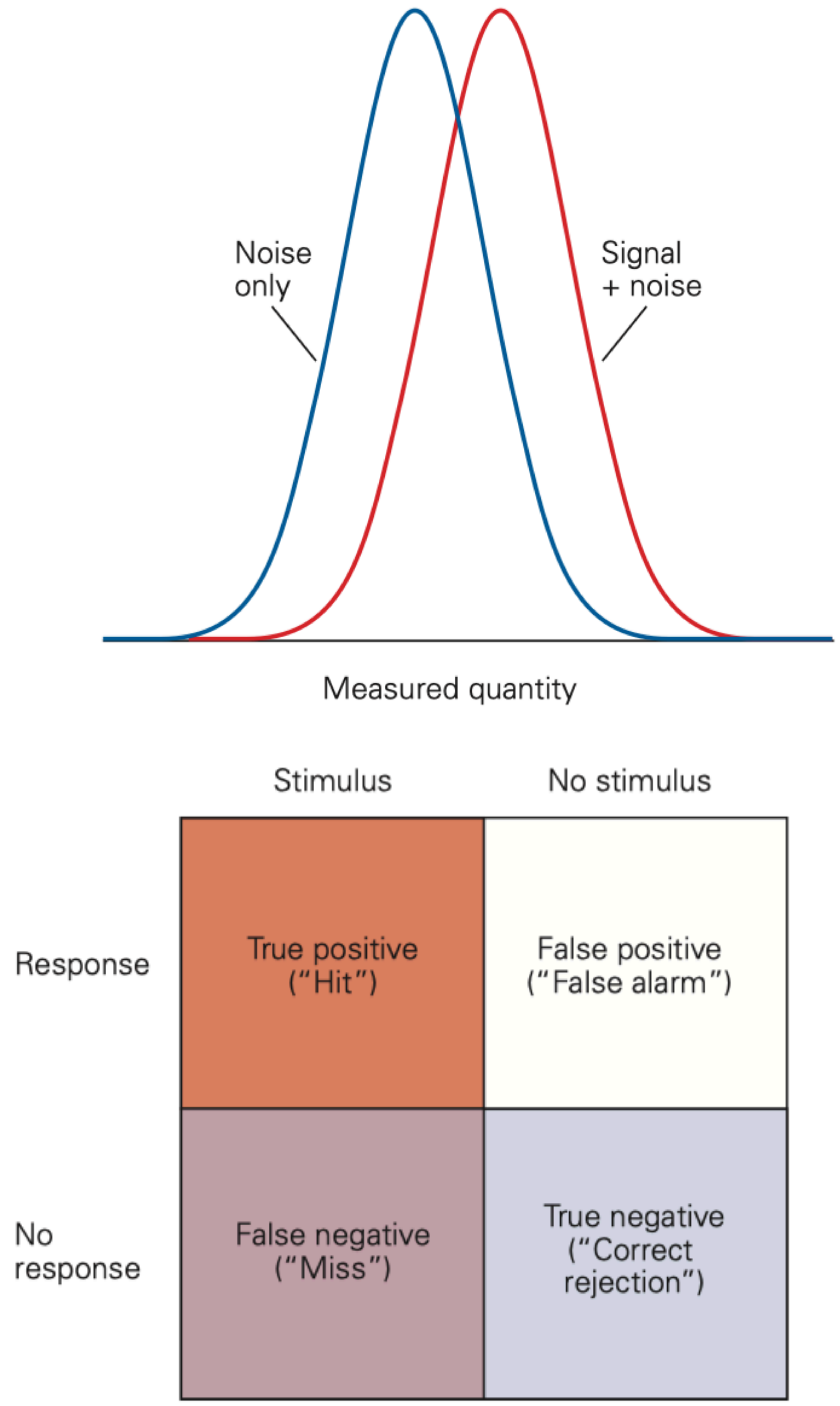
Kandel et al. 2021. Principles of Neural Science, Sixth Edition. Chapter 56, “Decision-Making and Consciousness.”



A decision is a commitment to a proposition, action, or plan based on evidence, prior knowledge, and expected outcomes.

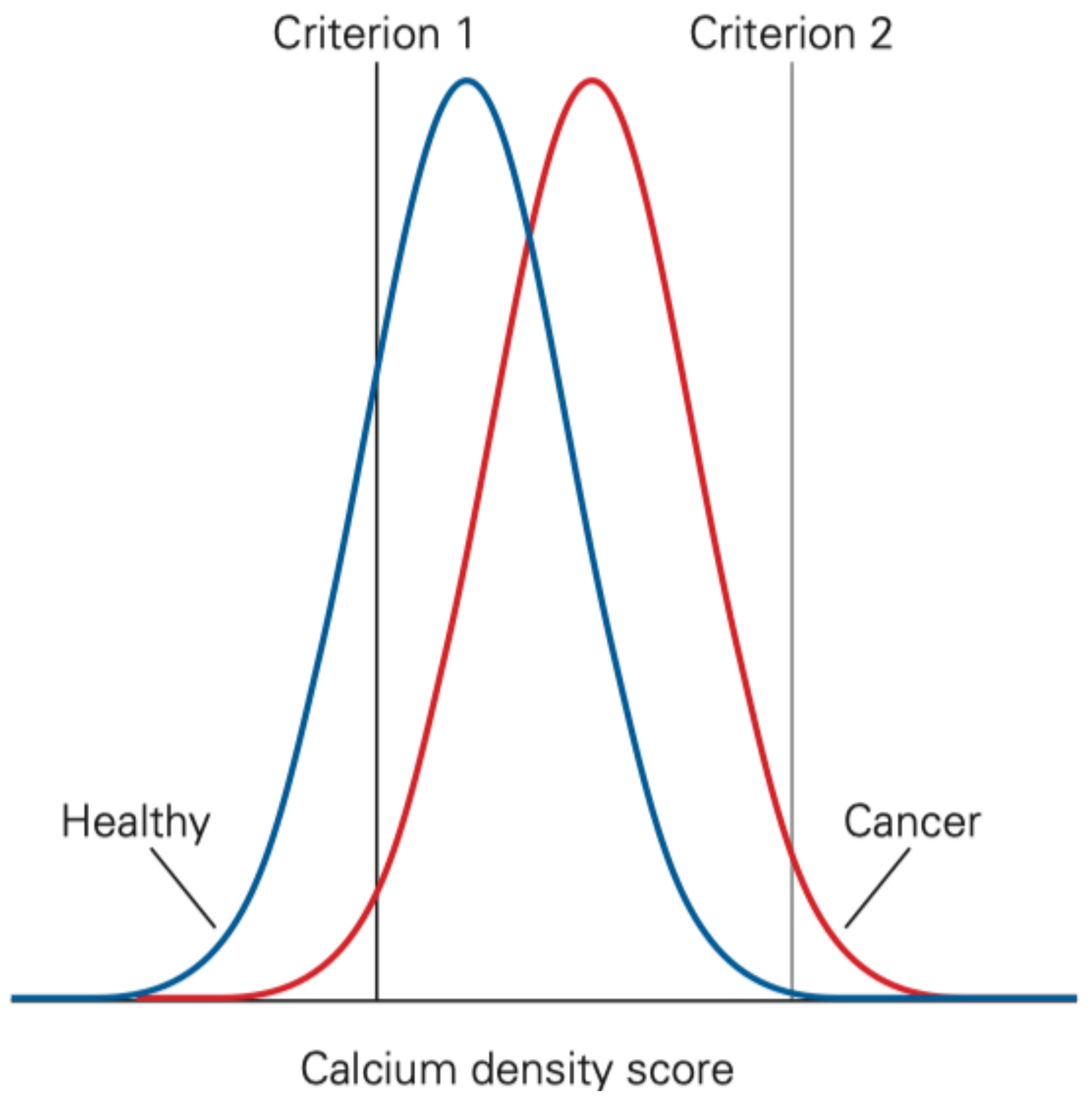
Perceptual Discrimination Requires a Decision Rule

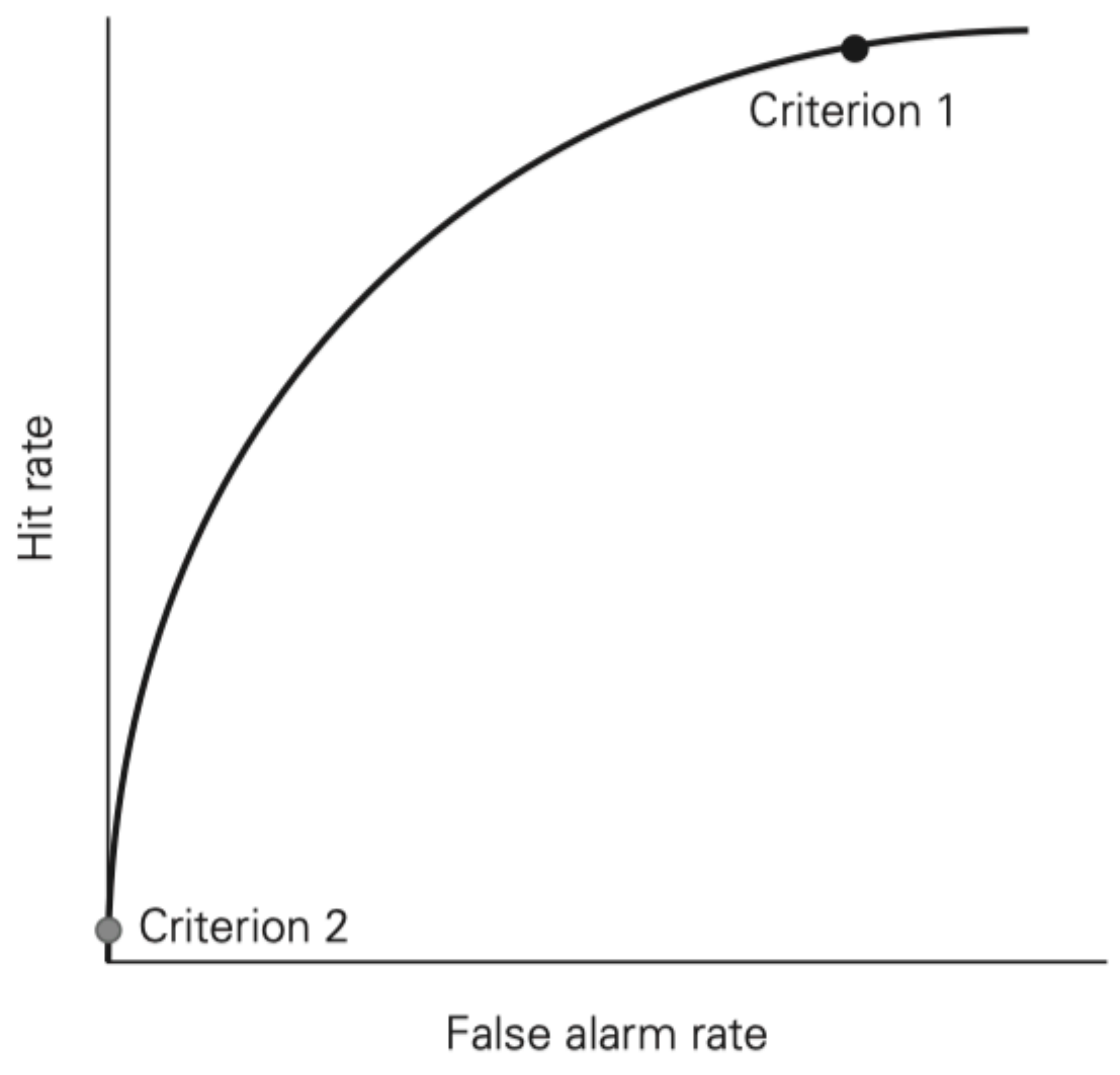
- The simplest type of decision involves the detection of a weak stimulus where the decision a subject must make is whether or not the stimulus is present—yes or no.
- If the stimulus is present, the evidence is a random sample drawn from the probability distribution of signal + noise. If the stimulus is absent, the evidence is a sample from the noise-only distribution.
- Subject choices can be tabulated in a four-cell *stimulus–response matrix*.



A Simple Decision Rule Is the Application of a Threshold to a Representation of the Evidence

- A simple decision rule is to say “yes” if the evidence exceeds some criterion or threshold.
- The criterion instantiates the decision-maker’s policy or strategy: laxity (criterion 1) vs. conservatism (criterion 2).
- The appropriate criterion depends on the relative cost of the two types of errors and the prior probability of encountering the signal.





Theoretical Excursion #1

Signal Detection

Encoding and decoding are related through a basic identity of probability theory.

Signal Detection

Encoding and Decoding

- $\mathbb{P}(s)$. Prior; probability of stimulus s being present
- $\mathbb{P}(r)$. probability of response r being recorded
- $\mathbb{P}(r, s)$. Joint probability; probability of stimulus s being present and response r being recorded
- $\mathbb{P}(r \mid s)$. probability of evoking response r, given that stimulus s was present
- $\mathbb{P}(s \mid r)$. probability of stimulus s being present, given that response r was recorded

$$\mathbb{P}(r) = \sum_s \mathbb{P}(r|s)\mathbb{P}(s)$$

$$\mathbb{P}(s) = \sum_r \mathbb{P}(s|r)\mathbb{P}(r)$$

$$\begin{aligned}\mathbb{P}(r, s) &= \mathbb{P}(r|s)\mathbb{P}(s) \\ &= \mathbb{P}(s|r)\mathbb{P}(r)\end{aligned}$$

$$\mathbb{P}(s|r) = \frac{\mathbb{P}(r|s)\mathbb{P}(s)}{\mathbb{P}(r)}$$

Signal Detection

Encoding and Decoding

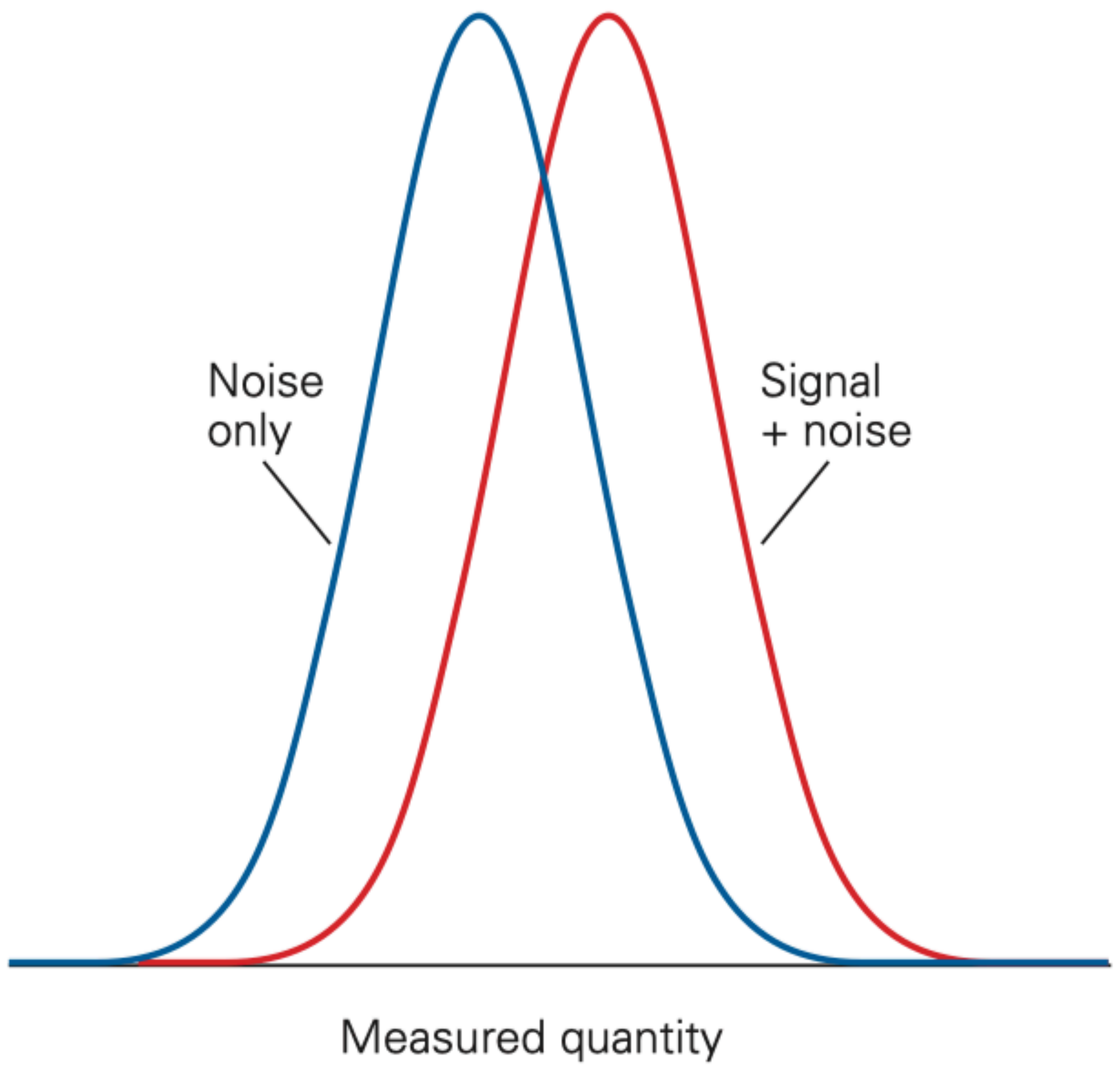
- Encoding is characterized by the set of probabilities $\mathbb{P}(r \mid s)$.
- Decoding is characterized by the set of probabilities $\mathbb{P}(s \mid r)$.
- $\mathbb{P}(s \mid r)$ can be obtained from $\mathbb{P}(r \mid s)$, but the stimulus probability $\mathbb{P}(s)$ is also needed.
- Decoding requires knowledge of the statistical properties of stimuli.

$$\mathbb{P}(s|r) = \frac{\mathbb{P}(r|s)\mathbb{P}(s)}{\mathbb{P}(r)}$$

Signal Detection

Detection and Discrimination

- A convenient measure of the separation between two Gaussian distributions is the discriminability *d'*.
- This is the distance between the means in units of their common standard deviation.
- The larger the *d'*, the more separated the distributions

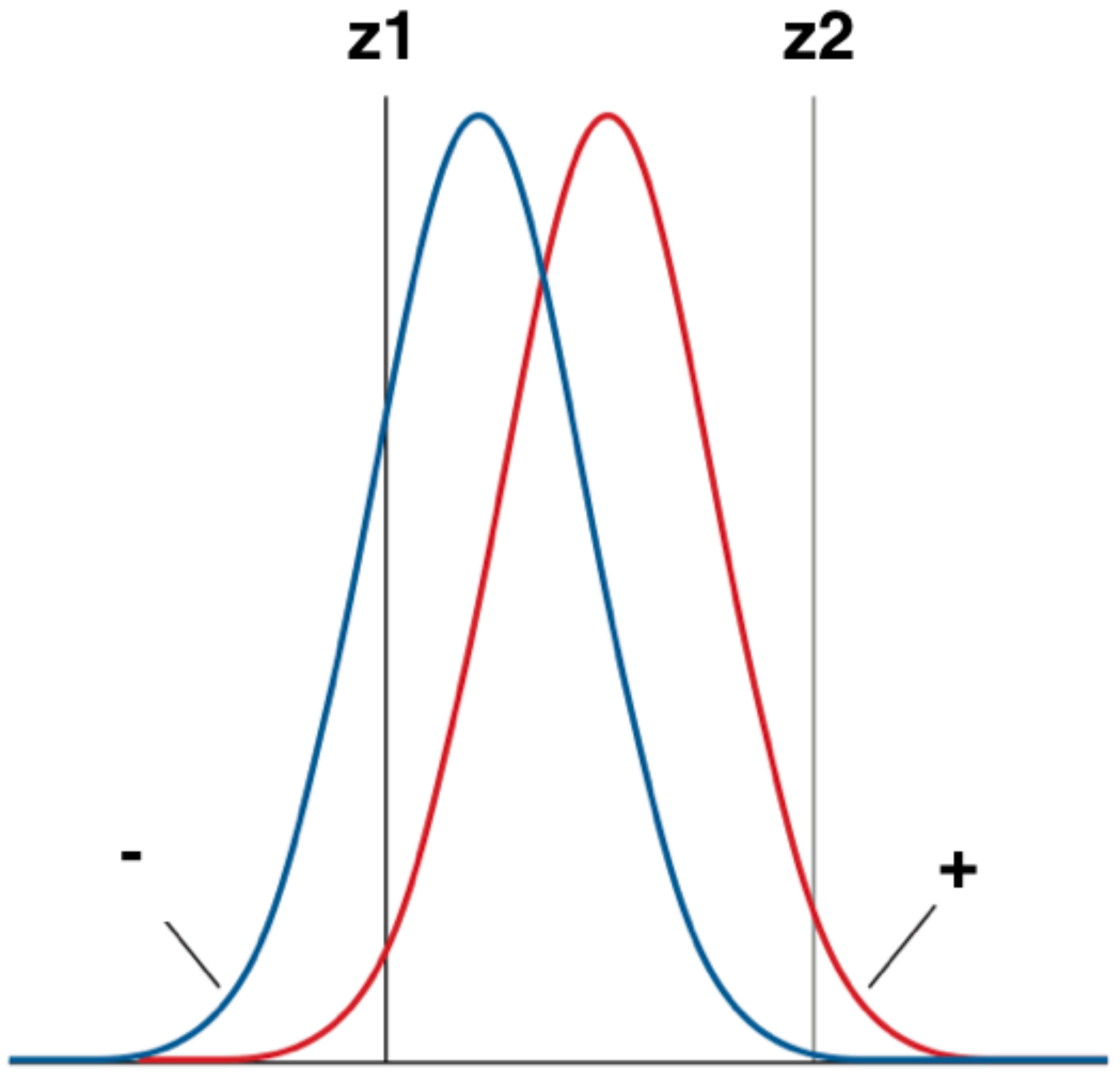


$$d' = \frac{\langle r \rangle_+ - \langle r \rangle_-}{\sigma_r}$$

Signal Detection

Detection and Discrimination

- A simple decoding procedure is to determine the firing rate r during a trial and compare it to a threshold number z. If $r \geq z$, we report "plus"; otherwise report "minus".
- In signal detection theory, the probability of this procedure generating the right answer in the presence of signal is called the *power* or hit rate and designated $\beta(z)$.
- The false alarm rate is also called the *size*, and designated $\alpha(z)$.



$$\beta(z) = \mathbb{P}(r \geq z|+)$$
$$\alpha(z) = \mathbb{P}(r \geq z|-)$$

Exercise 1

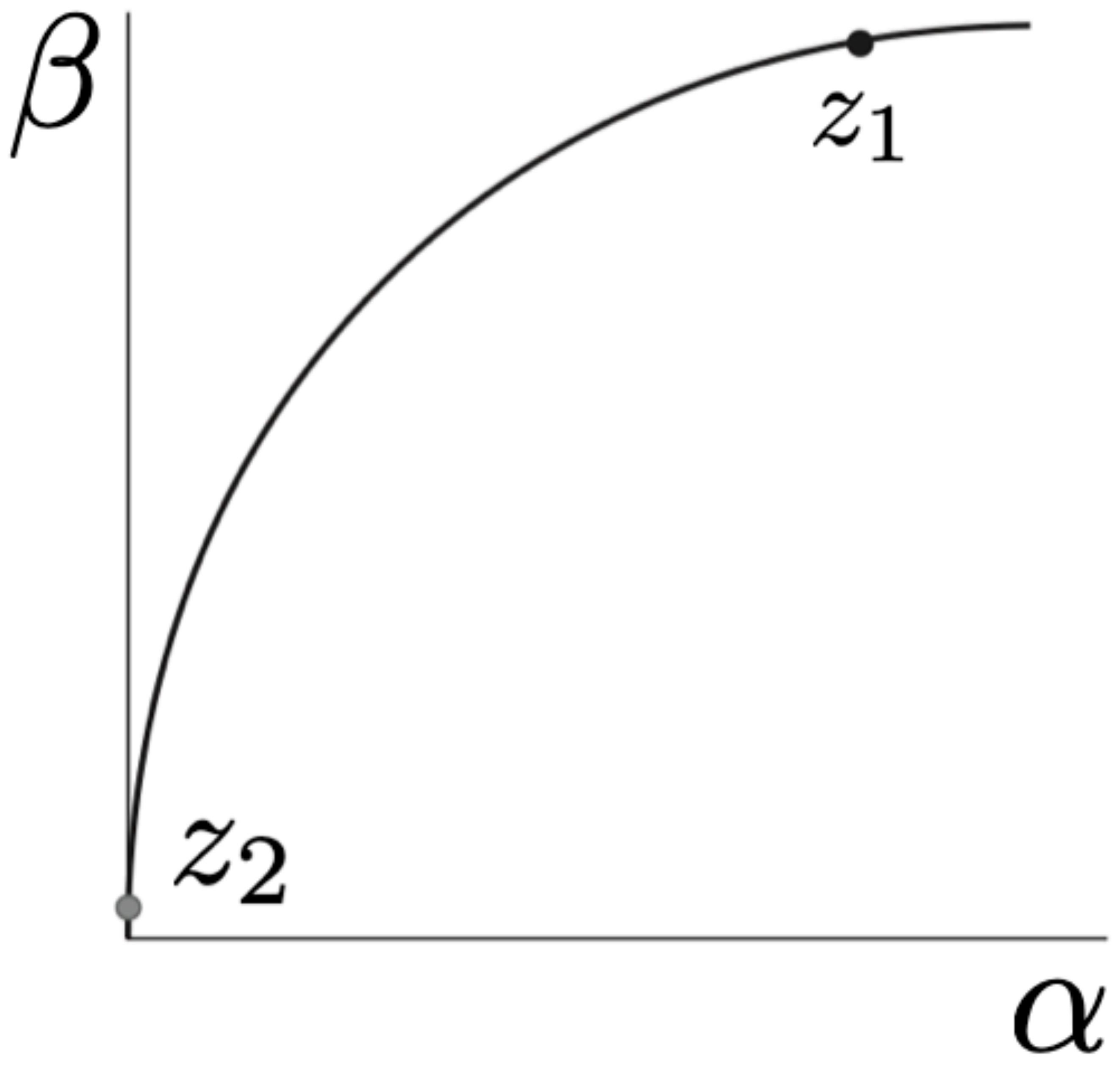
Assuming a 0.5 probability of signal presence, show

$$\mathbb{P}(\text{correct}) = \frac{\beta(z) + 1 - \alpha(z)}{2}.$$

Signal Detection

ROC Curves

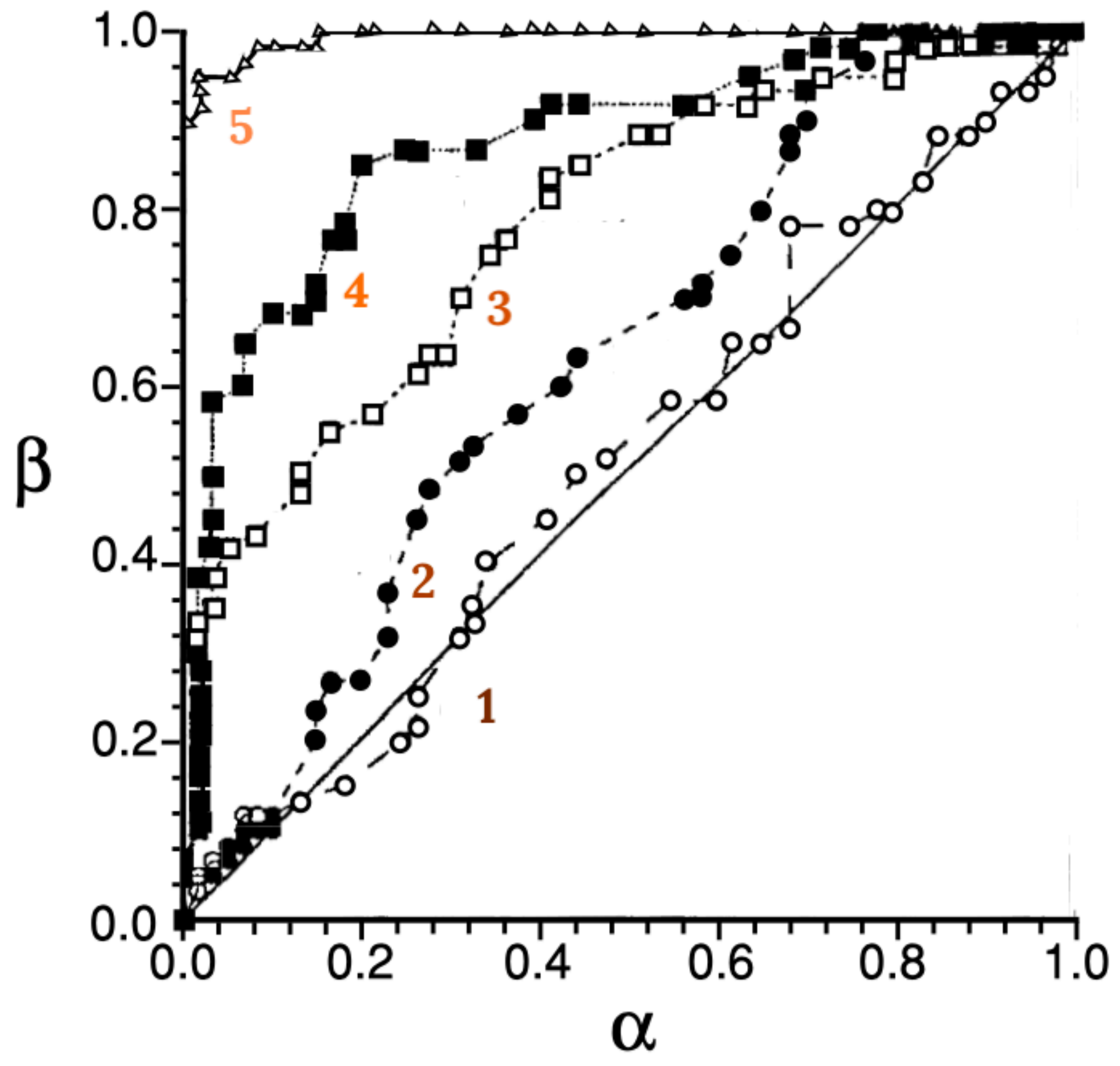
- Each point on a ROC curve corresponds to a different value of z. The x coordinate of the point is the test size for this value of z, and the y coordinate is its power.
- For $z = 0$, $\alpha = \beta = 1$.
- For $z \to \infty$, $\alpha = \beta = 0$.



Signal Detection

ROC Curves

- When signal presence is easily distinguishable from signal absence, the ROC curve rises rapidly as the threshold is lowered.
- For more difficult tasks, the curve rises more slowly as the threshold is lowered.
- If signal presence is indistinguishable from its absence, the curve will lie along the diagonal $\alpha = \beta$.
- The higher the probability of a correct response, the greater the area under the ROC curve.



Exercise 2

Show that the area under a ROC curve is precisely equal to the probability of a correct response.

$$\mathbb{P}(\text{correct}) = \int_0^1 \beta \, \mathrm{d}\alpha.$$

Signal Detection

The Likelihood Ratio Test

- *Neyman-Pearson lemma.* It is impossible to do better than to choose as the function test the ratio of probability densities, known as the likelihood ratio.
- Any other test that is monotonically increasing with respect to the likelihood ratio of r, such as r itself, is an equivalently optimal test.
- If $\mathbb{P}(r \mid +)$ and $\mathbb{P}(r \mid -)$ are Gaussians, the probability of signal presence given response r is a sigmoidal function of r, with d' as the slope.

$$\mathrm{LR}(r) = \frac{\mathbb{P}(r|+)}{\mathbb{P}(r|-)}$$

$$\mathbb{P}(+|r) = \frac{1}{1 + e^{\frac{-d'(r - r_{\text{ave}})}{\sigma_r}}}$$

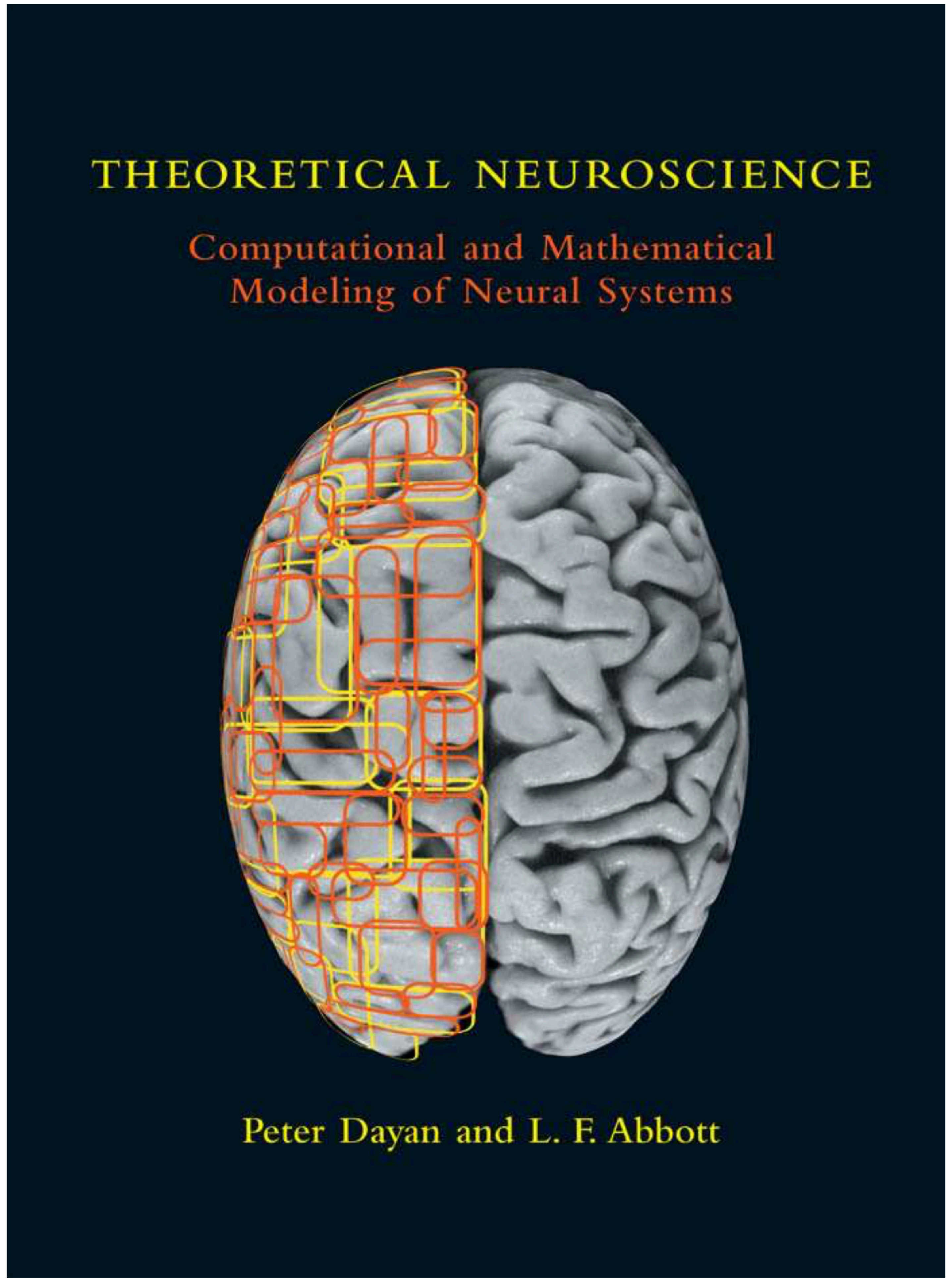
Exercise 3

Show that the slope of the ROC curve is the likelihood ratio.

$$\frac{\mathrm{d}\beta}{\mathrm{d}\alpha} = \mathrm{LR}(z).$$

Reference

Dayan and Abbott, 2001. Theoretical Neuroscience, Chapter 3, "Neural Decoding."

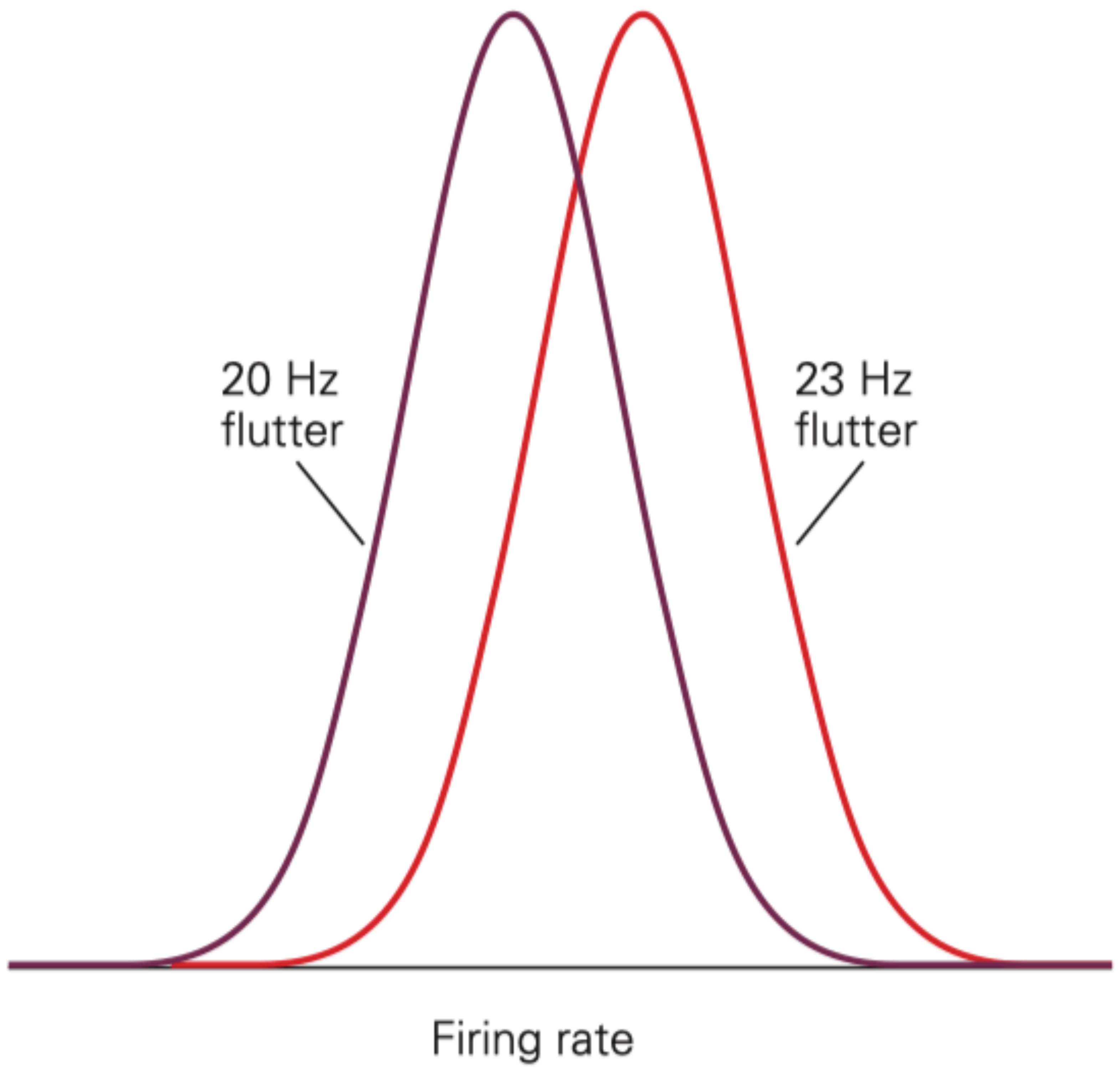


The challenge for neuroscience is to relate the terms *signal*, *noise*, and *criterion* to neural representations of sensory information and operations upon those representations that result in a choice.

Perceptual Decisions Involving Deliberation Mimic Aspects of Real-Life Decisions Involving Cognitive Faculties

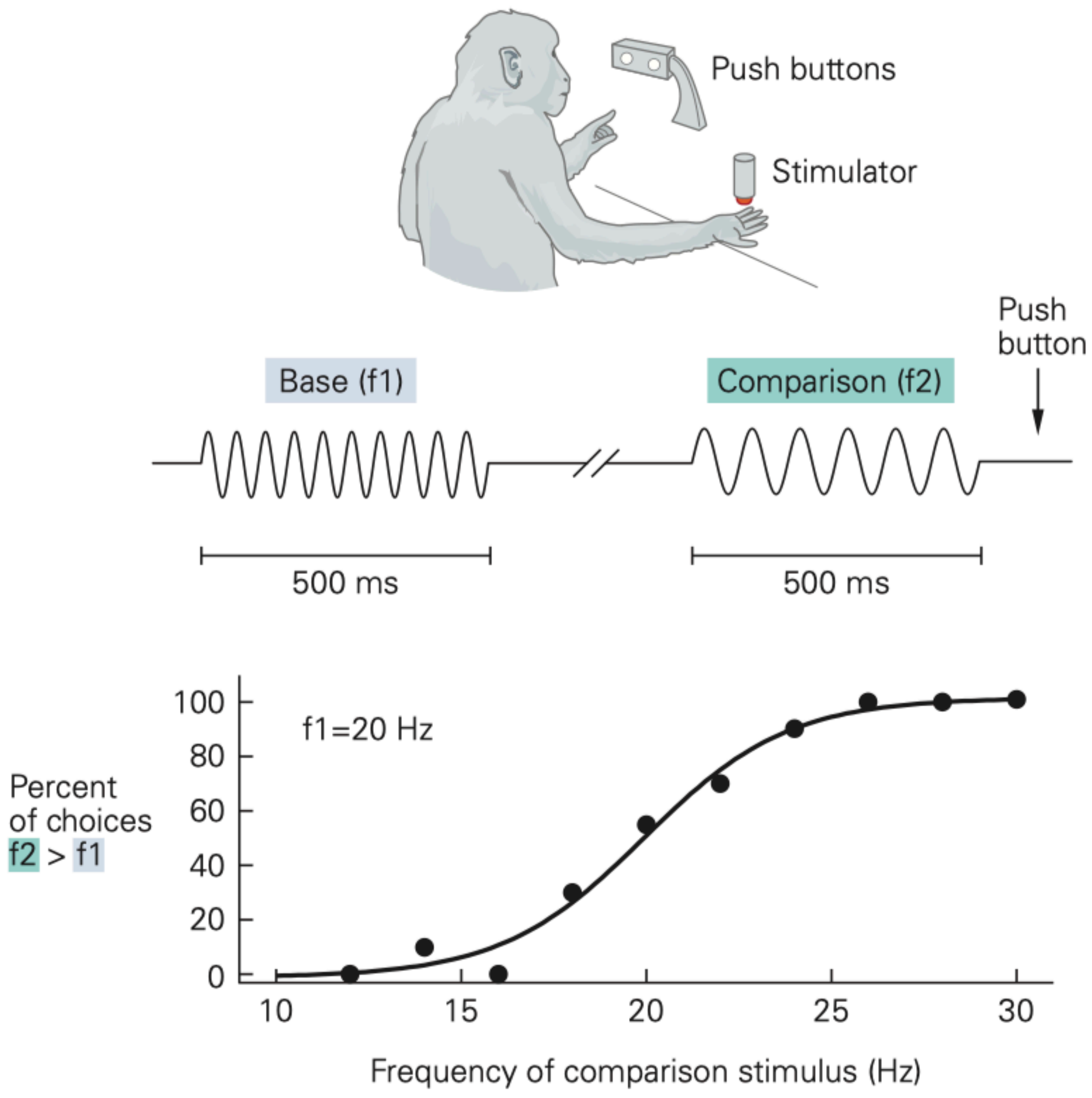
- The neural bases for more cognitive decisions have been examined by extending simple perceptual decisions in three ways:

  1. **Mountcastle; moving beyond detection to a choice between two or more competing alternatives**
  2. **Newsome; requiring the decision process to take time by involving consideration of many samples of evidence**
  3. considering decisions about matters involving values and preferences



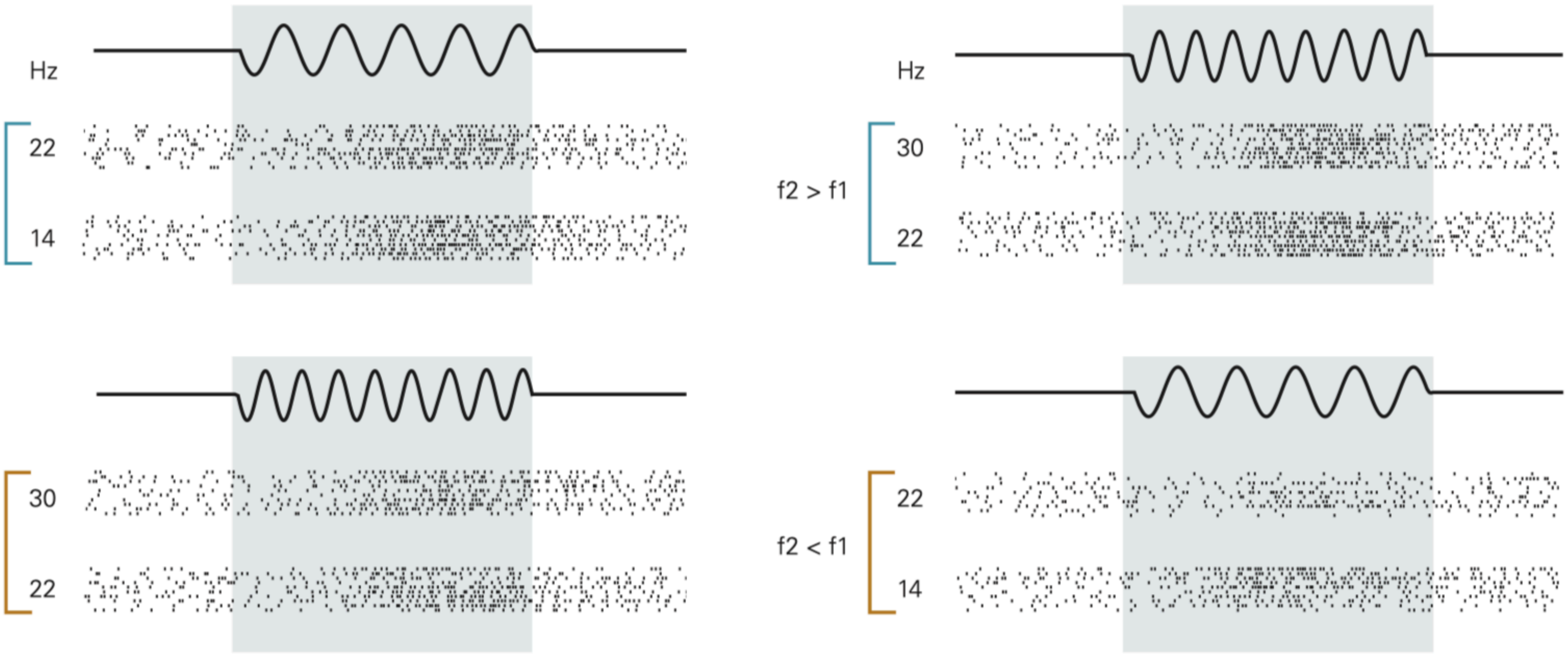
The discrimination of flutter-vibration frequency was the first perceptual decision studied in the central nervous system

- A 20-Hz vibratory stimulus is applied to the finger on the right hand.
- Following a delay period of several seconds, a second vibratory stimulus is applied.
- The monkey indicates whether the second vibration (f2) was at a higher or lower frequency than that of the first stimulus (f1) by pushing the left or right button with the other hand.



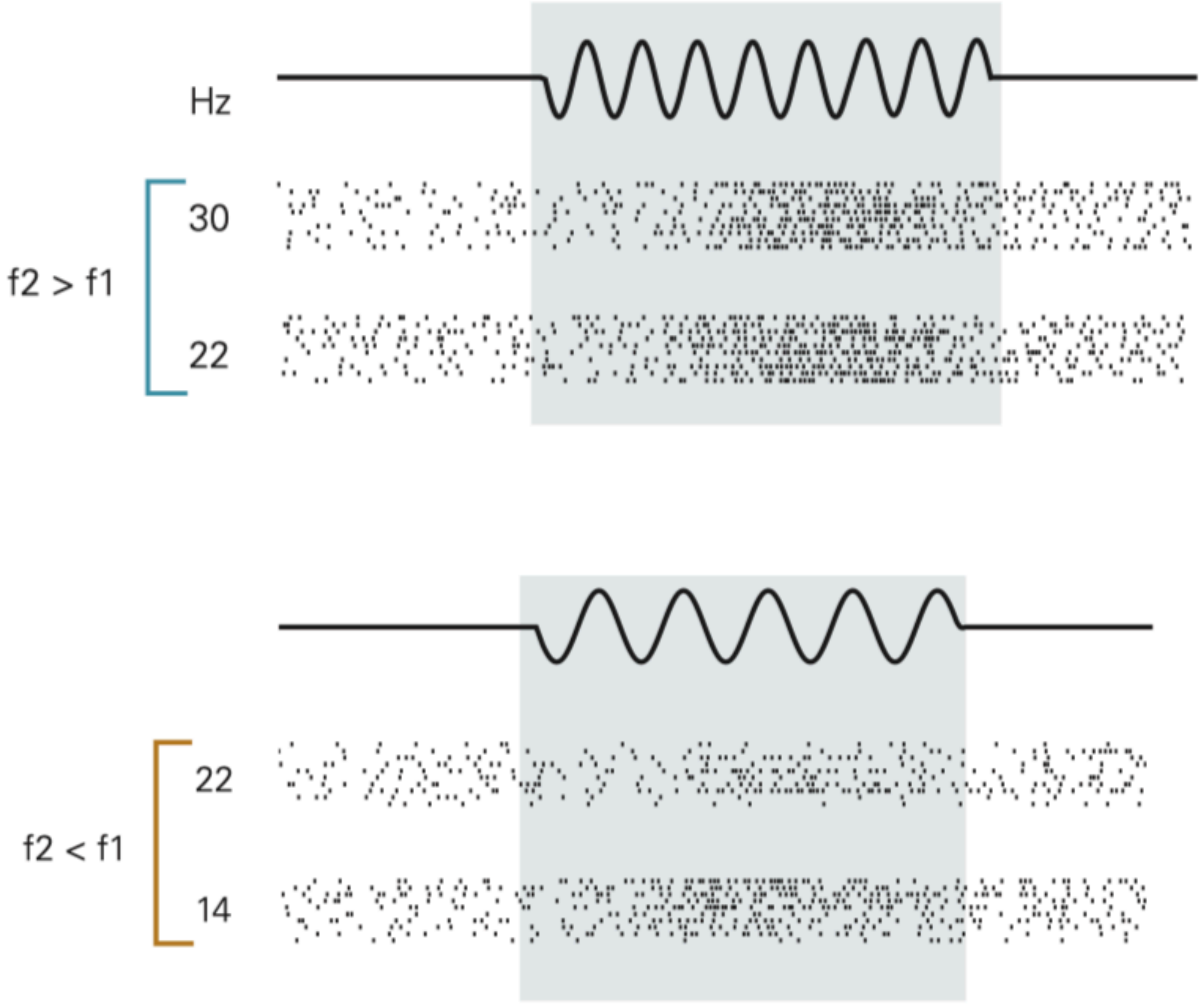
The discrimination of flutter-vibration frequency was the first perceptual decision studied in the central nervous system

- The neuron's response to f2 reflects the frequency of both f2 and f1.



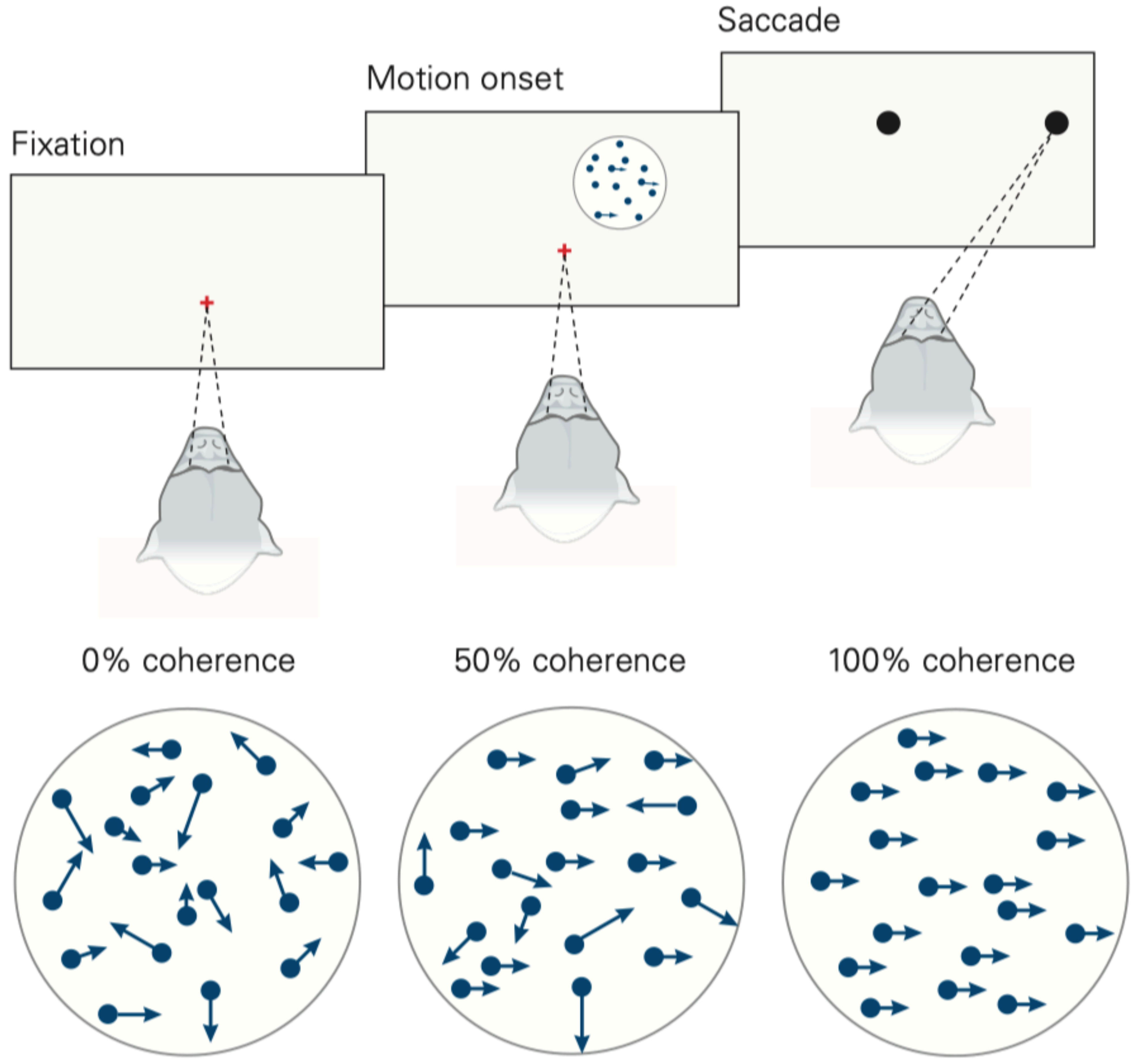
The discrimination of flutter-vibration frequency was the first perceptual decision studied in the central nervous system

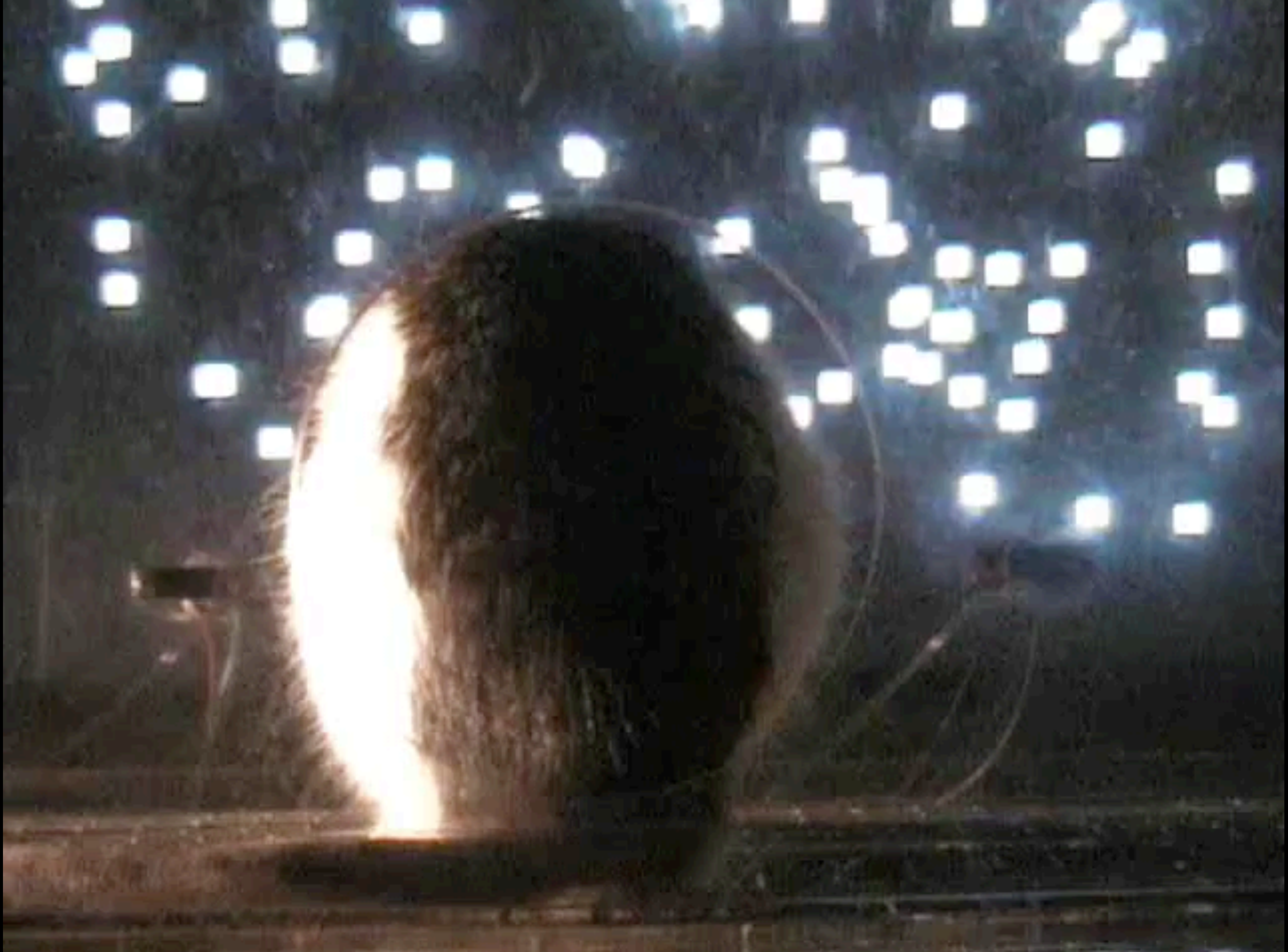
- When f2 > f1, the neuron fires at high rates during f2 and the animal reports that f2 is the higher frequency.
- When f2 < f1, the neuron fires at low rates during f2 and the animal reports that f1 is the higher frequency.
- The responses of neurons from the secondary somatosensory cortex reflect the animal's memory of an earlier event.



In the random dot motion discrimination task, the observer decides if the net motion of dots is in one direction or its opposite

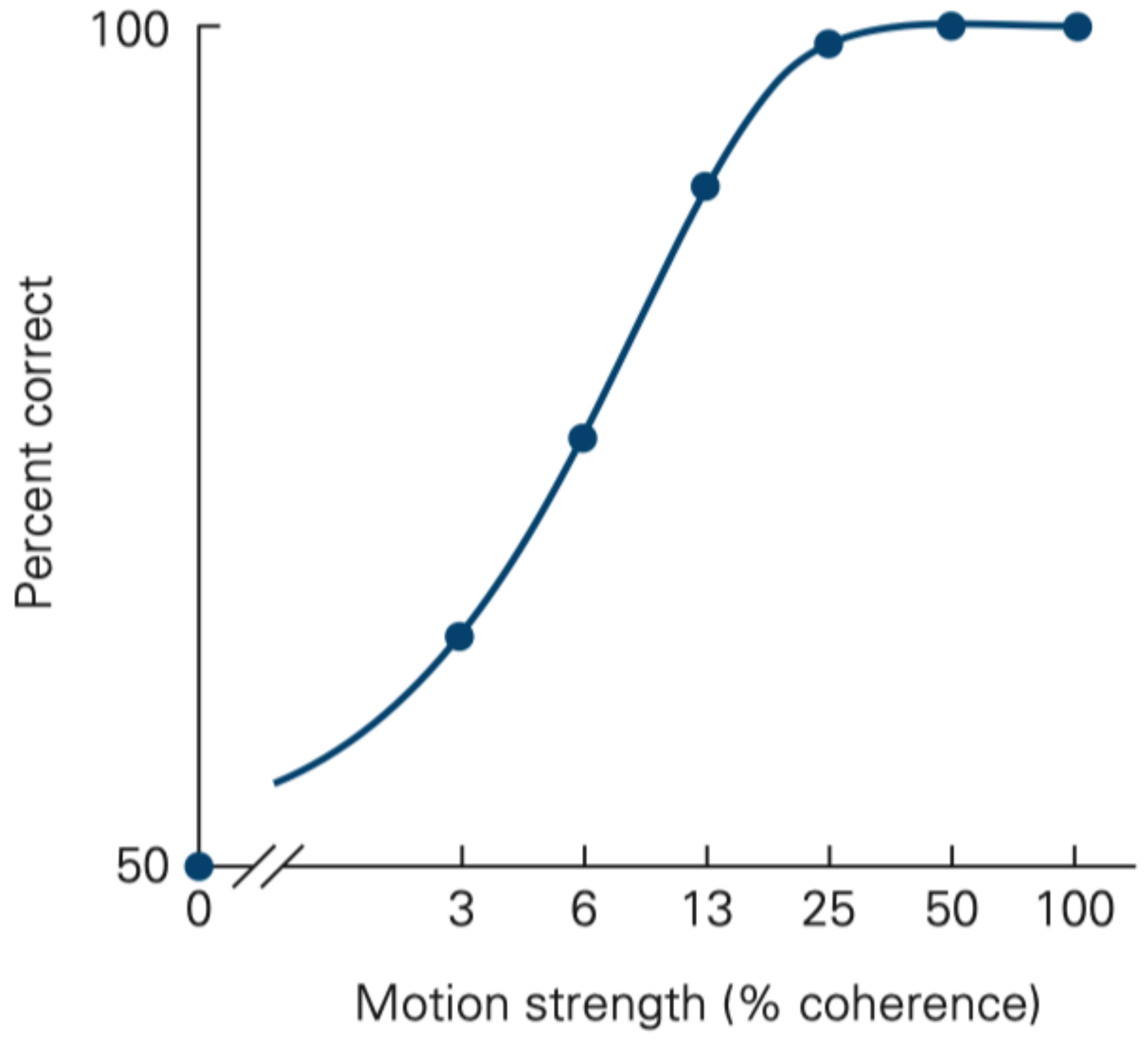
- William Newsome trained monkeys to decide whether a field of dynamic random dots had a tendency to move in one direction or its opposite.
- The decision is rendered difficult not by making the directions of motion more similar, but by degrading the signal-to-noise ratio of the random dots.
- This ratio is represented by the *coherence* of the stimuli.





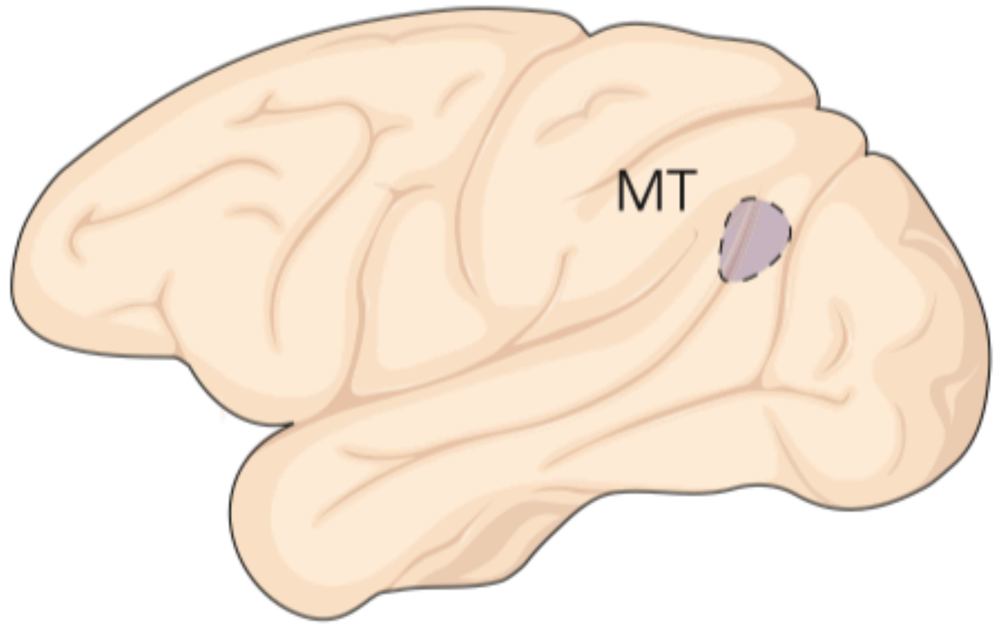
In the random dot motion discrimination task, the observer decides if the net motion of dots is in one direction or its opposite

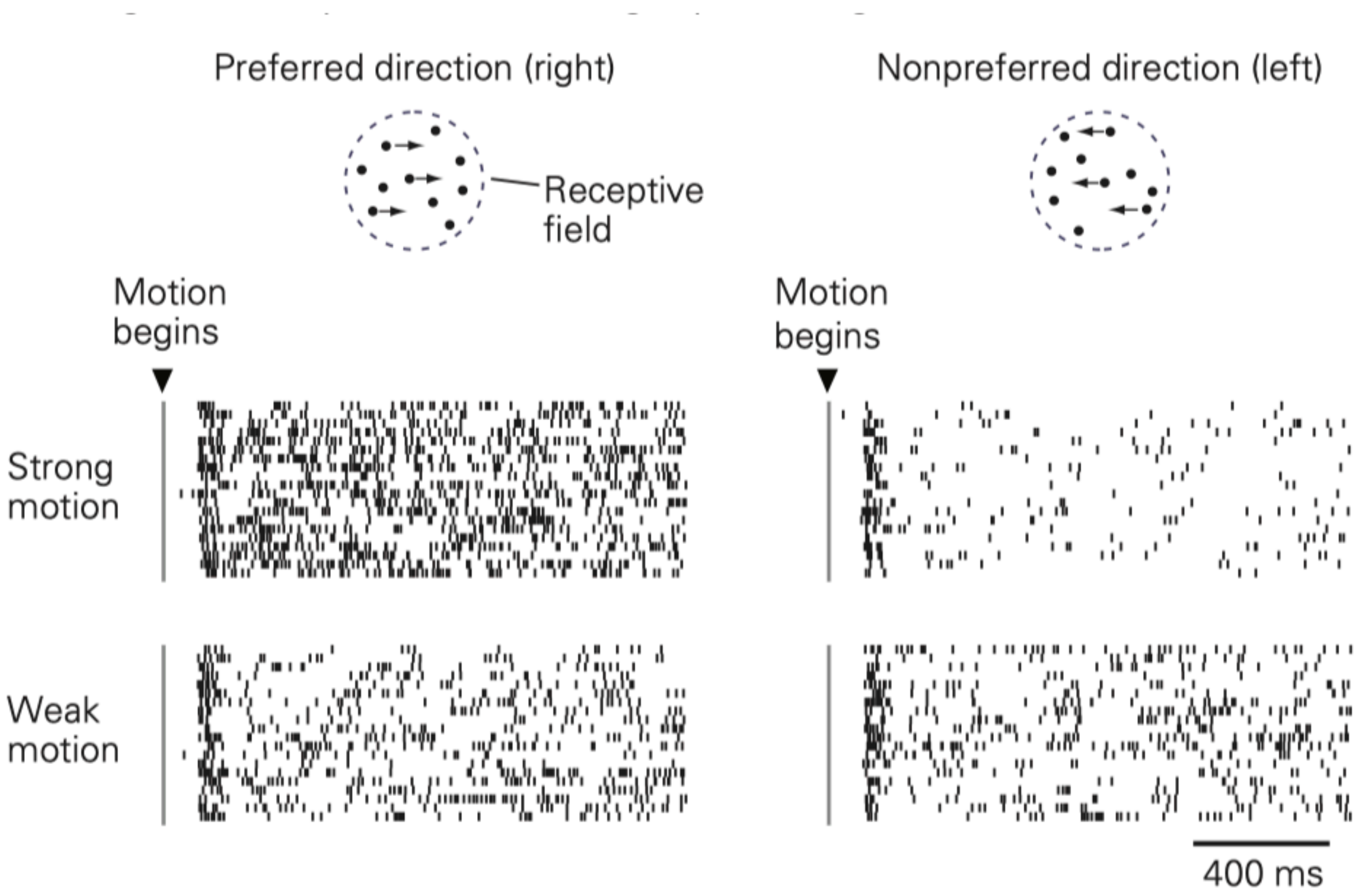
- The same neurons should inform the decision at all levels of difficulty.
- There is only one stimulus presentation: There is no need to remember anything between a reference and a test stimulus.
- Humans and monkeys perform this task at nearly identical levels



Neurons in Sensory Areas of the Cortex Supply the Noisy Samples of Evidence to Decision-Making

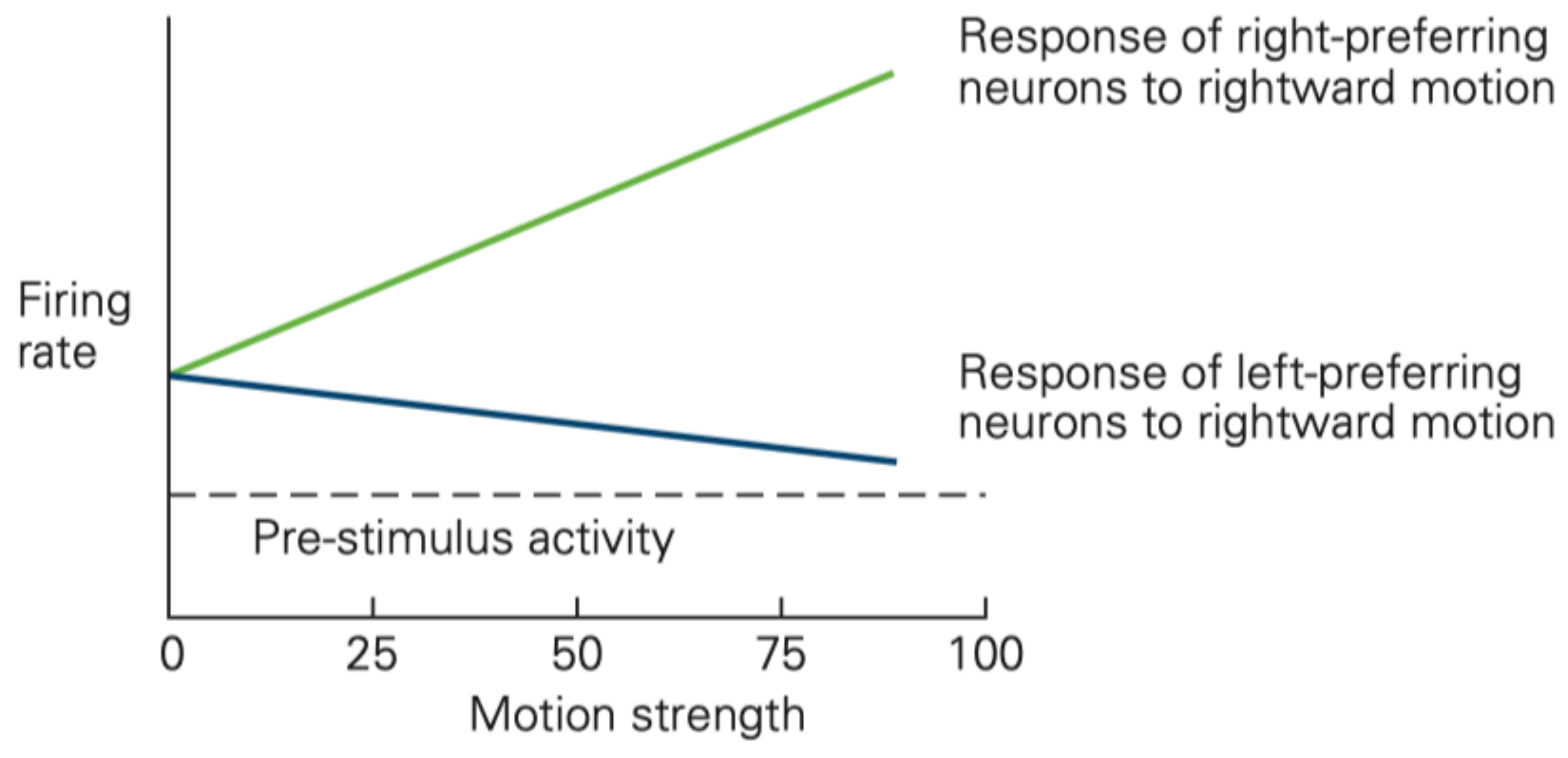
- Neurons in area MT contain a map of motion direction at each point of the visual field.
- Area MT (middle temporal) is a secondary visual processing area first discovered in New World monkeys.
- By showing RDM stimuli in the receptive field of MT neurons, we can identify their preferred directions of motion.
- MT neuron firing rates depend on motion strength and direction.

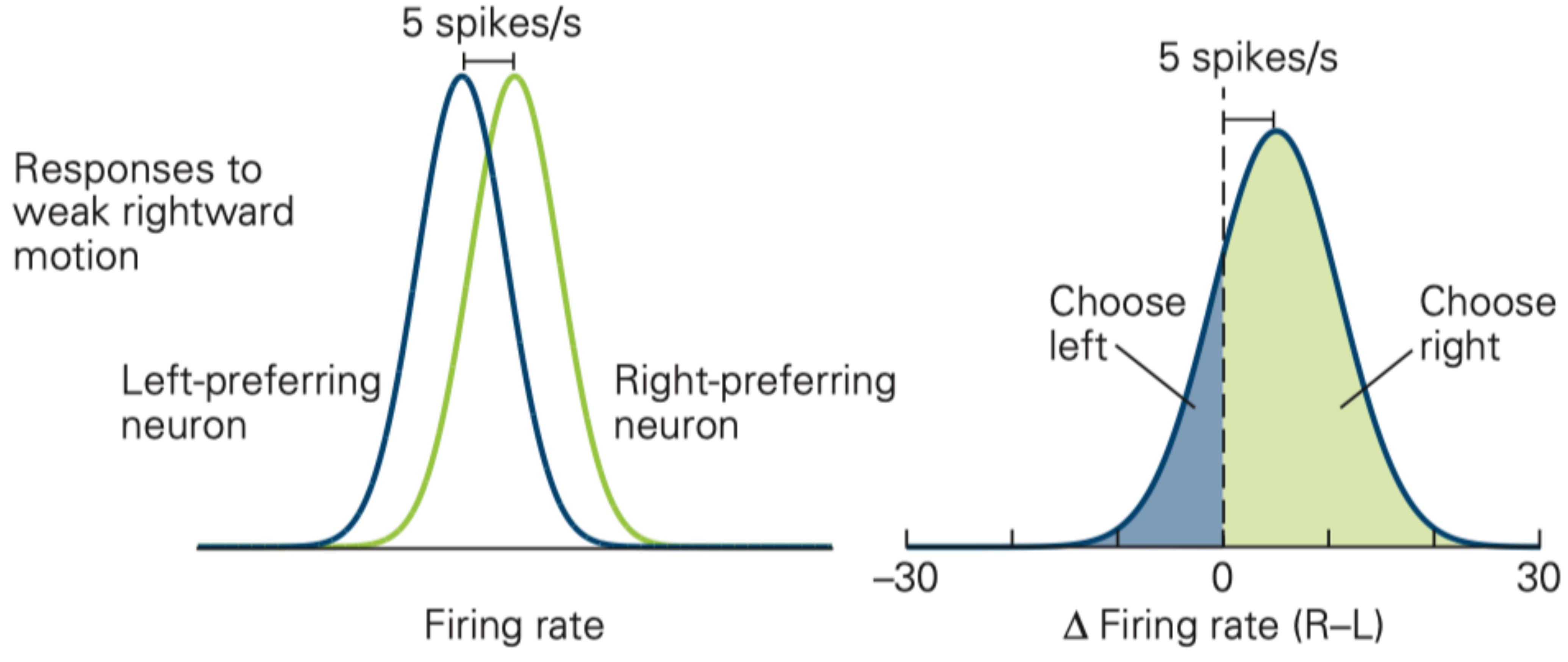




Neurons in Sensory Areas of the Cortex Supply the Noisy Samples of Evidence to Decision-Making

- Neurons that preferred rightward motion respond above baseline to the 0% coherence stimulus because the random noise contains all motion directions.
- Noisy neural evidence for left and right are conceptualized as random samples from probability distributions.
- We can characterize the evidence as the difference between the firing rates of the left- and right-preferring neurons, calling it the *decision variable*.



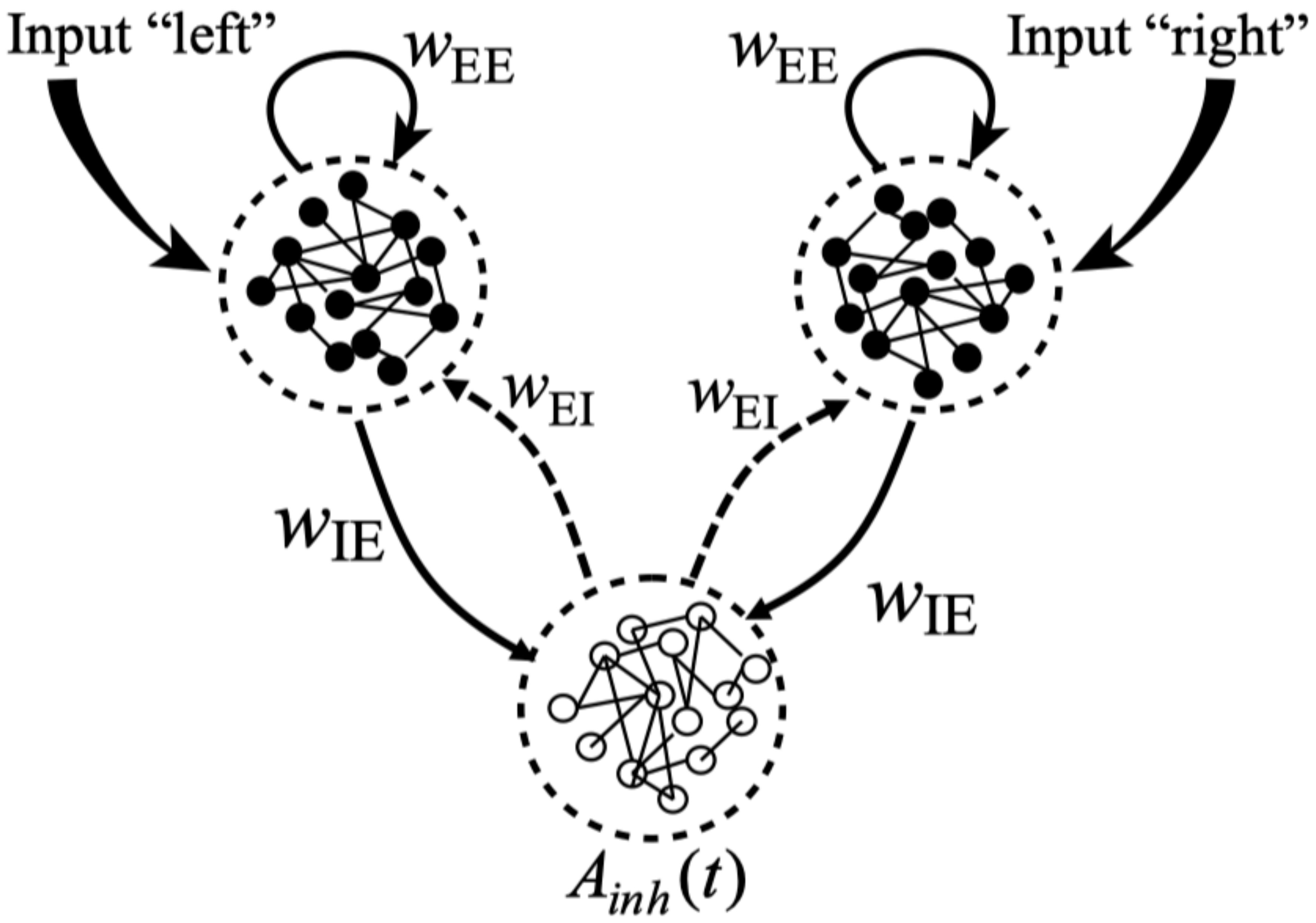


Theoretical Excursion #2

Competing Populations of Neurons

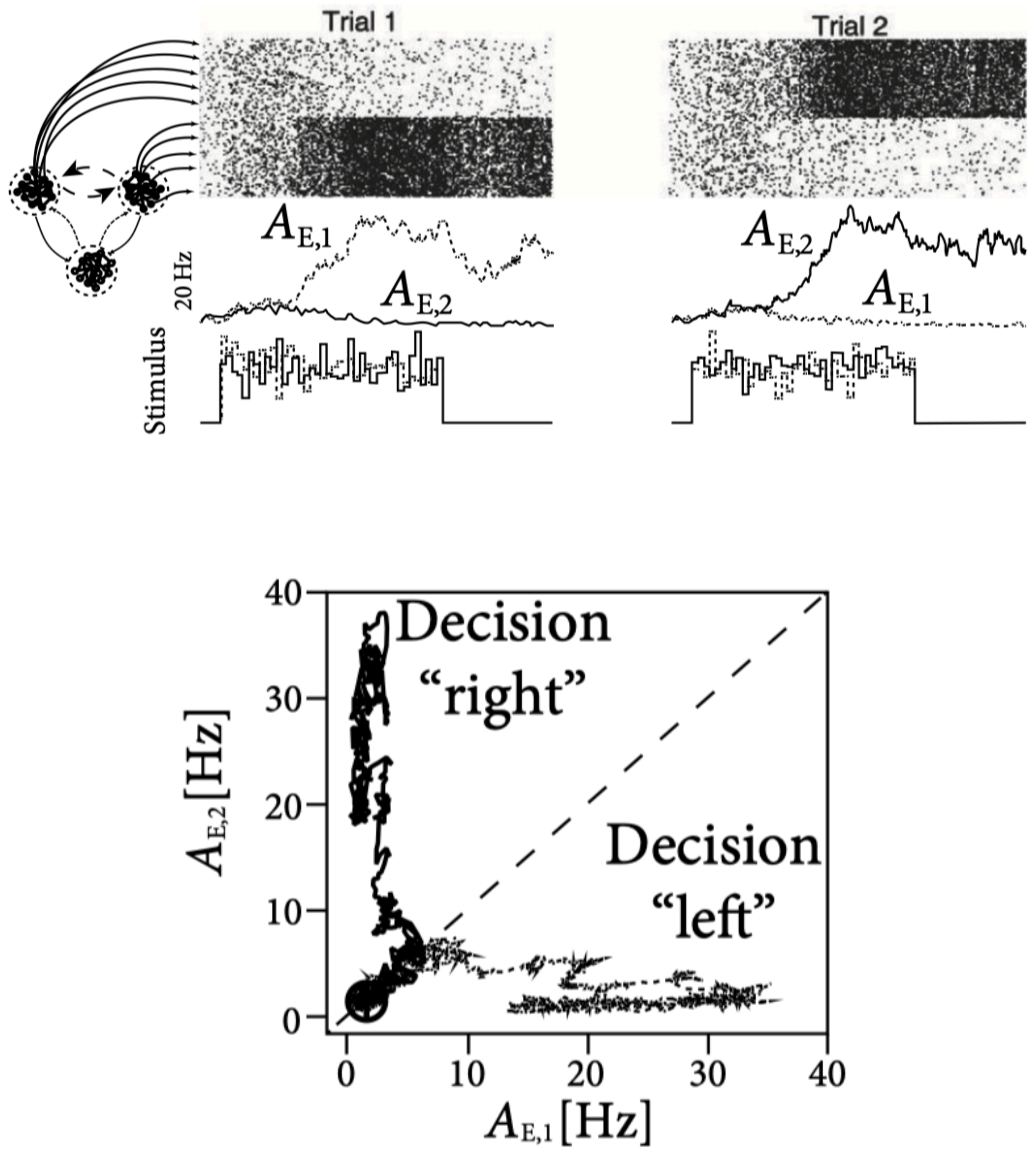
Competition through Common Inhibition

- The essential features described previously can be explained by a simple model where neuronal populations compete with each other through shared inhibition.
- Neuronal parameters and connection weights are adjusted such that, in the absence of external input, all neurons exhibit spontaneous activity at low firing rates.
- Competition means that at most one of the two populations can be active at the same time.



Competition through Common Inhibition

- If the external stimulus favors one of the two populations, the population receiving the stronger stimulus "wins" the competition.
- If both populations receive strong unbiased stimulation, they both increase their firing rates.
- Soon after, one of the activities grows further (the winner) at the expense of the other one, which is suppressed (the loser).



Dynamics of Decision Making

Model with Three Populations

- The population activity A in a stationary state of asynchronous firing can be predicted by the neuronal gain function $g_\sigma(I)$ of isolated neurons.

$$A(t) = F(h) \text{ where } F(h) = g_\sigma(h/R)$$

- The input potential h is the contribution to the membrane potential that is caused by the input.

$$h(t) = \frac{R}{\tau_m} \int_0^\infty e^{-\frac{s}{\tau_m}} I(t-s)\mathrm{d}$$

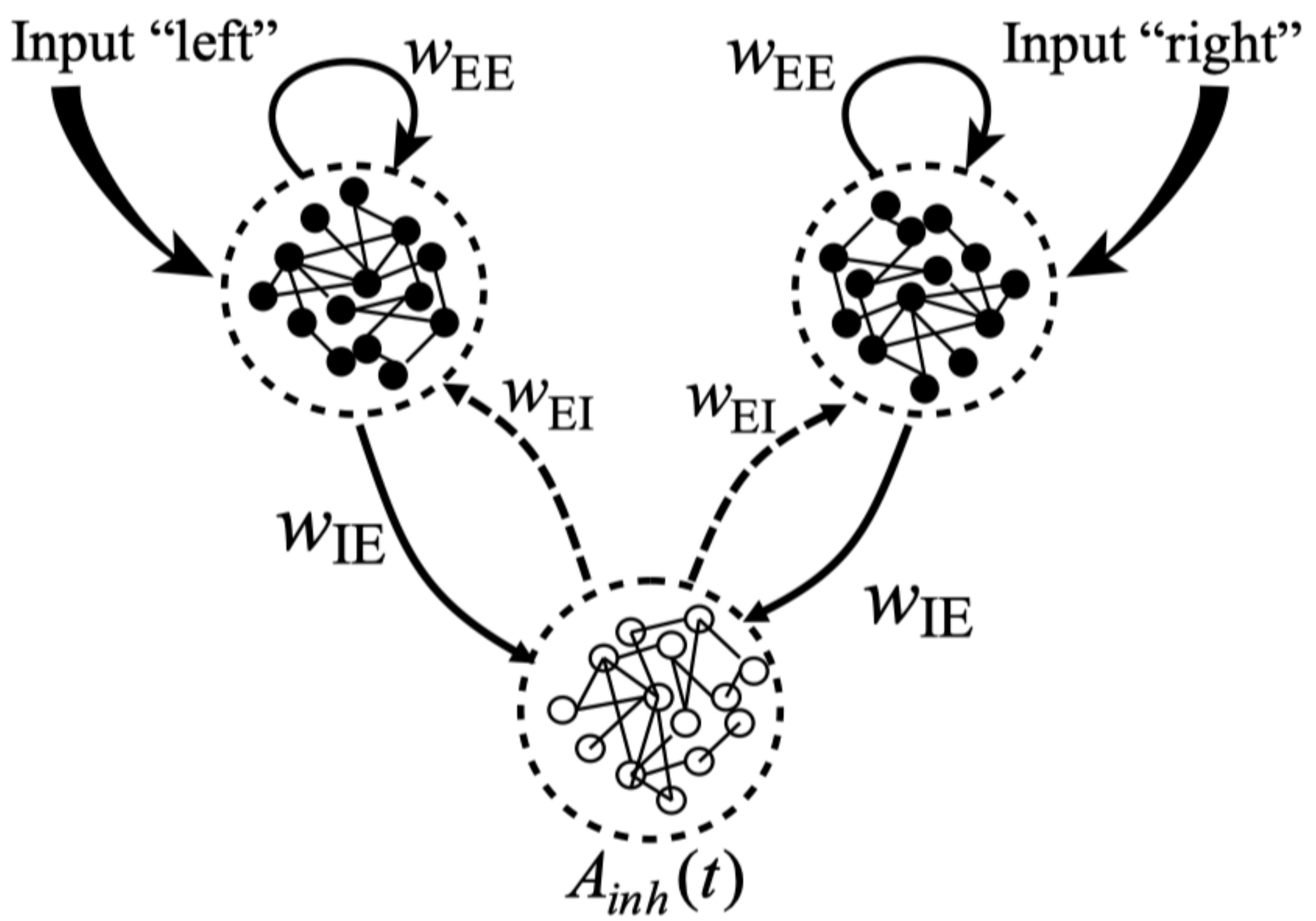
$$\tau_m \frac{\mathrm{d}h(t)}{\mathrm{d}t} = -h + RI(t)$$

Dynamics of Decision Making

Model with Three Populations

- The input potentials of the previously described model are expressed by three differential equations.

$$\tau_m \frac{\mathrm{d}h(t)}{\mathrm{d}t} = -h + RI(t)$$



$$\tau_E \frac{\mathrm{d}h_{E,1}}{\mathrm{d}t} = -h_{E,1} + w_{EE}g_E(h_{E,1}) + w_{EI}g_{inh}(h_{inh}) + RI_1$$
$$\tau_E \frac{\mathrm{d}h_{E,2}}{\mathrm{d}t} = -h_{E,2} + w_{EE}g_E(h_{E,2}) + w_{EI}g_{inh}(h_{inh}) + RI_2$$
$$\tau_E \frac{\mathrm{d}h_{inh}}{\mathrm{d}t} = -h_{inh} + w_{IE}g_E(h_{E,1}) + w_{IE}g_E(h_{E,2})$$

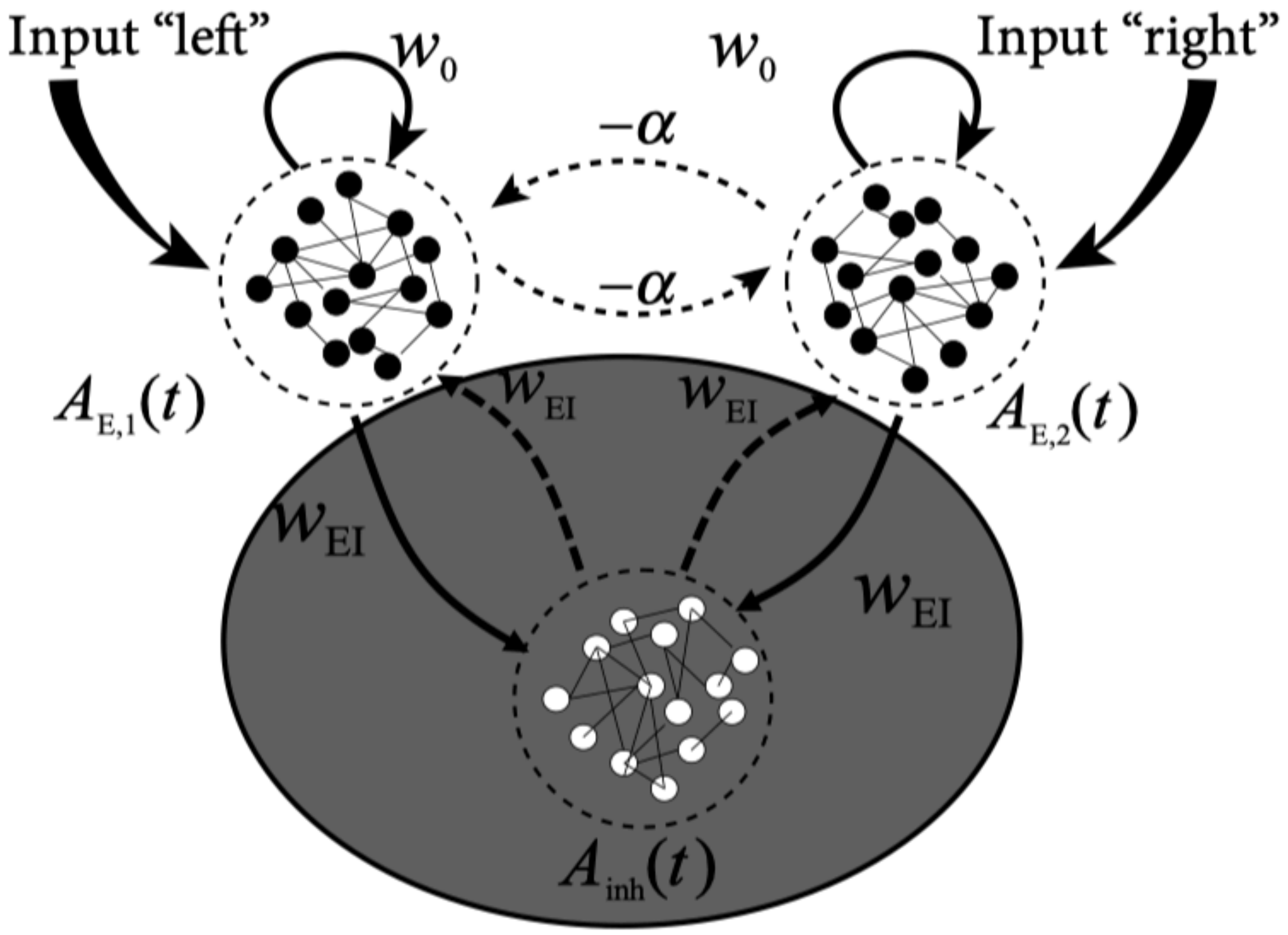
Dynamics of Decision Making

Effective Inhibition

- Two assumptions:

  1. Separation of time scales: $\tau_{\text{inh}} \ll \tau_E$ or $\dfrac{\tau_{\text{inh}}}{\tau_E} \to 0$
  2. Inhibitory gain function is linear: $g_{\text{inh}}(h_{\text{inh}}) = \gamma h_{\text{inh}}$

- In this way we reduce our description from three to two differential equations.



$$\tau_{\mathrm{E}} \frac{\mathrm{d}h_{\mathrm{E},1}}{\mathrm{d}t} = -h_{\mathrm{E},1} + (w_{\mathrm{EE}} - \alpha) g_{\mathrm{E}}(h_{\mathrm{E},1}) - \alpha g_{\mathrm{E}}(h_{\mathrm{E},2}) + RI_1$$

$$\tau_{\mathrm{E}} \frac{\mathrm{d}h_{\mathrm{E},2}}{\mathrm{d}t} = -h_{\mathrm{E},2} + (w_{\mathrm{EE}} - \alpha) g_{\mathrm{E}}(h_{\mathrm{E},2}) - \alpha g_{\mathrm{E}}(h_{\mathrm{E},1}) + RI_2$$

Exercise 4

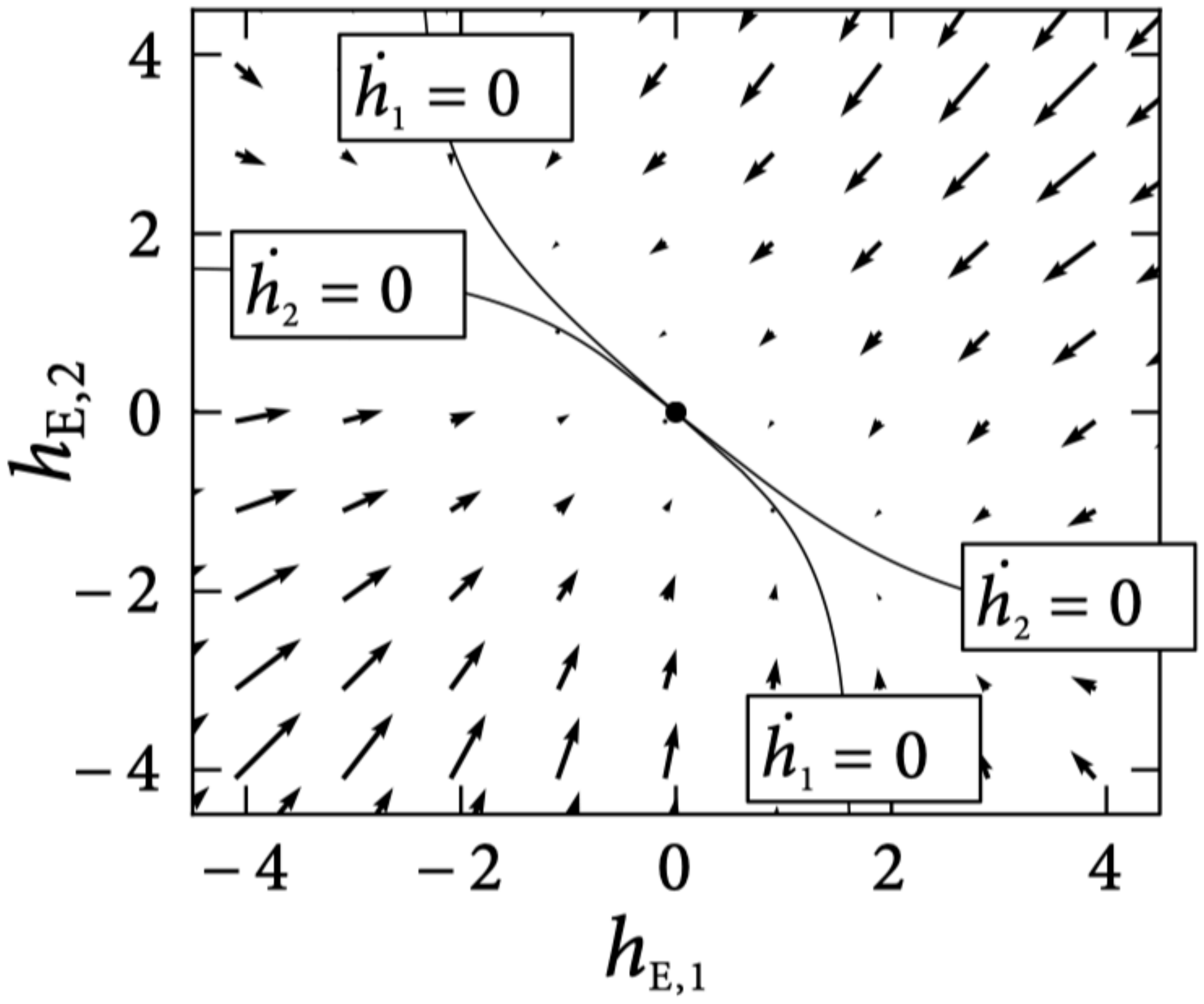
What is α's sign?

Dynamics of Decision Making

Phase Plane Analysis

- In the absence of stimulation, there exists only a single fixed point $h_{\mathrm{E},1} = h_{\mathrm{E},2} \approx 0$, corresponding to a small level of spontaneous activity

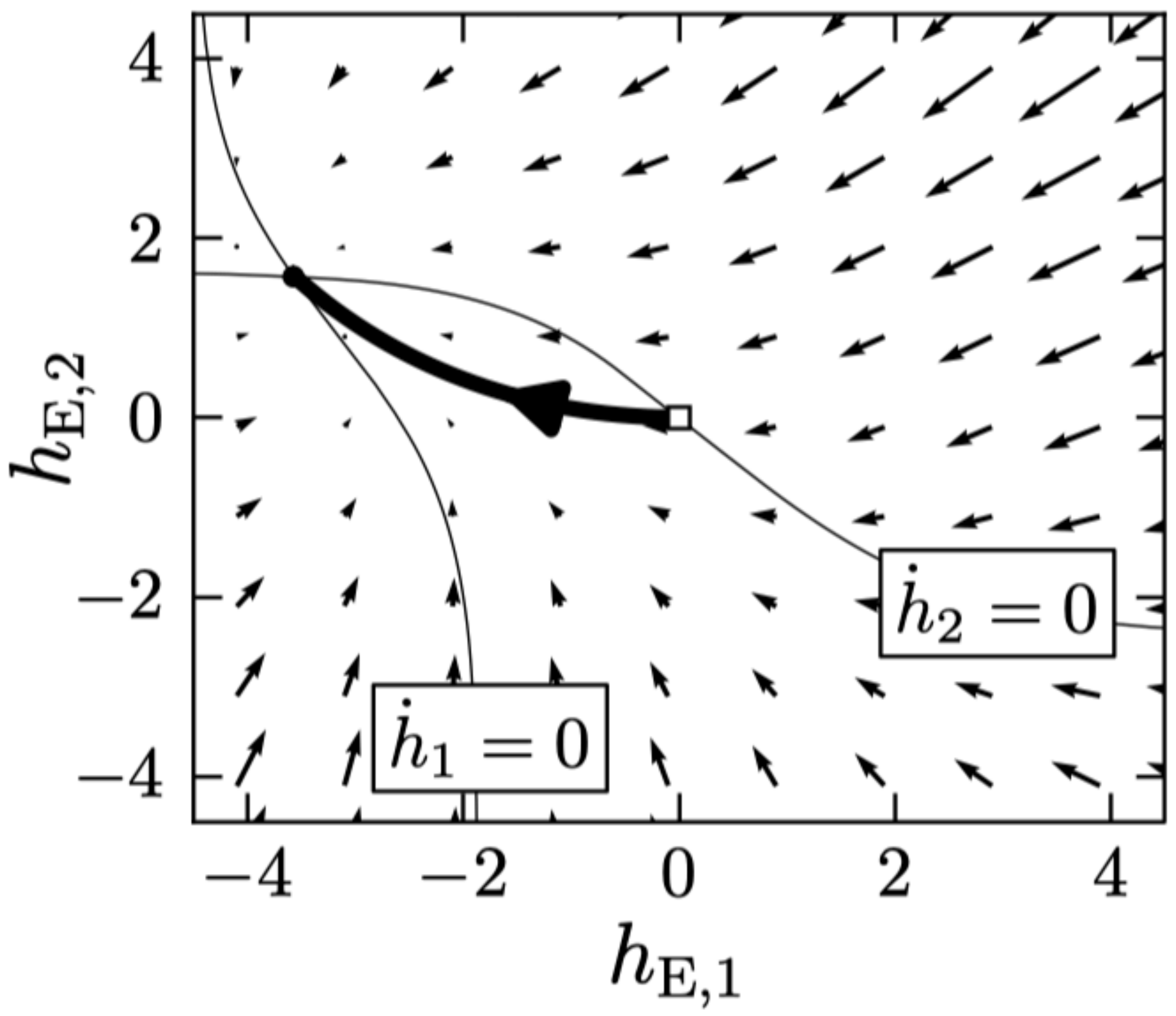
$$\tau_{\mathrm{E}} \frac{\mathrm{d}h_{\mathrm{E},1}}{\mathrm{d}t} = -h_{\mathrm{E},1} + (w_{\mathrm{EE}} - \alpha) g_{\mathrm{E}}(h_{\mathrm{E},1}) - \alpha g_{\mathrm{E}}(h_{\mathrm{E},2}) + RI_1$$
$$\tau_{\mathrm{E}} \frac{\mathrm{d}h_{\mathrm{E},2}}{\mathrm{d}t} = -h_{\mathrm{E},2} + (w_{\mathrm{EE}} - \alpha) g_{\mathrm{E}}(h_{\mathrm{E},2}) - \alpha g_{\mathrm{E}}(h_{\mathrm{E},1}) + RI_2$$

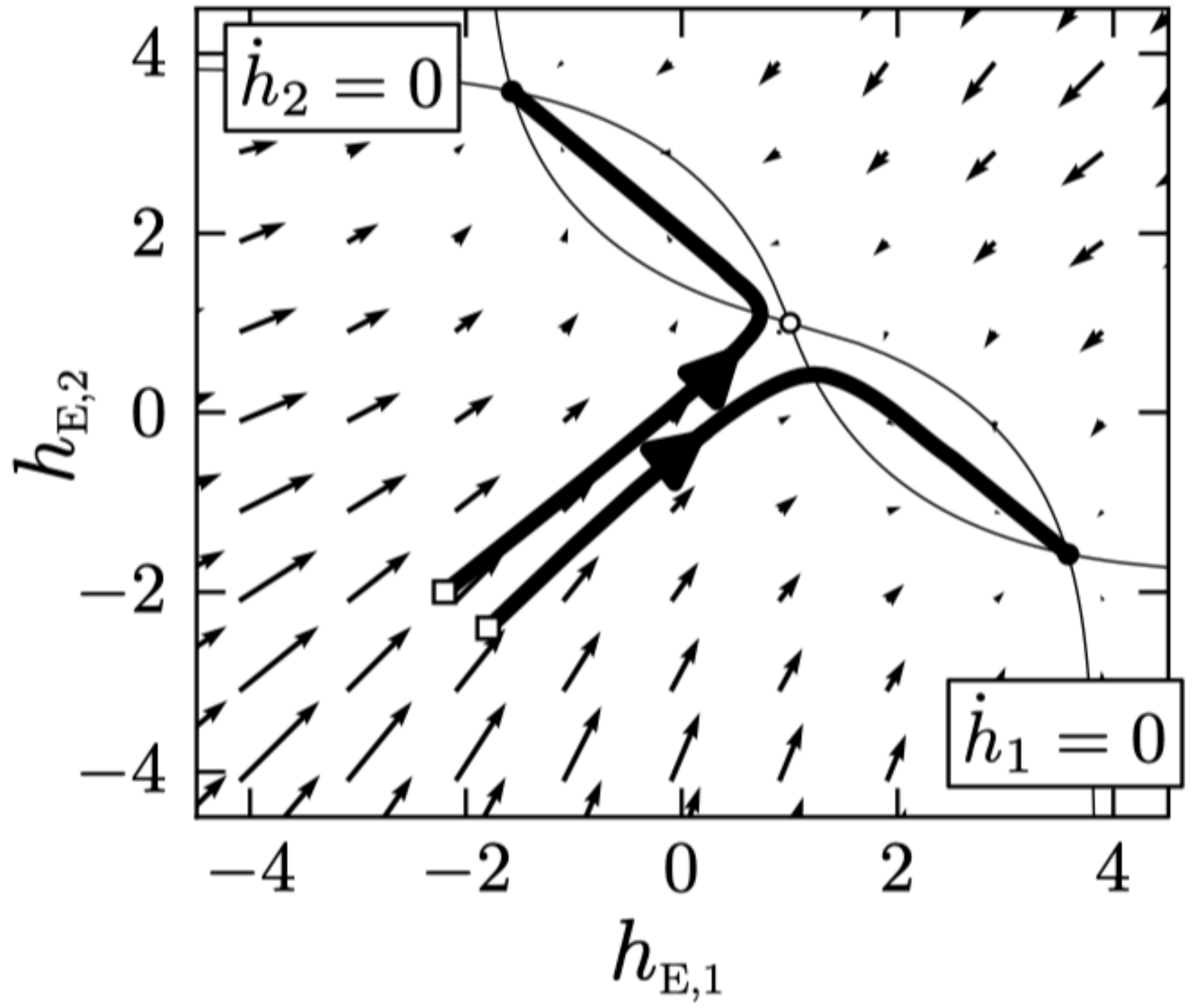


Dynamics of Decision Making

Phase Plane Analysis

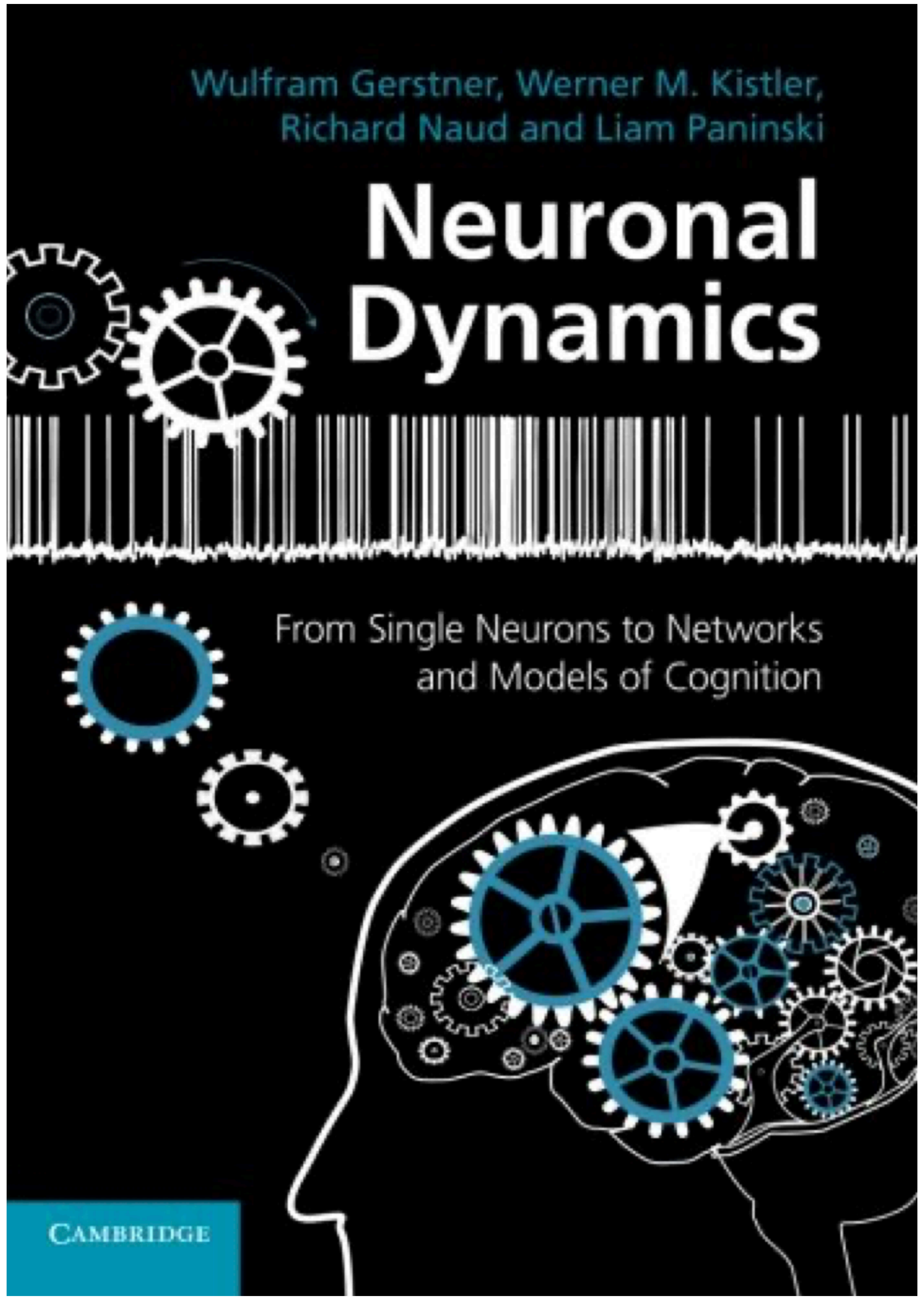
- If a stimulus $I_2 > 0$ favors the first population, the fixed point moves to an asymmetric position where population 2 exhibits much stronger activity than population 1.
- With a strong unbiased stimulus $I_1 = I_2 \gg 0$ three fixed points exist:
  - Saddle point: $h_{E,1} = h_{E,2}$
  - Two other fixed points occur at equivalent positions symmetrically to the left and right of the diagonal





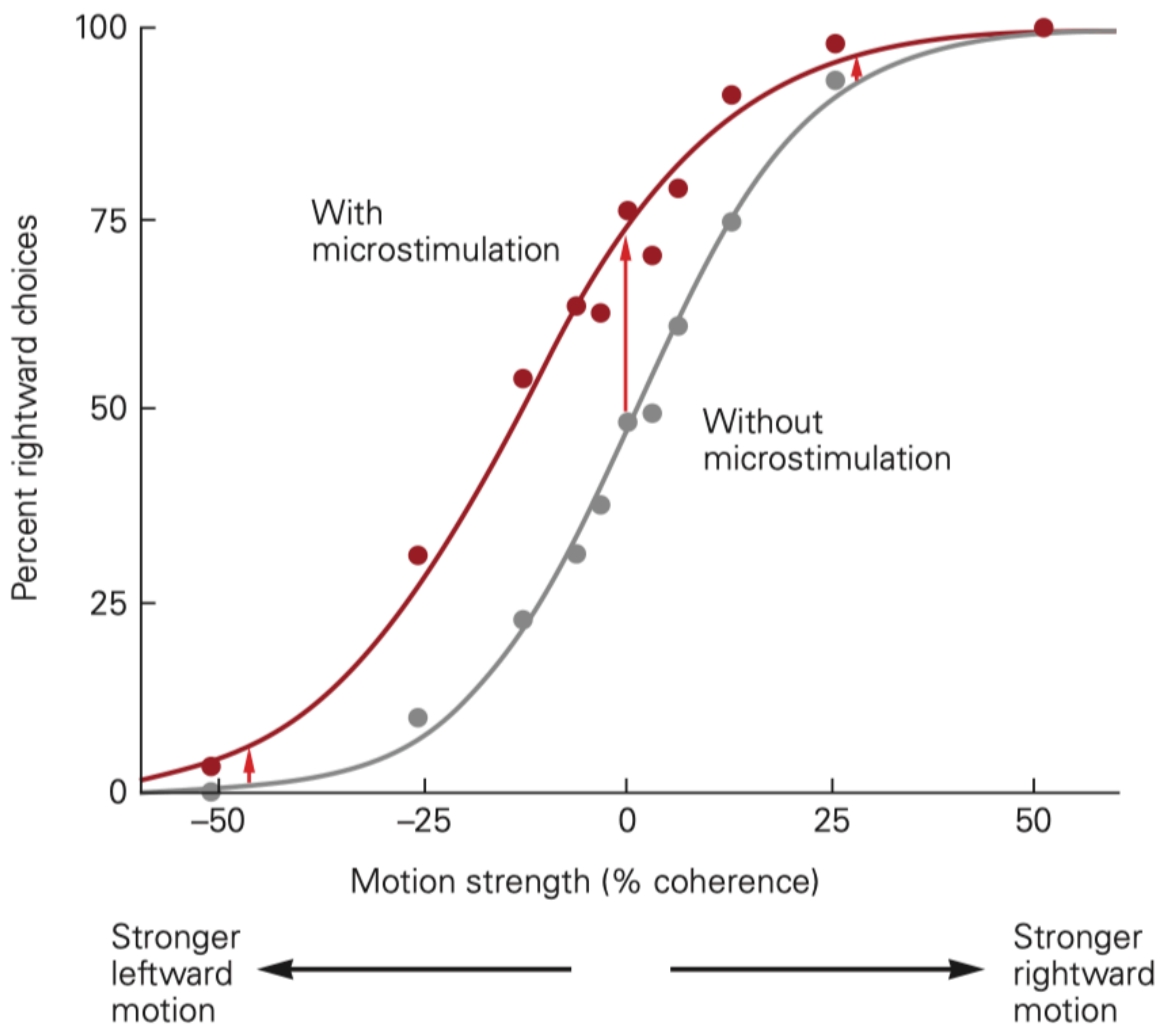
Reference

Gerstner et al. 2014. Neuronal Dynamics, Chapter 16, "Competing populations and decision making."



Neurons in Sensory Areas of the Cortex Supply the Noisy Samples of Evidence to Decision-Making

- We can investigate the causal contribution of MT activity to decision-making using *microstimulation*.
- Stimulating neurons that preferred rightward motion caused the monkey to decide more often in favor of right.
- The microstimulation exerted its largest effect on choices when the motion strength was weakest.
- The stimulated neurons do not necessarily need to affect the decision directly; they only have to participate in a neural circuit that lies in a causal chain.

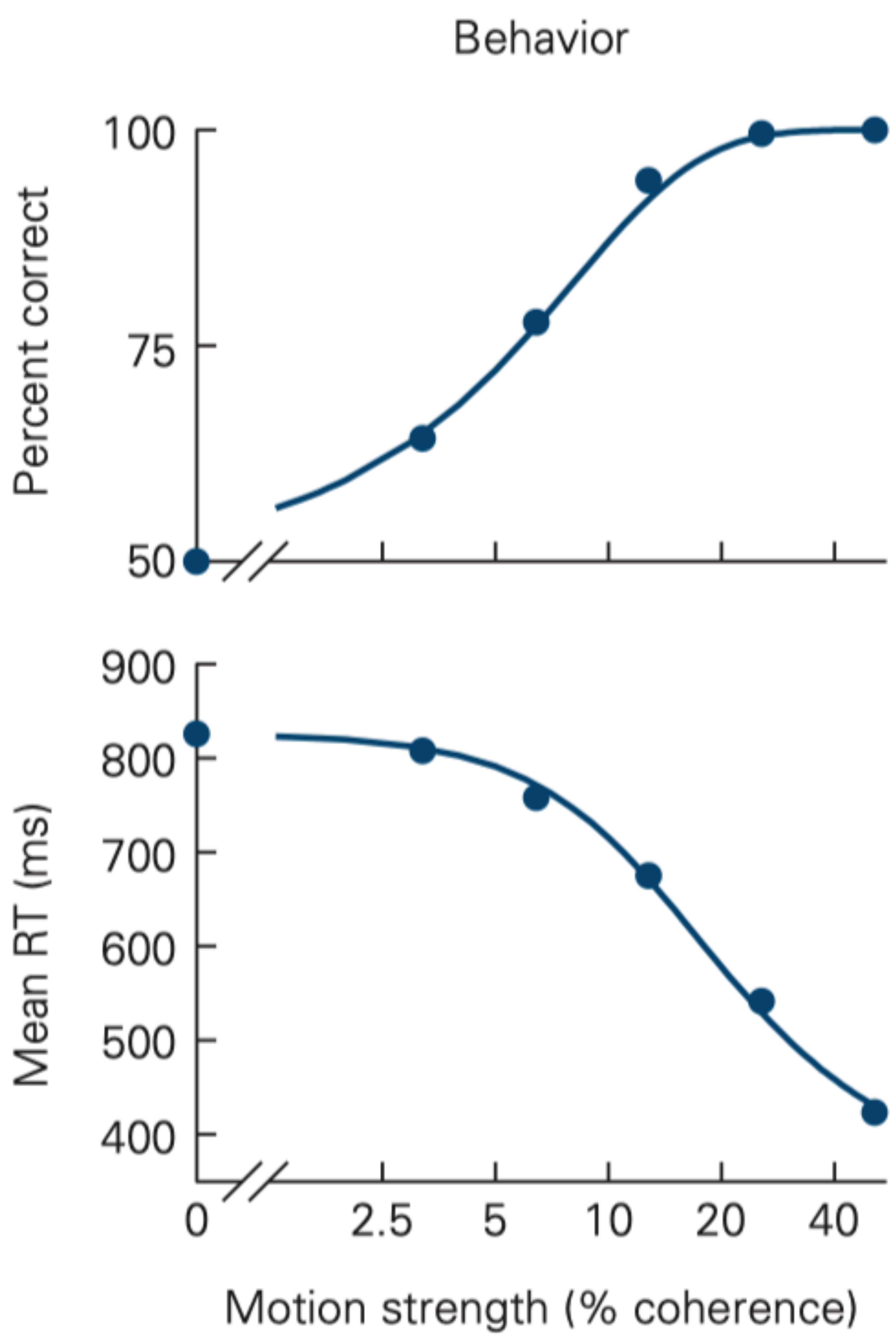


Accumulation of Evidence to a Threshold Explains the Speed Versus Accuracy Trade-Off

- The difference in firing rates of left- and right-preferring direction-selective neurons supplies the momentary evidence to another process that accumulates this noisy evidence as a function of time.
- The accumulation of noisy evidence follows a path comprising random steps on top of a constant bias determined by the coherence and direction of the moving dots: This is a biased random walk or a drift-diffusion process.
- When one of the accumulations reaches an upper stopping bound, a choice is made.

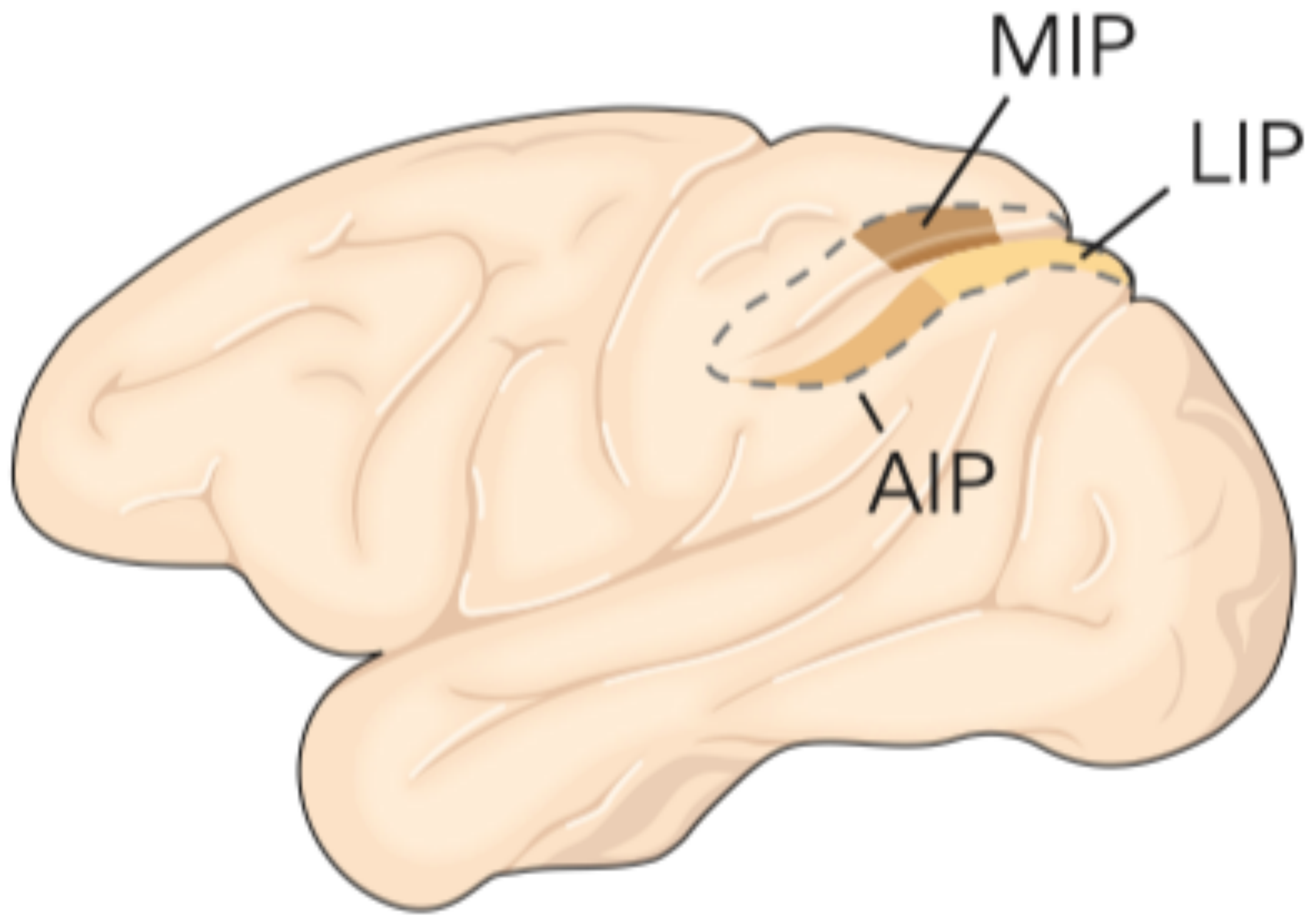
Accumulation of Evidence to a Threshold Explains the Speed Versus Accuracy Trade-Off

- The stopping bounds explain an important feature of the decision—the time it takes to make it.
- If the stopping bounds are close to the starting point of the accumulation, the decision will be based on very little evidence—fast but error prone.
- If the stopping bounds are further from the starting point, more accumulated evidence is needed to stop—slower but more likely to be correct.



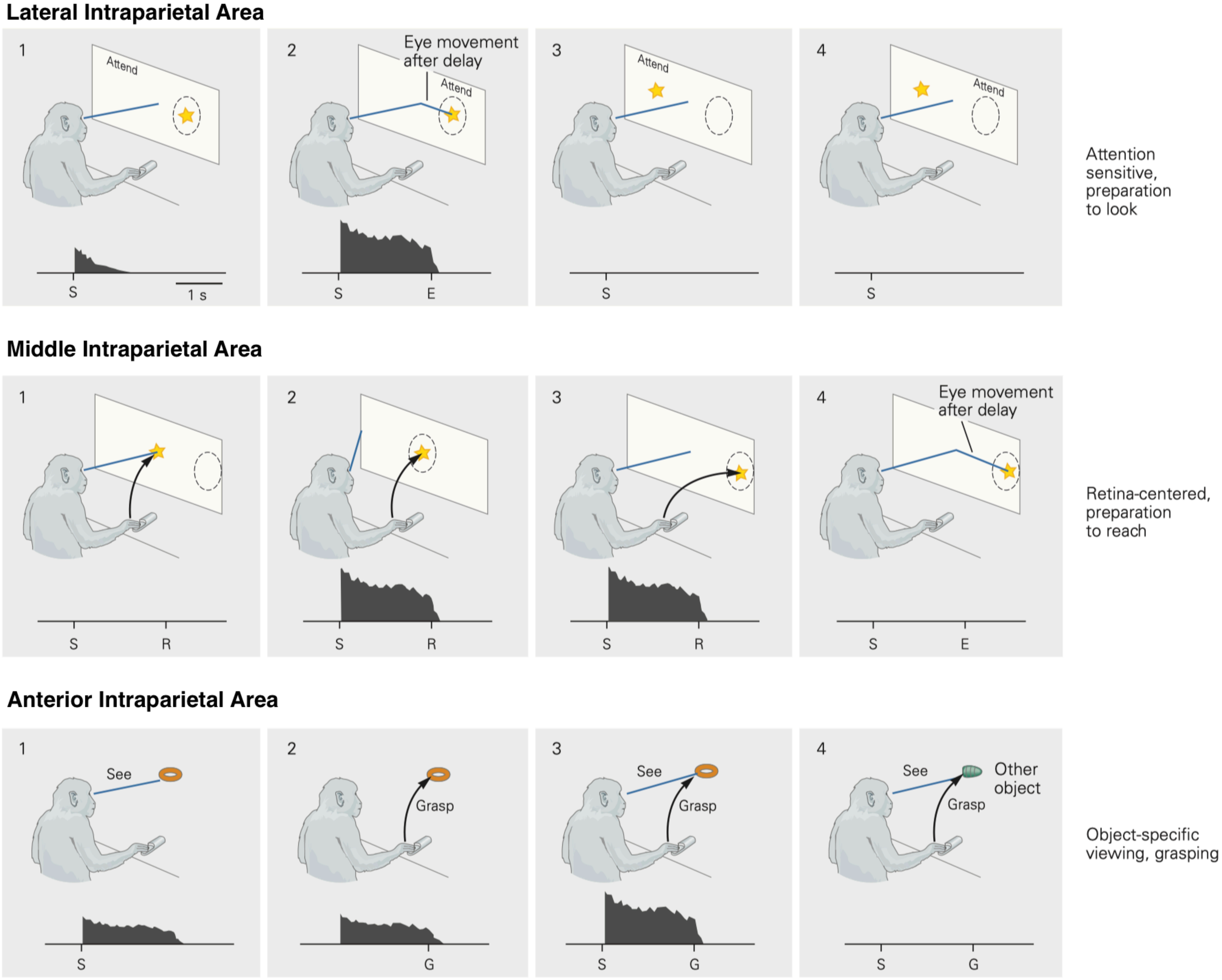
Neurons in the Parietal and Prefrontal Association Cortex Represent a Decision Variable

- The neurons that represent the accumulation differ from sensory neurons in two important ways.
  1. Persistent activity: they can continue to respond for several seconds after a sensory stimulus has come and gone.
  2. Motor connections: they tend to be associated with circuits that control the learned behavioral response (e.g. eye movement, reaching, etc.)



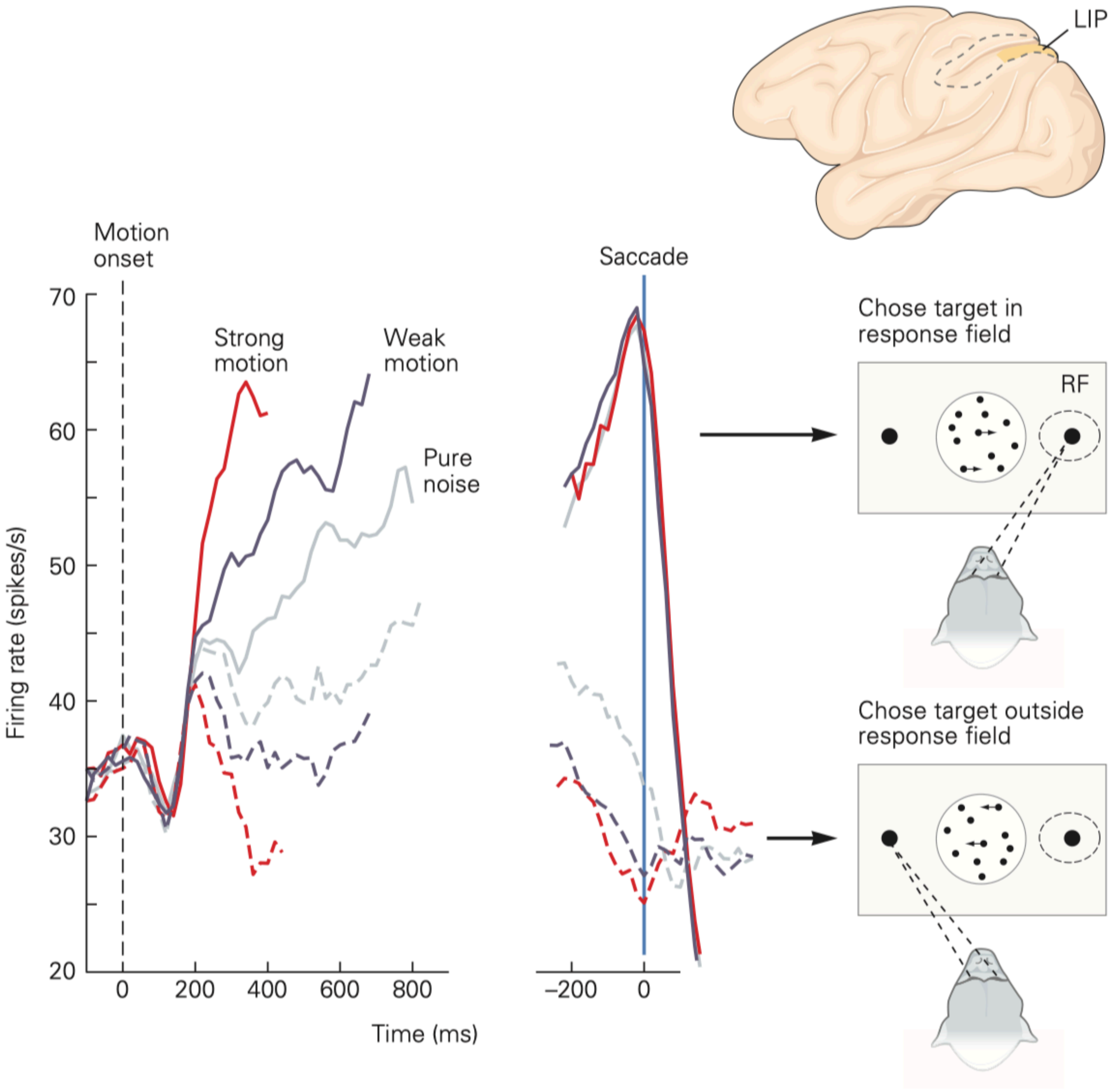
Neurons in the Parietal and Prefrontal Association Cortex Represent a Decision Variable

- Neurons in the LIP fire when a monkey is preparing to make an eye movement to an object or when the monkey directs attention to the object's location.
- Neurons in the MIP fire when the monkey is preparing to reach for a visual target.
- Neuron in the AIP fire when the monkey is looking at or preparing to grasp an object and are selective for objects of particular shapes



Neurons in the Parietal and Prefrontal Association Cortex Represent a Decision Variable

- It seemed possible that neurons whose activity represents a plan to act might also represent the formation of that plan during decision making.
- Evidence accumulation: Neurons that represent the evolving decision increase their firing rates gradually as the evidence mounts for one of the choices.
- Threshold: The firing rate appears to reach the same level on trials regardless of stimulus strength.



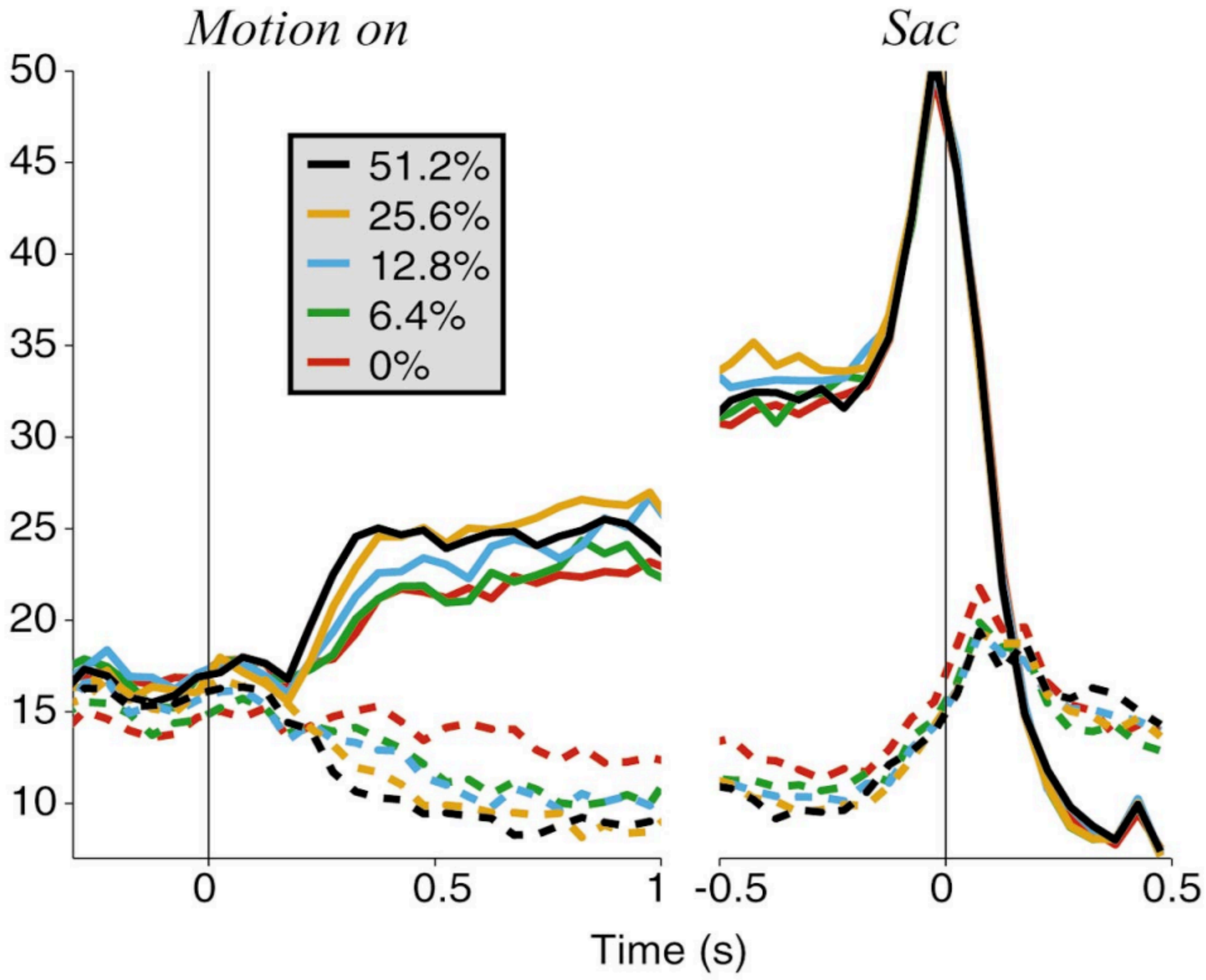


FIG. 8. Population response from 104 LIP neurons the direction discrimination task. The average firing plotted as a function of time during the motion-viewi delay periods. Solid and dashed curves are from t which the monkey judged direction toward and away fi RF, respectively. Error trials are not shown. Both tl course and magnitude of the response are affected strength of random-dot motion, particularly during tl tion-viewing period.

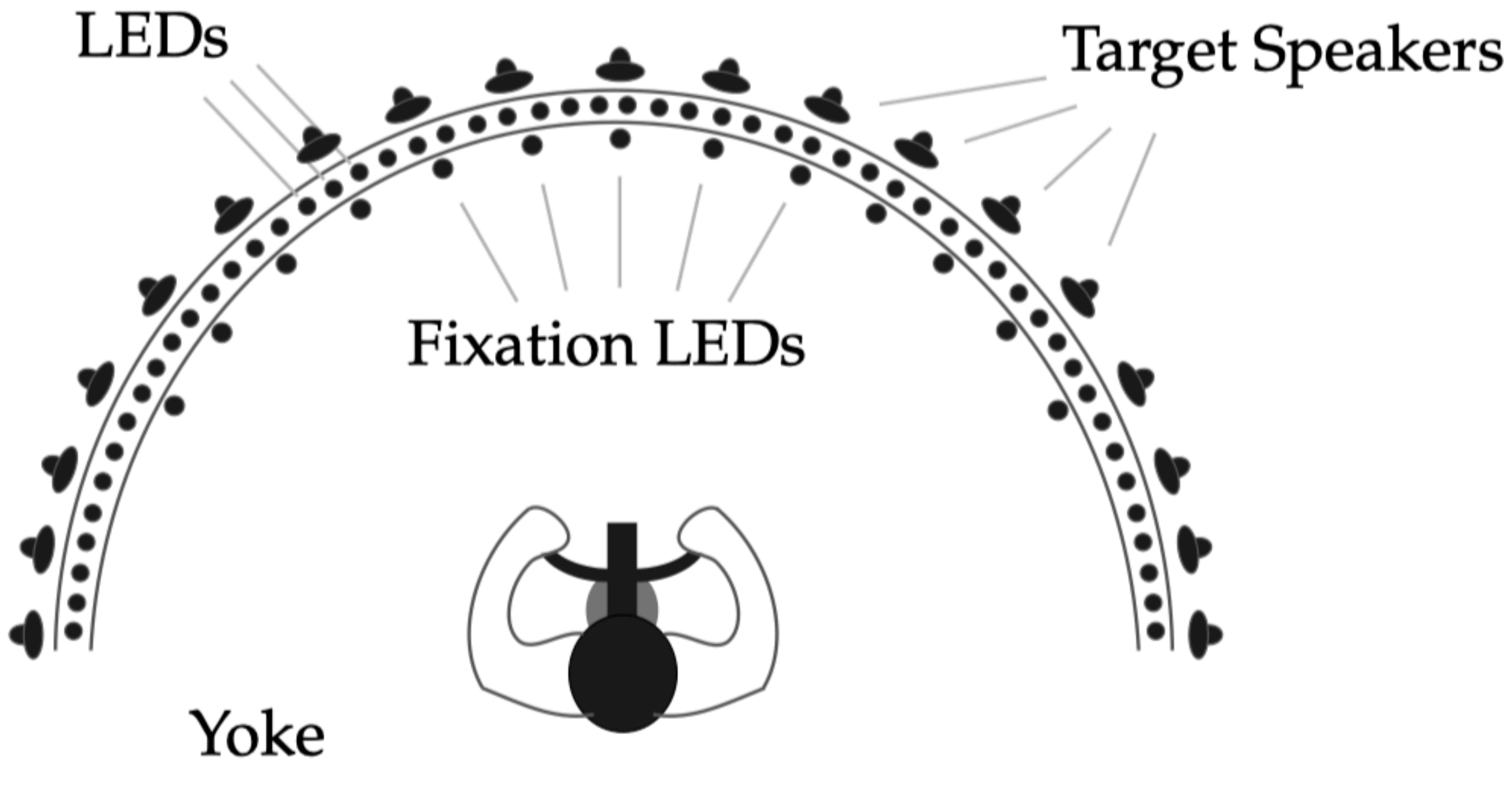
Shadlen 2001. Neural Basis of a Perceptual Decision in the Parietal Cortex (Area LIP) of the Rhesus Monkey

Theoretical Excursion #3

Cue Combination in Bayesian Decisions

What is Cue Combination?

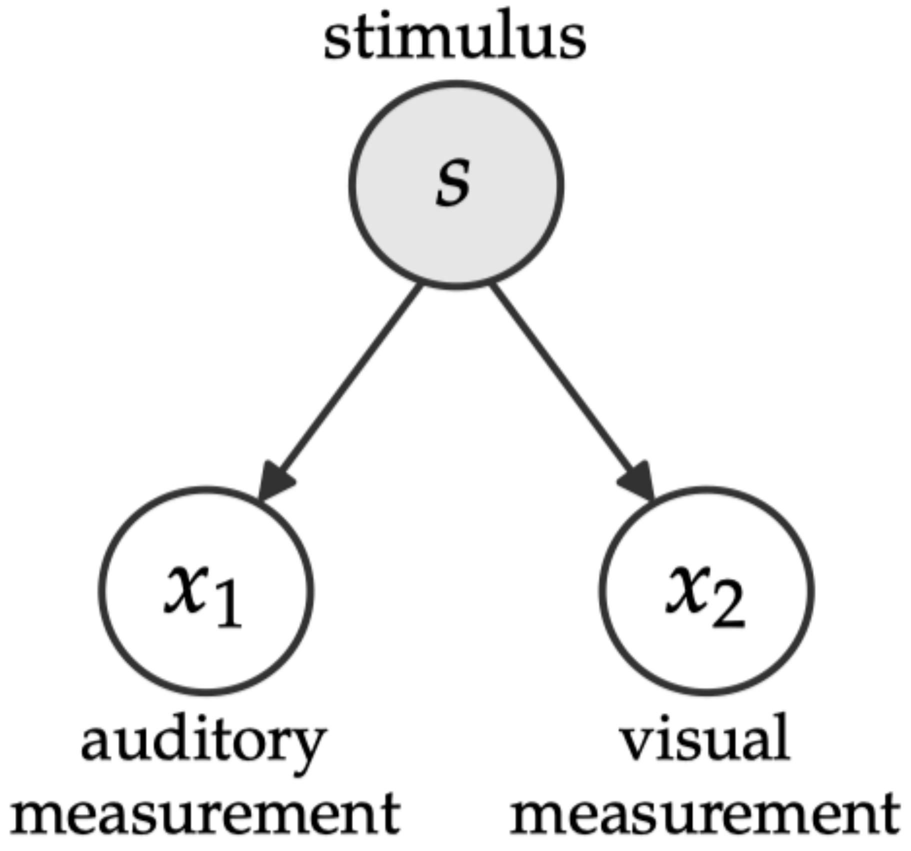
- Why should we combine cues?
  - Our sensorineural responses are noisy.
  - Even when sensorineural noise does not impose serious limitations, an individual cue is often ambiguous.
- We can study cue combination in the lab using the auditory-visual location estimation task.
- When the beep and flash occur at the same location, subjects use the visual stimulus to help estimate the location of the auditory stimulus, even when they are instructed to ignore it.



Formulation of the Bayesian Model

Step 1: Generative Model

- 3 nodes: stimulus s and 2 measurements x_1 and x_2
- Flat prior distribution $\mathbb{P}(s)$
- Measurements are conditionally independent: $\mathbb{P}(x_1, x_2 \,|\, s) = \mathbb{P}(x_1 \,|\, s)\, \mathbb{P}(x_2 \,|\, s)$
- Each individual measurement is a Gaussian



$$\mathbb{P}(x_1|s) = \frac{1}{\sqrt{2\pi\sigma_1^2}} e^{\frac{-(x_1-s)^2}{2\sigma_1^2}}$$

$$\mathbb{P}(x_2|s) = \frac{1}{\sqrt{2\pi\sigma_2^2}} e^{\frac{-(x_2-s)^2}{2\sigma_2^2}}$$

Exercise 5

Assuming only the product rule for probabilities, show that when random variables X and Y are independent given Z, then

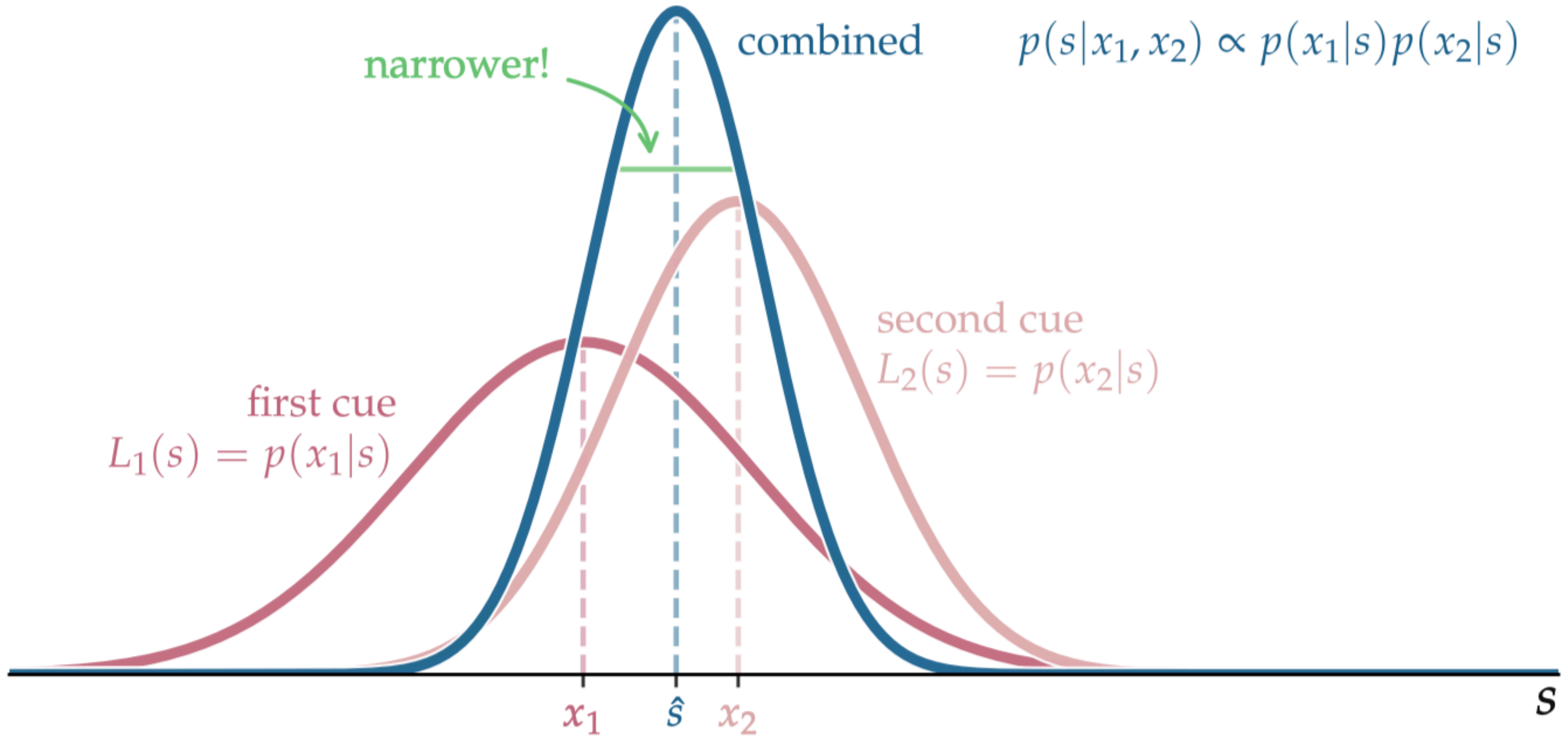
$$\mathbb{P}(x, y \mid z) = \mathbb{P}(x \mid z)\, \mathbb{P}(y \mid z).$$

Formulation of the Bayesian Model

Step 2: Inference

- The posterior distribution over the stimulus is computed from Bayes' rule and considers the conditional independence of the measurements:

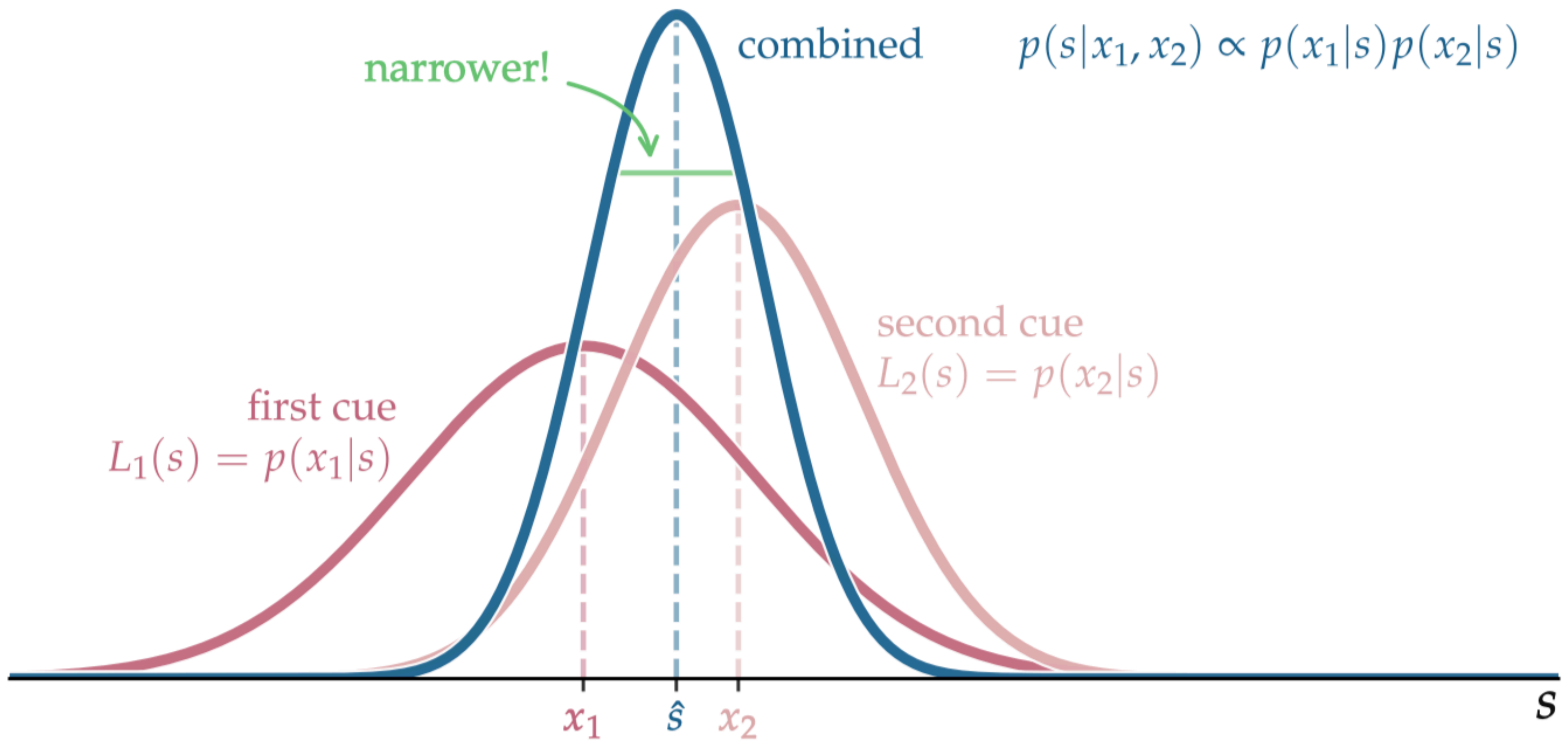
$$\mathbb{P}(s|x_1, x_2) \propto \mathbb{P}(s)\mathbb{P}(x_1, x_2|s)$$
$$\mathbb{P}(s|x_1, x_2) \propto \mathbb{P}(s)\mathbb{P}(x_1|s)\,\mathbb{P}(x_2|s)$$
$$\mathbb{P}(s|x_1, x_2) \propto \mathbb{P}(x_1|s)\,\mathbb{P}(x_2|s)$$



Formulation of the Bayesian Model

Step 2: Inference

- By substituting the two Gaussian distributions into these equations we can see that the variance of the posterior is never larger than either of the components.



$$\mathbb{P}(s|x_1, x_2) = \frac{1}{\sqrt{2\pi\sigma_{\text{post}^2}}} e^{\frac{-(s-\mu_{\text{post}})^2}{2\sigma_{\text{post}^2}}}$$

where

$$\mu_{\text{post}} = \frac{J_1 x_1 + J_2 x_2}{J_1 + J_2}$$

$$\sigma^2_{\text{post}} = \frac{1}{J_1 + J_2}$$

Exercise 6

Why is the variance of the posterior never larger than that of either component?

Generalization to Multiple Cues

- When combining N conditionally independent cues with the same underlying stimulus, the posterior is

$$\begin{aligned}\mathbb{P}(s|x_1 \dots x_N) &\propto \mathbb{P}(s)\mathbb{P}(x_1|s)\dots\mathbb{P}(x_N|s) \\ &= \mathbb{P}(s)\prod_{i=0}^{N} \propto \mathbb{P}(x_i|s)\end{aligned}$$

with mean $\dfrac{J_s\mu + \sum_{i=1}^{N} J_i s_i}{J_s + \sum_{i=1}^{N} J_i}$ and variance $\dfrac{1}{J_s + \sum_{i=1}^{N} J_i}$.

Evidence Accumulation

- Mathematically, evidence accumulation is cue combination over time and can be described using the same formalism → the variance of the posterior will shrink continuously to 0 as more evidence is accumulated:

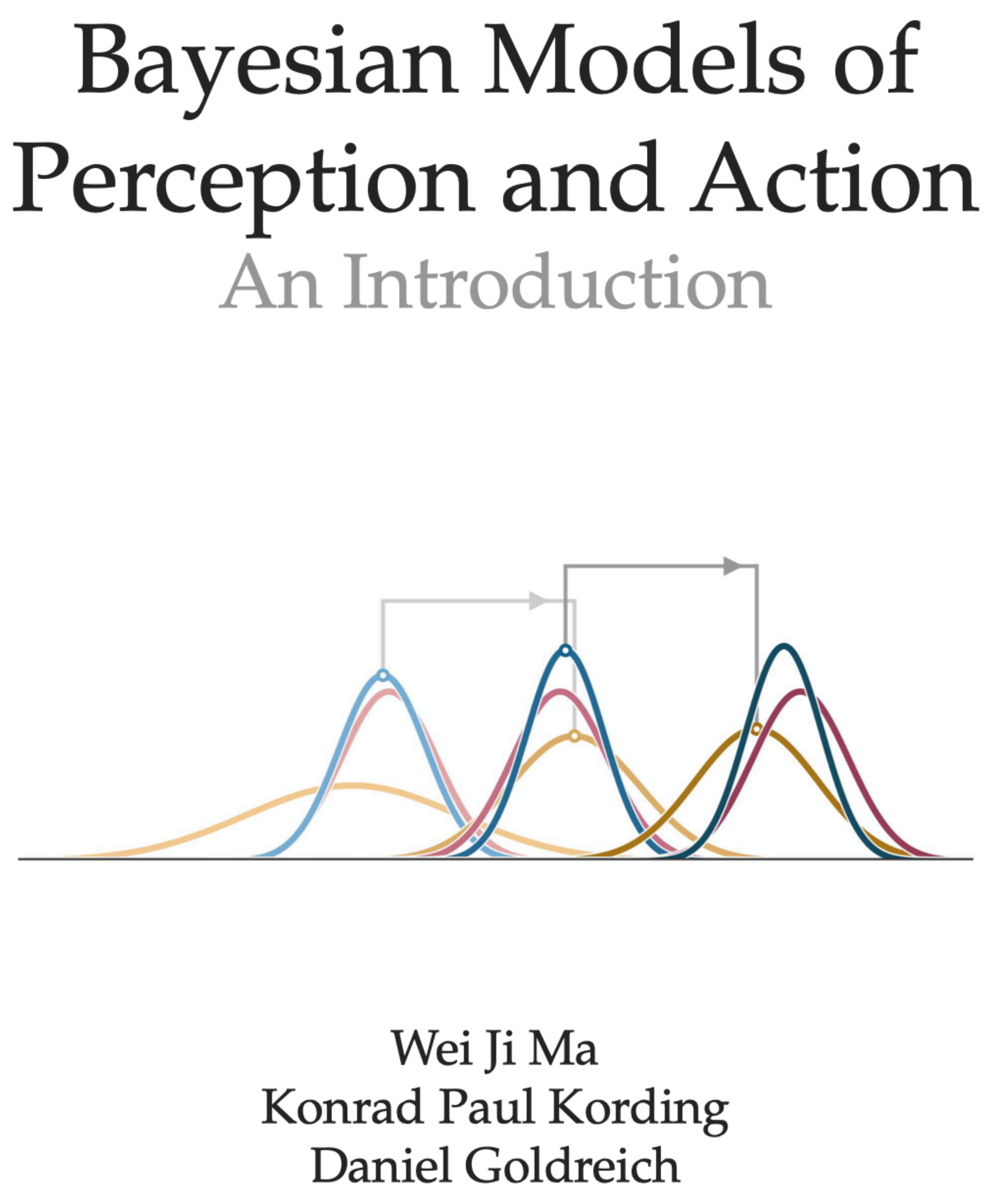
$$\begin{aligned}\mathbb{P}(s|x_1 \dots x_T) &\propto \mathbb{P}(s)\mathbb{P}(x_1|s)\dots\mathbb{P}(x_T|s) \\ &= \mathbb{P}(s)\prod_{i=0}^{T} \propto \mathbb{P}(x_i|s)\end{aligned}$$

- It makes sense to think of the computation of the posterior as a recursive process, as expressed in the *bayesian update equations*

$$\mathbb{P}(s|x_1 \dots x_{t+1}) \propto \mathbb{P}(s|x_1 \dots x_t)\mathbb{P}(x_{t+1}|s)$$

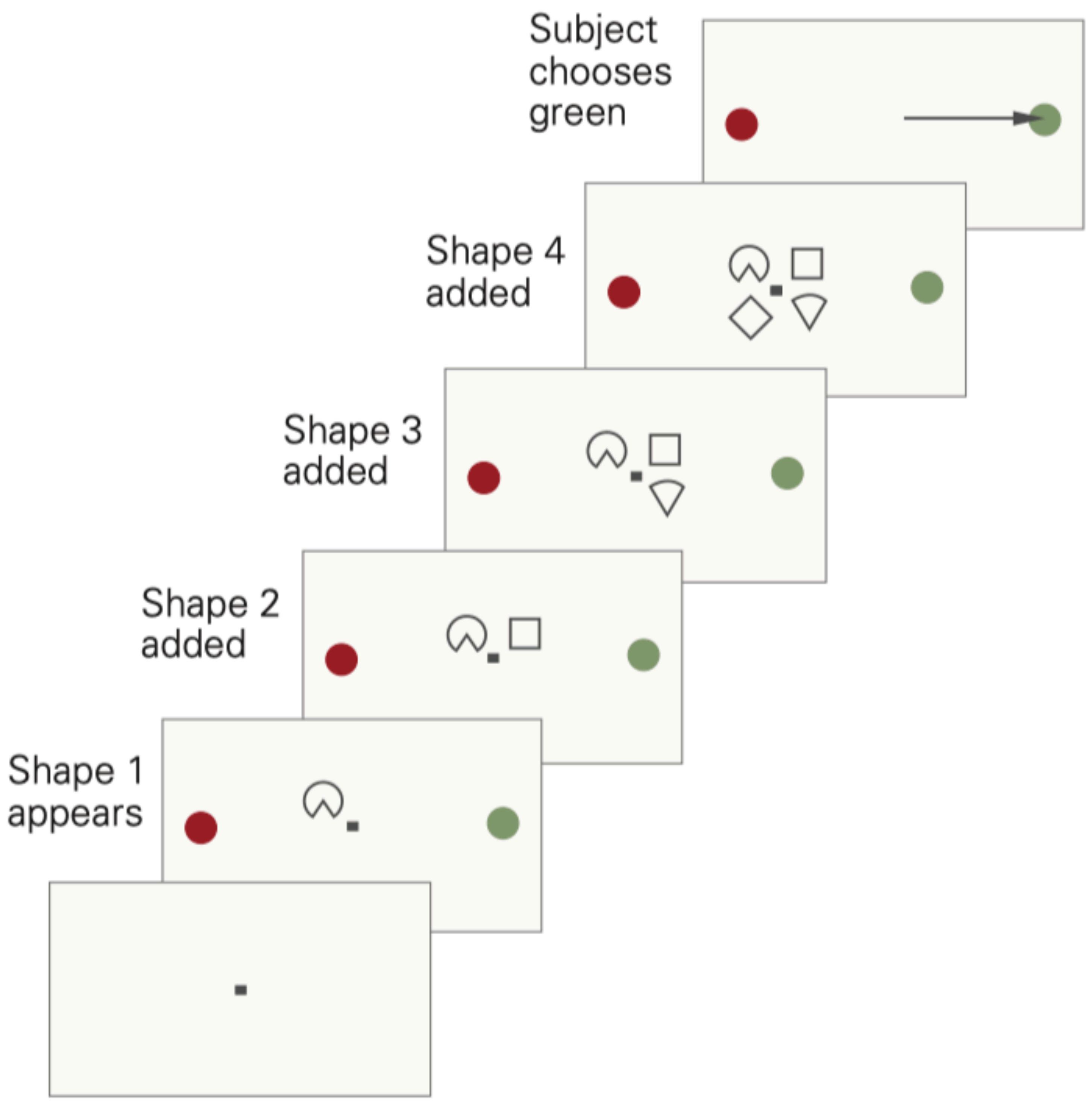
Reference

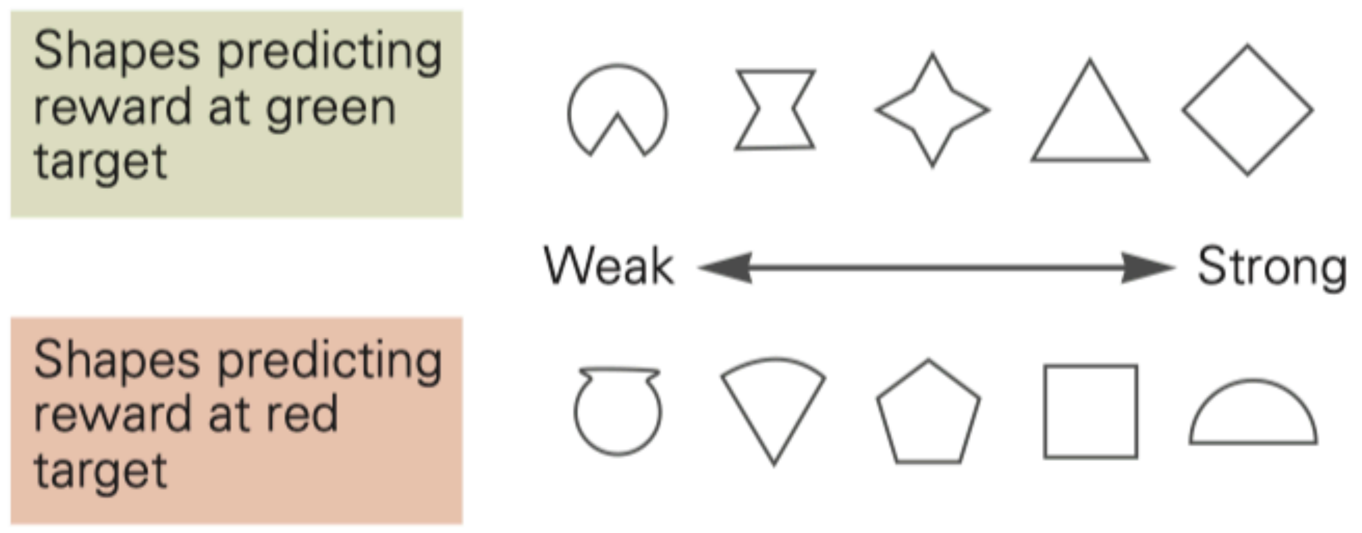
Ma et al. 2021. Bayesian Models of Perception and Action, Chapter 5, “Cue combination and evidence accumulation.”



Perceptual Decision-Making Is a Model for Reasoning From Samples of Evidence

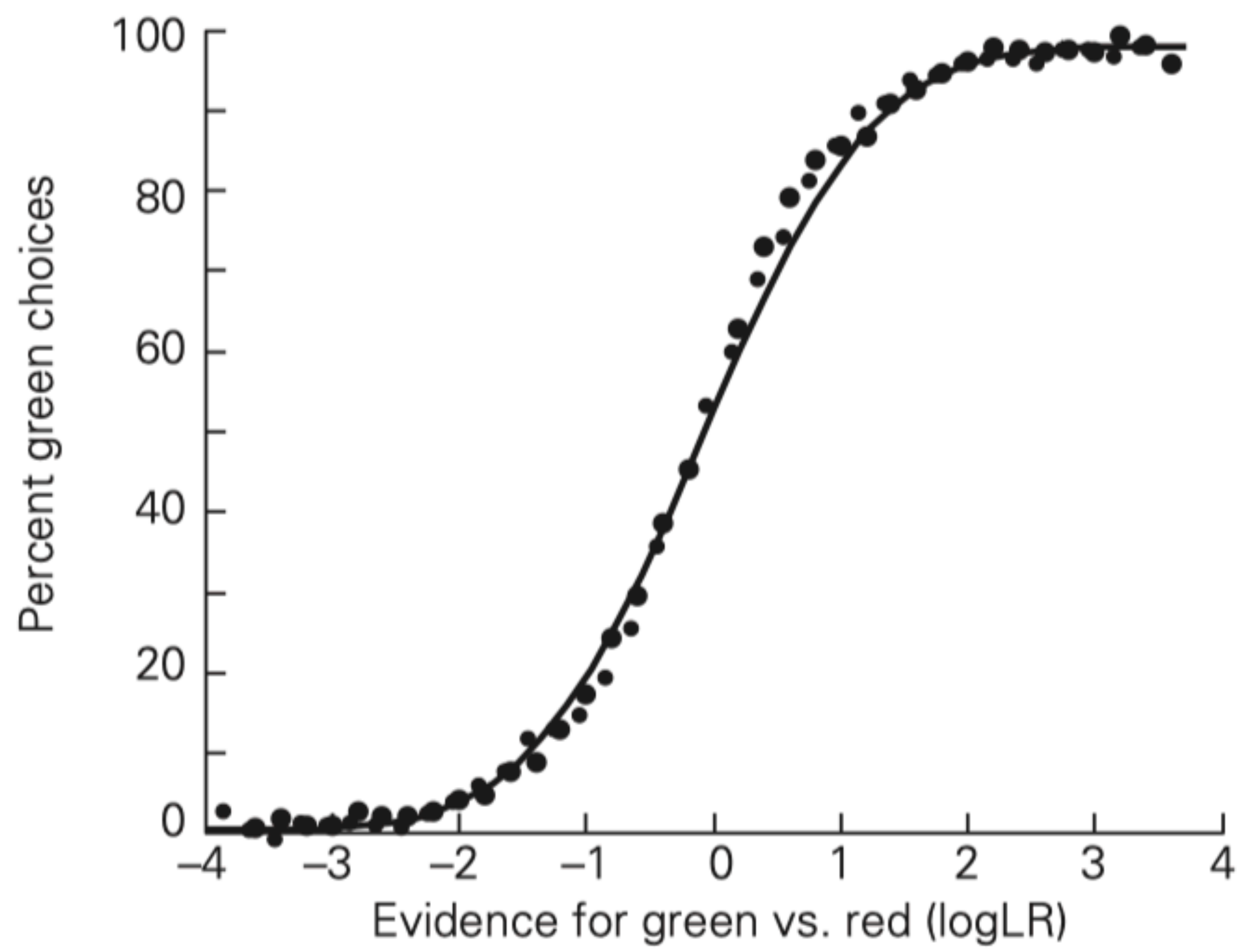
- Most of the decisions animals and humans make are not about weak or noisy sensory stimuli, but rather about activities, purchases, and propositions: the *weather prediction* task.
- The right way to make this decision is to consider each of the shapes and ask how likely they would be if the reward is in the red target or conversely the green target.
- The ratio of these two probabilities is termed the likelihood ratio, and it is computationally useful to take their logarithms (logLR).

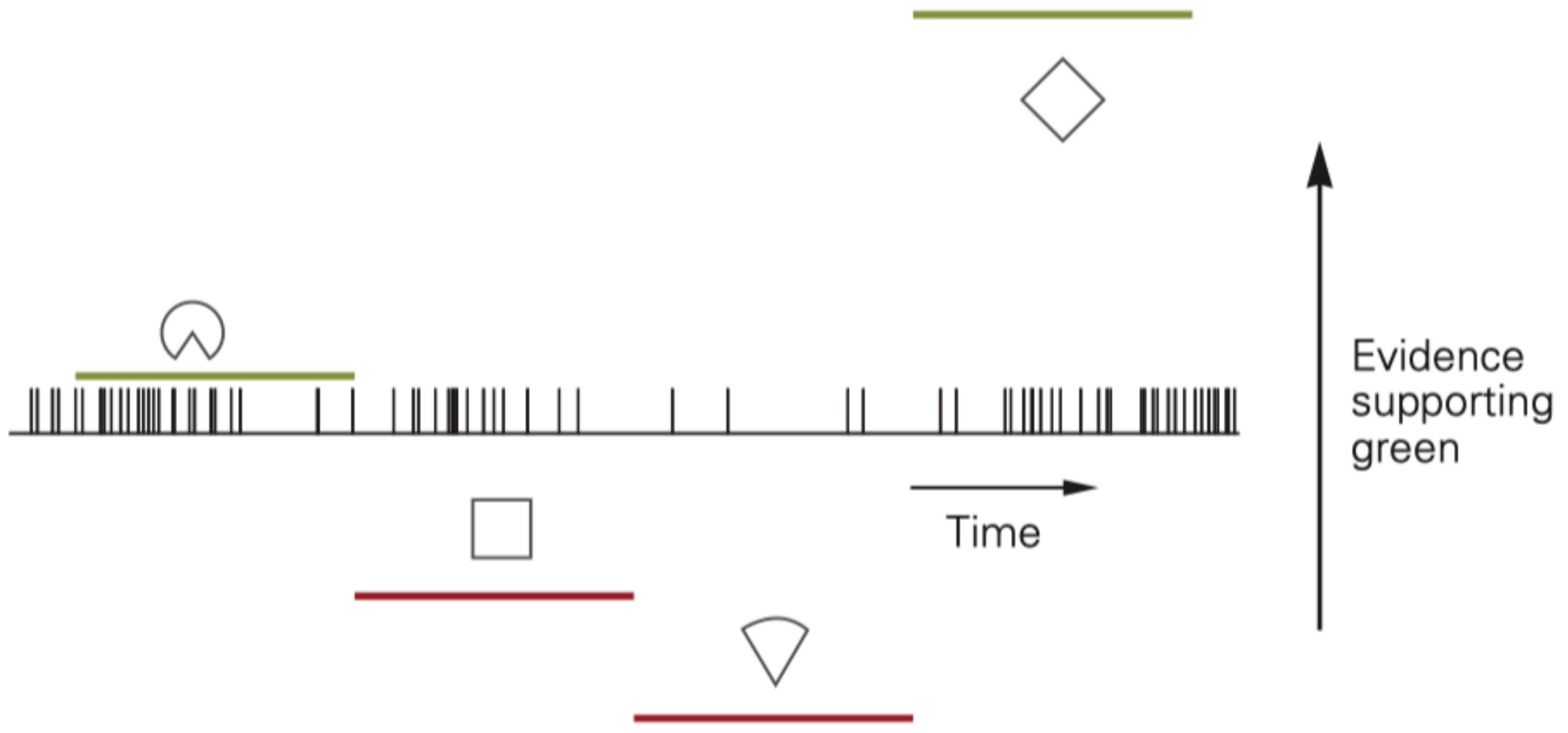




Perceptual Decision-Making Is a Model for Reasoning From Samples of Evidence

- The response changed discretely when each of the four shapes was presented, and it did so by an amount commensurate with the degree of reliability.
- The increment (or decrement) was proportional to the logLR assigned by the experimenter to the shape.
- If the monkey is allowed to view as many shapes as it wants, it will typically stop when the accumulated evidence (in units of logLR) reaches a criterion level.





Highlights

1. A decision is formed by applying a rule to the state of evidence bearing on the alternatives.
2. A simple decision rule for choosing between two alternatives employs a criterion. If the evidence exceeds the criterion, then choose the alternative supported by the evidence; if not, choose the other alternative.
3. The accuracy of many decisions is limited by considerations of the signal strength and its associated noise.
4. For neural systems, this noise is attributed to the variable discharge of single neurons, hence the variable firing rate of small populations of neurons that represent the evidence.
5. Many decisions benefit from multiple samples of evidence, which are combined across time. Such decision processes take time and require neural representations that can hold and update the accumulated evidence (ie, the decision variable).
6. Neurons in the prefrontal and parietal cortex, which are capable of holding and updating their firing rates, represent the evolving decision variable.
7. The speed–accuracy trade-off is controlled by setting a bound or threshold on the amount of evidence required to terminate a decision.
8. The log-likelihood-ratio provides a natural unit for belief.