

Figure 56-2 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 (f_2) was at a higher or lower frequency than that of the first stimulus (f_1) by pushing the left or right button with the other hand. The plots show that the proportion of trials in which the monkey decided that the comparison stimulus was greater than the reference depended on the magnitude and sign of the difference. With larger differences, the monkey almost always chose correctly, but when the difference was small, the choices were often incorrect. (Adapted from Romo and Salinas 2001.)

about whether the stimulus is present or absent but whether the vibration rate is fast or slow. On every trial of the experiment, the monkey experienced a reference frequency, f_1 , equal to 20 cycles per second (Hz). The pressure cycles are too fast to count; they feel more like a buzzing. The reference was then turned off, and after a few seconds, a second test stimulus, f_2 , was applied. The frequency of f_2 was chosen from a range of values from 10 to 30 Hz. The monkey was rewarded for indicating whether the test frequency was higher or lower than the f_1 reference.

We can represent the process conceptually using the same type of signal and noise distributions we drew for the detection problem (Figure 56-1D). Here, the “noise-only” distribution represents a quantity that is sampled in association with the 20-Hz reference, whereas the red distribution represents a quantity that is sampled in association with a test stimulus with a flutter frequency

greater than 20 Hz. Mountcastle favored the idea that the brain obtained two samples of evidence—one accompanying the 20-Hz reference and the second from the test. The decision, higher or lower, could arise by evaluating the inequality—greater than or less than—or, equivalently, by subtracting the two samples and answering based on the sign of the difference. This was a terrific insight, but the neural recordings were out of step with the theory. Mountcastle’s neural recordings explained the monkey’s ability to detect vibratory stimulation as a function of intensity and frequency (Chapter 17)—a yes/no decision—but they were unable to explain the mechanism for the comparison between the two alternatives, whether f_2 is greater or less than f_1 .

Two key elements were missing. First, to evaluate f_2 versus f_1 , the brain needs a representation of frequency. Mountcastle found neurons in the somatosensory cortex and thalamus with firing rates that were phase-locked to frequencies of the flutter, and they could measure the reliability of this frequency locking, but they did not find neurons that were tuned to particular frequencies less than or greater than 20 Hz. Second, both representations need to be available at the same time in order to compare them. However, the neural responses to f_1 lasted only as long as the flutter vibration. Mountcastle failed to observe neural responses that conveyed the representation of the reference frequency through the delay period up to the time that the test stimulus was presented. It was therefore impossible to study the neural operations corresponding to the decision process, which seemed to require some trace of the reference stimulus during analysis of the test.

These obstacles were overcome using a simpler task design and a different sensory modality. Inspired by Mountcastle, William Newsome trained monkeys to decide whether a field of dynamic random dots had a tendency to move in one direction or its opposite (eg, left or right). The random dot motion stimulus is constructed such that at one easy extreme all dots share the same direction of motion, say to the right. At the other easy extreme, all dots move to the left, and in between, the direction can be difficult to discern because many dots contribute only noise (Figure 56-3A).

Unlike the flutter vibration task, where a decision is rendered difficult by making the comparison frequencies more similar, the two directions of motion remain fixed and opposite for all levels of difficulty. The two directions were rendered less distinct by degrading the signal-to-noise ratio of the random dots. Each random dot appears only briefly, and then either reappears at a random location or at a displacement to support a consistent direction and speed. The probability of the latter (displacement) determines the motion

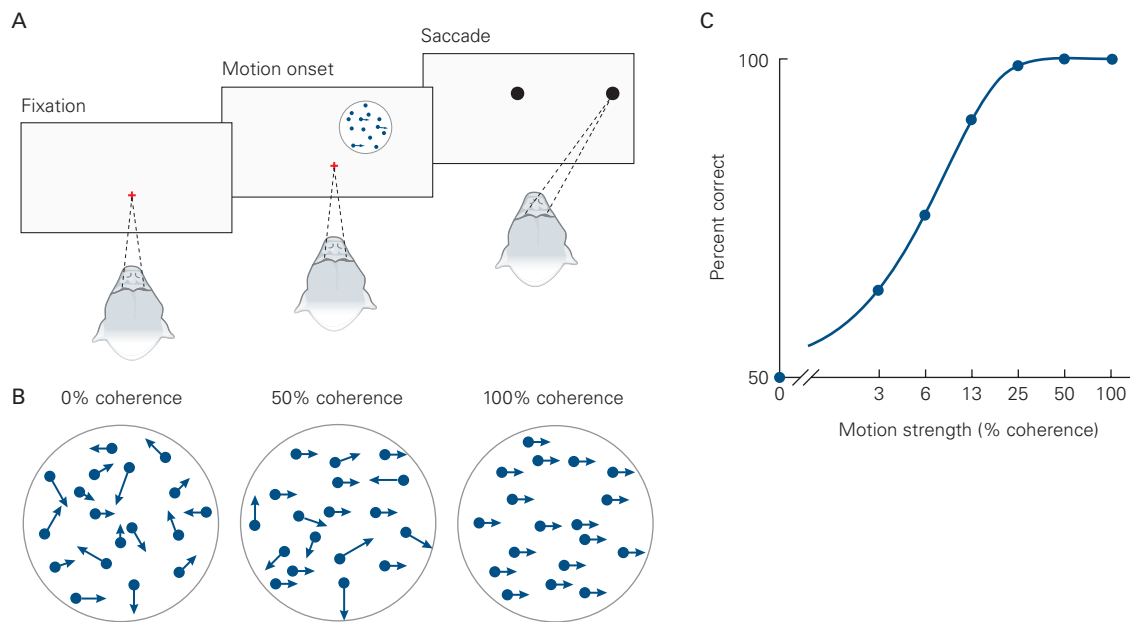


Figure 56-3 In the random dot motion discrimination task, the observer decides if the net motion of dots is in one direction or its opposite (eg, right or left).

A. The monkey maintains its gaze on a cross while viewing the random dot motion display. When the stimulus and fixation cross are extinguished, the monkey indicates its decision by shifting the gaze to the left or right choice targets and receives a reward if the decision is correct.

B. The difficulty of the decision is controlled by the coherence of dot motion. Each dot appears for only a few milliseconds at

a random location and then reappears 40 ms later, either at a new random location or at a displacement consistent with a chosen speed and direction. The probability that a dot present at time t_1 undergoes displacement in the same direction at t_2 establishes the motion strength (% coherence). (Reproduced, with permission, from Britten et al. 1992. Copyright © 1992 Society for Neuroscience.)

C. The decision is more likely to be correct when the motion is stronger.

strength, which is commonly expressed on a 0 to 100 scale, termed the percentage coherence. At the most difficult extreme, 0% coherence, all dots are plotted at random locations in each successive frame, giving the appearance of dancing snowflakes with no dominant direction. At intermediate levels of difficulty, the dancing snowflakes give rise to a weak sense that the wind might be blowing them ever so slightly to the right or left. Any one dot is unlikely to be displaced more than once, so there is no feature to track.

This simple stimulus was originally developed by Anthony Movshon to promote a decision strategy that would benefit from integrating visual information across its spatial extent and as a function of time. Moreover, it satisfied another desideratum: The same neurons should inform the decision at all levels of difficulty. For a left versus right decision, direction-selective neurons in the visual cortex that are, say, sensitive to leftward motion emit signals that are relevant to the decision at all levels of difficulty. That would not be the case if difficulty were controlled by the angular difference between the two directions. Another

advantage of this task over the vibration-flutter task is that there is only one stimulus presentation. There is no need to remember anything between a reference and a test stimulus. Finally, humans and monkeys perform this task at nearly identical levels. They answer perfectly for the strong-motion trials and make more errors when the strength of motion is reduced (Figure 56-3C). This establishes a platform for a quantitative reconciliation of decisions and neural activity. Is there a way to explain the likelihood that a decision will be accurate from measurements of the signal-to-noise ratio in the appropriate sensory neurons?

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

In higher mammals and primates, neurons that respond differentially to the direction of motion are first encountered in the primary visual cortex (area V1). They are a subset of the orientation-tuned simple

and complex cells discovered by Hubel and Wiesel (Chapter 22). These neurons project to a secondary visual cortical area, area MT.¹

Area MT contains a complete map of the contralateral visual field, and almost all the neurons in area MT are direction selective. Neurons with similar direction preferences cluster together so that MT contains a map of both space and motion direction at each point in the visual field. Their receptive fields are larger than those of V1 neurons, and some manifest properties that are not evident in V1 (eg, pattern motion; Chapter 23), but most respond as if they integrate signals from V1 that share the same direction selectivity over a larger patch of the visual field. In Newsome's experiments, the random dot motion stimulus was contained in a circular aperture that matched the size of an MT neuron's receptive field. It was thus possible to measure the response of a neuron perfectly situated to convey evidence to the decision process on single trials.

It seemed possible that the neurons with receptive fields aligned to the random dot motion stimulus and a firing preference for one or the other direction under consideration might contribute the evidence used to make the decision. Indeed, we can begin to understand the monkey's perception of motion by applying the same signal-to-noise considerations to the MT neural responses. We consider two types of direction-selective neurons (Figure 56–4). One type responds better to rightward motion than to leftward motion, and it yields higher firing rates when the rightward motion is stronger. It also responds above baseline to the 0% coherence stimulus because the random noise contains all motion directions including leftward and rightward, and it yields lower firing rates (compared to 0% coherence) when the leftward motion is stronger (Figure 56–4B). The other type of neuron responds well to leftward motion. It exhibits the same pattern as the right-preferring type, only with the direction preferences reversed. The neural responses are noisy, so the firing rates on any trial or in any epoch may be conceptualized as a random draw from one of the distributions in Figure 56–4C. These distributions can be interpreted in two ways. The two curves might represent the possible firing rates of a rightward-preferring neuron when weak motion is to the right or left, respectively. They

might also represent the possible firing rates of right- and left-preferring neurons, respectively, to the same weak rightward stimulus.

Because the responses of the two classes of neurons are available at the same time, we are able to characterize the evidence as the difference between the firing rates of the left- and right-preferring neurons. (The brain in fact relies on the difference between the averages from many left- and many right-preferring neurons.) We refer to such a quantity as a decision variable because the decision could be made by applying a criterion to this difference. Here, the criterion would be at zero. Thus, if the decision variable is positive, answer right; if it is negative, answer left.

Notice that when the stimulus is purely random (0% coherence), there is no correct answer. The monkey is rewarded randomly by the experimenter on a random half of the trials, and the monkey answers right and left with about equal probability. This is not because the monkey is guessing but because fluctuation in the random dot motion stimulus and the noisy firing rates of the right- and left-preferring neurons lead to variability in the evidence used to make the decision. This makes sense because the right- and left-preferring neurons respond equivalently to this type of stimulus. On some trials, the right-preferring neurons respond more than the left-preferring neurons, and the brain interprets this as evidence for rightward motion. On other trials, the left-preferring neurons respond more and the monkey chooses left.

Neuroscientists have been able to use a network of small populations of neurons to model the relation between the accuracy of an animal's choice versus motion strength, known as the *psychometric function*. The success of such models gives support to the idea that the signal and noise properties of cortical neurons can explain the fidelity of a perceptual decision, just as Mountcastle had hoped. This achievement was possible because of a clever experimental design that allowed the same neuron to participate in decisions across a wide range of difficulty. But are these neurons actually used to make the decision? Do they actually supply the noisy evidence that the monkey uses to make its decision?

We now know that they do. Because of the columnar organization of direction-selective neurons in area MT, it is possible to apply small currents through a microelectrode to excite a cluster of neurons sharing the same receptive field property. Newsome and colleagues placed the electrode in the middle of a cluster of neurons with receptive fields that were exactly aligned to the random dot motion stimulus. He reasoned that at weak stimulating currents the majority of stimulated

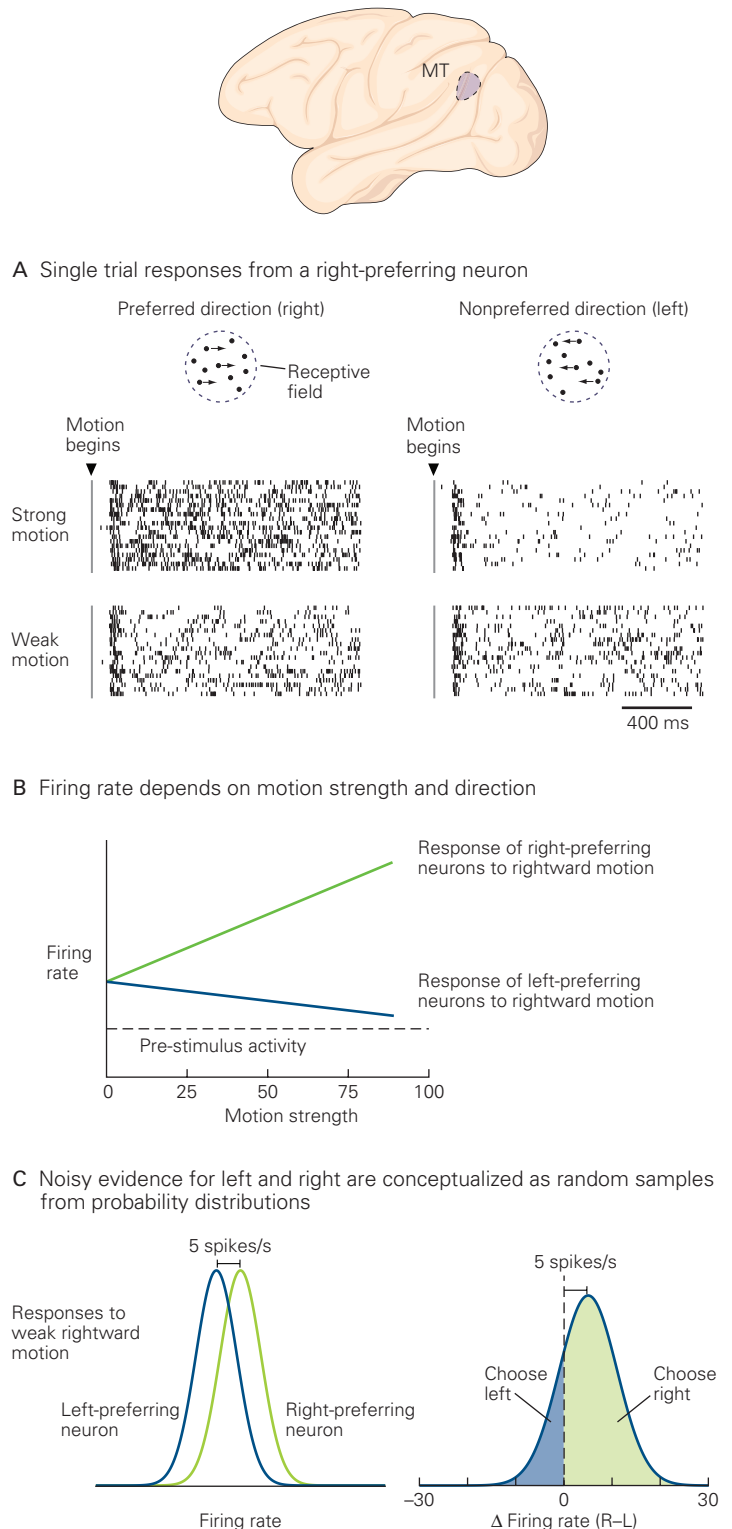
¹The letters MT stand for middle temporal, a sulcus in the species of New World monkey in which the area was first discovered. This sulcus does not exist in Old World monkeys and humans, but the homologous area does, and it retains its original name. Area MT is sometimes referred to as area V5 (the fifth visual area) in humans. The name is unimportant, but the area is!

Figure 56–4 Neurons in area MT provide noisy evidence bearing on the direction of motion.

A. Responses from a right-preferring neuron during the discrimination task. The random dot movie is in the receptive field of the neuron. The panels in the left column of the 2×2 panel display show the neuron's responses to motion in its preferred direction, and panels in the right column show its responses to the nonpreferred direction. The panels in the top row show the neuron's responses to strongly coherent motion, and the bottom panels show the responses to weakly coherent motion. In each panel, the time of each action potential (spike) is represented by a small vertical tick mark. Each row of spikes in a panel shows the neuron's response to the motion stimulus in a single trial. (Adapted with permission from Mazurek et al. 2003.)

B. The mean firing rate varies as a function of motion strength. The neuron increases its firing rate above baseline even in response to the 0% coherence stimulus because the dynamic random dots contain all directions of motion, including the neuron's preferred direction. The firing rate then increases with stronger rightward motion. It decreases, relative to the response to 0% coherence, with stronger leftward motion. The responses of this right-preferring neuron to leftward motion are mirrored by the responses of a left-preferring neuron to rightward motion.

C. Probability distributions of the firing rates from left-preferring and right-preferring neurons to weak rightward motion. The right-preferring neuron tends to respond more, but the overlap of the distributions shows that it is possible for the left-preferring neuron to respond more than the right-preferring neuron on any given trial. These same considerations apply to the pooled signals from populations of right- and left-preferring neurons. The plot on the right shows the distribution of the difference between firing rates of the left-preferring neuron and the right-preferring neuron measured in response to the same stimulus over many trials. The decision is to choose right if this difference is positive and to choose left if it is negative. This rule would lead to correct rightward choices on 80% of the trials.



neurons were likely to share the same receptive field and the same direction preference. Newsome had the monkey decide between this direction and its opposite. For example, if these neurons preferred rightward motion, the weak currents caused the monkey to decide more often in favor of right (Figure 56–5).

We now refer to such weak stimulation, designed to affect a cluster of neurons within a 50- to 100 μ m radius, as *microstimulation*. Notably, microstimulation did not cause a hallucination of visual motion. It biased the monkey's decisions, which were guided mainly by the random dot motion stimulus. The monkey did not respond when the stimulus was not shown, and microstimulation did not affect the monkey's decisions when the random dots were presented at a location of the visual field outside the receptive field of the stimulated neurons. The microstimulation exerted its largest effect on choices when the motion strength was weakest. The stimulated neurons simply added a small amount of evidence for rightward motion, which is effectively evidence against leftward motion, as discussed below.

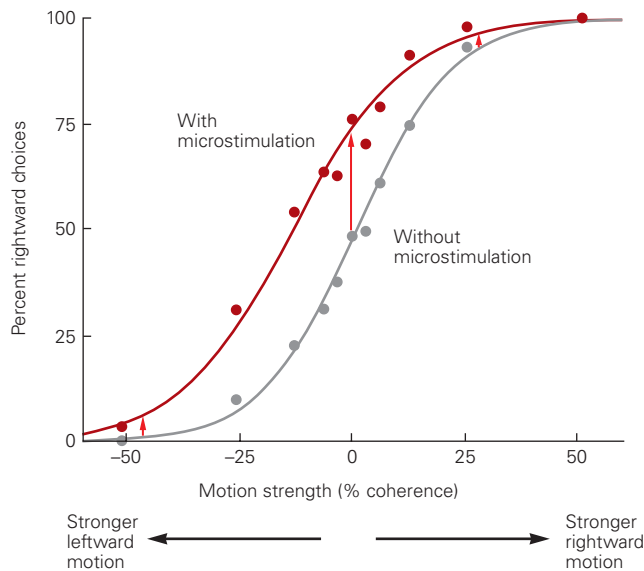


Figure 56–5 Artificial activation of neurons that respond preferentially to rightward motion causes a monkey to decide that motion is rightward. In the experiment, an electrode is placed in the middle of a patch of neurons in area MT that prefer the same direction of motion, say rightward. The random dot motion is shown in the receptive field of these neurons. A weak alternating current is applied on half of the trials during the presentation of the random dots movie. The amount of current activates about 200 to 400 neurons within 50 to 100 μ m of the electrode tip. On trials with microstimulation, the monkey is more likely to choose the preferred direction of the simulated neurons. The effect is most pronounced when the decision is more difficult (middle red arrow). (Adapted, with permission, from Ditterich, Mazurek, and Shadlen 2003.)

The microstimulation experiment shows that the direction-selective neurons in area MT contribute evidence to the perceptual decision. However, 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. In addition, many more neurons in MT were not affected by the electrical stimulation but nonetheless responded to the same random dot patch in the same direction-selective manner. They are in other columns with receptive fields that are not centered on the stimulus but overlap it. If the electrode is moved to stimulate these neurons, they too cause the monkey to choose the preferred direction more often. These findings imply that in any one experiment the microstimulation only affects a small fraction of the neurons that contribute to the decision. Most respond at their usual firing rates to the random dot motion. The microstimulation only changes the total signal that the brain uses to make its decision by a small amount. No wonder the effect is only evident when the decision is difficult.

There is an important principle to be learned here. Had Newsome used only the easier conditions, the electrical stimulation would have yielded a null effect, and thus, the causal relationship between the neural activity and behavior would not have been established. The same pattern of effects has recently been established using techniques to turn neurons off. Silencing induces a bias in choices against the direction of the silenced neurons, but this too is only apparent on trials when the motion is difficult. Without evidence for sufficiency or necessity, a neuroscientist might conclude that the neurons in MT do not cause changes in perceptual decisions. This would be a mistake, notably one that is likely to be made in any experiment in which perturbations are restricted to a subset of the neurons involved in a computation. That is the rule, not the exception, for studies of higher cortical functions. It is only mitigated by studying behavior in conditions when a small difference to the total pool of neural signals might make a difference, as in the difficult (low signal-to-noise) regime employed in Newsome's experiments.

To summarize so far, the perceptual decision arises from a simple *decision rule*: the application of a criterion to the noisy evidence supplied by noisy direction-selective neurons in the visual cortex. We have characterized the noisy evidence as a single number: the difference in the mean firing rates from two opposing pools of direction-selective neurons. This account leaves out two important points: The operations that establish the decision variable must be carried out by neurons that receive information directly or indirectly from area MT, and these operations take time. As we will see, time is the key to understanding

decision-making, and it is also the factor that relates decision-making to higher cognitive function.

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

The decision rule considered so far is appropriate if the brain received only a brief snapshot of the motion, say for a tenth of a second. However, decision-making normally takes some time, so that when the viewing duration is longer, decisions tend to be more accurate. In fact, the strength of motion that is required to support 75% accuracy, termed the *sensory threshold*, decreases as a function of viewing duration. With more time, the decision-maker can achieve this level of accuracy with a weaker motion strength. Put another way, the sensitivity to weak motion improves as a function of viewing duration, t . Indeed, the sensitivity improves as a function of the square root of time (\sqrt{t}), which is the rate of improvement in the signal-to-noise ratio that one obtains by accumulating or averaging. The suggestion then is that 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—in this case, two processes that accumulate evidence for left and right, respectively.

The accumulation of noisy evidence follows a path comprising random steps in both the positive and negative direction on top of a constant bias determined by the coherence and direction of the moving dots. This is termed a *biased random walk* or *drift plus diffusion* process (Figure 56–6). Because evidence for left is evidence against right (and vice versa), the two random walks are anticorrelated, albeit imperfectly so. The accumulations evolve with time and continue to do so until the stimulus is turned off or until one of the accumulations reaches an upper *stopping bound*, which determines the answer, left or right. Even the 0% coherence (pure noise) stimulus will reach a stopping bound eventually, but it is equally likely that the left or right accumulation will do so. When the random dot motion favors one direction, it is more likely that the corresponding accumulation determines the choice, and increasingly so with stronger motion. Such accumulations of noisy evidence are dynamic versions of the decision variable. The decision rule remains similar: Choose right if there is more evidence for right than left, and vice versa. The stopping bounds also explain another important feature of the decision—the time it takes to make it.

This simple idea thus explains the observed trade-off between the speed and accuracy of a decision. It

specifies the exact relationship between the probability that each motion strength will lead to a correct choice and the amount of time that is taken, on average, to respond, termed the reaction time (Figure 56–6C). 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. If the flow of information is cut off before either bound has been reached, the decision-maker may feel she has not yet reached an answer, but may nonetheless answer based on the accumulation that is closer to its stopping bound. This mechanism, termed *bounded evidence accumulation*, explains the effect of task difficulty on choice accuracy and the associated reaction times on a variety of perceptual tasks. It explains the degree of confidence that a decision-maker has in a decision and why such confidence depends on both the amount of evidence and deliberation time. It also explains the rate of improvement in accuracy when the experimenter controls viewing duration by \sqrt{t} , mentioned above, and it explains why this improvement saturates with longer viewing durations. The brain stops acquiring additional evidence when the accumulated evidence reaches a stopping bound.

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

Neurons in several parts of the brain, including the parietal and prefrontal cortices, change their firing rates to represent the accumulation of evidence—in the case of visual motion from area MT—bearing on the direction decision. The neurons that represent the accumulation differ from sensory neurons in two important ways. First, they can continue to respond for several seconds after a sensory stimulus has come and gone. Moreover, they seem to be capable of holding a firing rate at one level and then increasing or decreasing that level when new information arrives. This is exactly the type of feature one would like to see in a neuron that represents the accumulation of evidence. Second, such neurons tend to be associated with circuits that control the behavioral response that the monkey has learned to use to communicate its decision. Such neurons were first identified for their capacity to maintain persistent activity in the absence of a sensory stimulus or ongoing action. They were therefore thought to play a role in working (short-term) memory, planning an action, or maintaining attention at a location in the visual field (Figure 56–7).

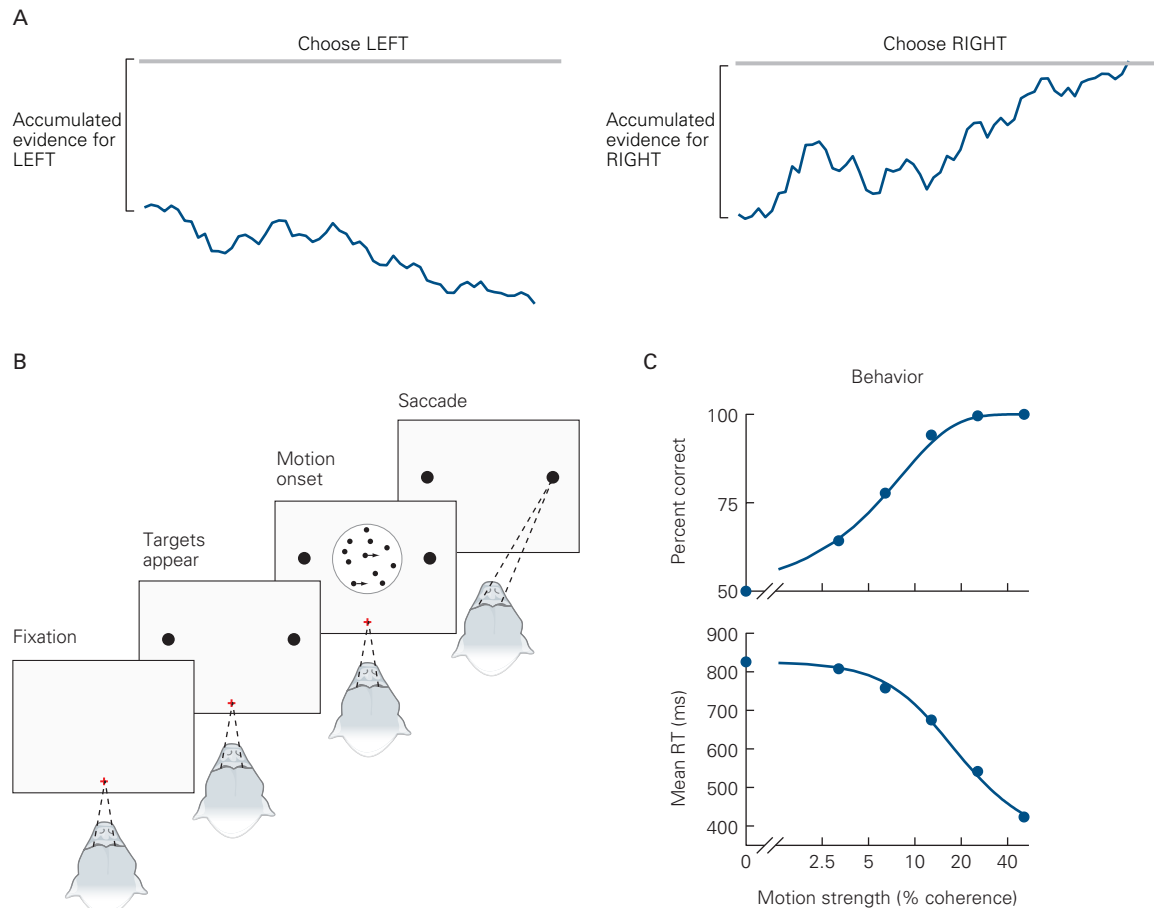


Figure 56-6 The speed and accuracy of a decision are explained by a process of evidence accumulation.

A. A decision and the time it takes to reach it are both explained by the accumulation of evidence, as a function of time, until there is sufficient evidence to terminate the decision in favor of one or the other choice. The cartoon illustrates a decision for rightward motion because the “choose right” accumulation was the first to reach the stopping bound (**thick gray lines**). Because the evidence is noisy, the accumulations resemble biased random walks, also known as drift-diffusion processes. For the decision between left and right motion, there are two accumulations. The one shown on the left accumulates evidence for left and against right. The one shown on the right accumulates evidence for right and against left. For this process, the bias (or drift rate) is the mean of the evidence samples depicted by the distribution of differences (right minus left) in Figure 56-4C. The process is a random walk because even if the motion is rightward, left-preferring neurons in area MT might respond more than right-preferring neurons at any instant. The two processes tend to evolve in an anticorrelated fashion because the random dot motion stimulus supplies the

same noisy samples of evidence to both accumulations via the visual cortex. They are not perfectly anticorrelated because right- and left-preferring neurons introduce additional noise. Were the anticorrelation perfect (eg, if all the noise comes from the motion stimulus), the two processes could be represented by one accumulation that terminates at either an upper or lower stopping bound.

B. In a choice-reaction time task, the decision-maker reports a decision whenever ready with an answer. In this case, the monkey signals its choice by the direction of a saccade.

C. Graphs show a typical data set. In addition to the proportion of correct choices, the reaction time (RT), the time from onset of motion to the beginning of the eye movement response, also depends on the strength of motion. The total length of RT is the time to reach a decision, explained by the process in **A**, plus the time required to convey sensory information from the stimulus to the neurons that compute the decision and the time required to convert the decision to a motor response. (Adapted, with permission, from Gold and Shadlen 2007.)

It seemed possible that neurons whose activity represents a plan to act might also represent the formation of that plan during decision making. For example, if a monkey has learned to answer “rightward” by moving its hand to a target on a touch screen, the neurons of interest will tend to be active in association with that movement and they will decrease their activity if the monkey plans to reach to the opposite “leftward” target. Those neurons project to brain areas that command reach movements. If the monkey has learned to answer with an eye movement, the neurons that help to plan eye movements to the choice-target represent the decision variable. Such neurons have been studied extensively in the lateral intraparietal area (LIP). Indeed, these LIP neurons provided neuroscientists with the first view of a decision process as it unfolds in time.

Neurons that represent the evolving decision increase their firing rates gradually as the evidence mounts for one of the choices, and they decrease gradually when the evidence favors the other option (Figure 56–8). Their firing rates, plotted as a function of time, approximate a ramp: a baseline rate plus a constant multiplied by time, where the constant is proportional to the strength of the momentary evidence (eg, the average difference in the firing rates of the right- and left-preferring MT neurons). This captures the average firing rates across many trials, but it leaves out the critical point that the decision variable is an accumulation of both signal and noise. The signal is the mean of the difference. The noise is the variance—that is, the spread around the mean. The accumulated noise is obscured by the averaging in Figure 56–8, but it is apparent in the variability of firing rates across multiple decisions.

The responses start at a common level and evolve as the brain acquires more and more information, until something stops the process. A neural signature of the stopping rule is apparent in the responses aligned to the eye movement itself. The firing rate appears to reach the same level on trials that take as little as a few tenths of a second and trials that take as much as a full second. The level is achieved less than a tenth of a second before the eyes start to move. Of course, it takes less time to achieve this level if the firing rates are increasing at a rapid pace (eg, solid red trace in Figure 56–8). This suggests that the brain terminates the decision when the representation of accumulated evidence reaches a threshold. That is exactly what the bounded accumulation framework predicts. There appears to be no common level of activity in neurons that signal a rightward movement when the monkeys choose the opposite direction. Instead, another population of neurons that accumulate evidence for left (and

against right) reaches their threshold and terminates the decision process when the monkey answers left (Figure 56–6A). The neurons that favor the right choice simply stop accumulating evidence at a time determined by the left choice neurons. This explains why the downward traces in Figure 56–8 do not reach a common level of activity around the time of the eye movement. It is not yet known where in the brain the threshold operation is applied. Computational theorists have proposed that a likely candidate is the striatum, a brain area involved in selecting between competing actions (Chapter 38), but there are many other candidate structures, including movement areas of the cortex and brainstem.

Area LIP is not the only part of the brain that represents the accumulation of evidence toward a decision, and LIP itself is not limited to making decisions about random dot motion. Many neurons in the parietal and prefrontal cortex exhibit persistent firing. In fact, the first brain areas shown to exhibit this type of activity were in the frontal lobe, rostral to the primary motor cortex, and some neurons with this property were found in the motor cortex itself. The persistent activity was thought to represent working memory for a location in space or a rule, category, or plan of action, as discussed in Chapter 52. But these neurons are also capable of representing graded levels of activity, suggesting a capacity to represent more analog quantities, like an evolving decision variable, the expected value of making an action, or working memory of a sensory quality, as we next consider.

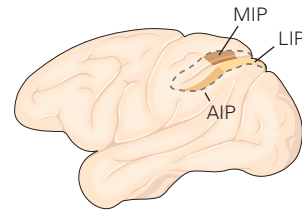
Twenty years after Mountcastle published his studies of flutter-vibration discrimination, his student Ranulfo Romo rejuvenated this line of research by focusing on neurons in the prefrontal cortex, which had the kind of persistent activity we have been discussing. Romo modified the task. The monkeys were still presented with two vibrating stimuli, separated by a delay, and were required to decide whether the vibration frequency of the second stimulus (f_2) was greater or less than the vibration frequency of the first stimulus (f_1). However, instead of using the same 20-Hz reference stimulus on all trials, the flutter frequency was varied across trials. He found that many neurons in the prefrontal cortex respond in a graded and persistent manner to the frequency of the first flutter-vibration stimulus during the delay period while the monkey awaited the second stimulus. Some neurons increased their firing rate as a function of the vibration frequency of f_1 , while others were more active with lower frequencies. These persistent neural responses were not observed by Mountcastle in his original studies. There is evidence that a decision variable is constructed in the ventral premotor cortex, where neurons respond

to the difference, $f_2 - f_1$. This is challenging to study because the decision variable does not evolve over a long time scale. There is no need to acquire many samples of evidence. All that is needed is an estimate of f_2 and the application of a threshold. The flutter-vibration task complements the motion decision task by demonstrating the diverse functions of persistent activity. In the motion task, the persistence supports the computation of the decision variable—the accumulated evidence bearing on the decision alternatives. In the flutter-vibration task, the persistent activity represents

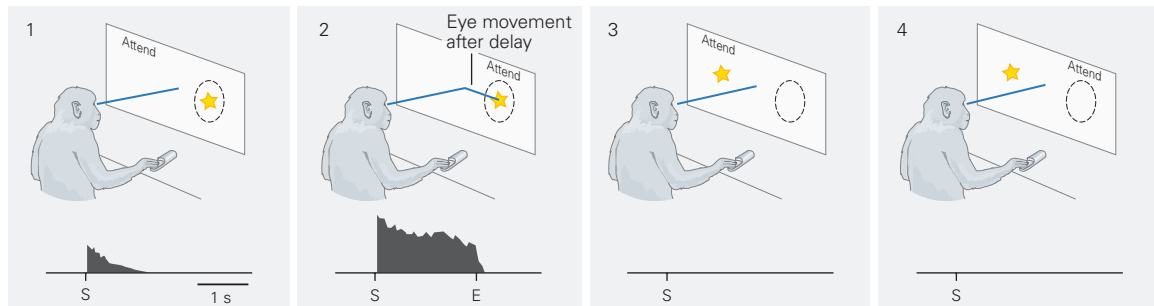
a sensory quality—the frequency of the reference stimulus—through a delay period.

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. They are about activities, purchases, propositions, and menu items. They are informed by knowledge and



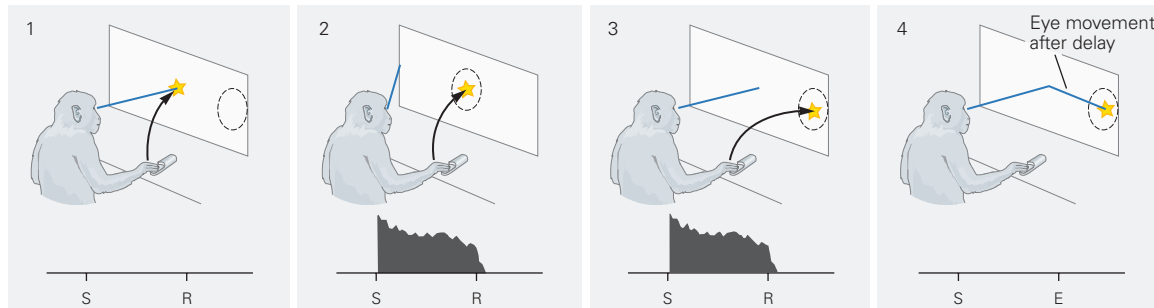
A Lateral intraparietal area



Receptive field characteristics

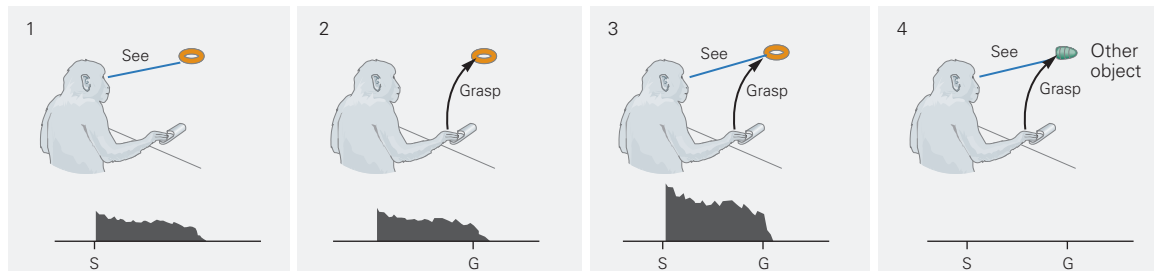
Attention sensitive, preparation to look

B Medial intraparietal area



Retina-centered, preparation to reach

C Anterior intraparietal area



Object-specific viewing, grasping