

## Chapter 56: Decision-Making and Consciousness

### Introduction

IN THE EARLIER CHAPTERS, WE HAVE SEEN how sensory input is transformed into neural activity that is then processed by the brain to give rise to immediate percepts and how those percepts can be stored as short- and long-term memories (Chapters 52, 53, 54). We have also examined in detail how movement is controlled by the spinal cord and brain. Here, we begin to consider one of the most challenging aspects of neuroscience: the transformation of sensory input to motor output through the higher-order cognitive process of decision-making. In doing so, we are afforded a glimpse of the building blocks of higher thought and consciousness.

Outside neuroscience, the term *cognitive* typically connotes some distinction from reflexes and dedicated routines, and yet as we shall see, neuroscience recognizes the rudiments of cognition in simple behaviors that display two types of flexibility—contingency and freedom from immediacy. Contingency means that a stimulus does not command or initiate an action in the way it does for a reflex. A stimulus might motivate a particular behavior, but the action may be delayed, pending additional information, or it may never occur. This freedom from immediacy of action means there are operations that transpire over time scales that are not immediately beholden to changes in the environment or the real-time demands of control of the body.

Both types of flexibility—contingency and time—are on display when we make decisions. Of course, not all decisions invoke cognition. Many behavioral routines—swimming, walking, feeding, and grooming—have branch points that may be called decisions, but they proceed in an orderly manner without much flexibility or control of tempo. They are governed mainly by the time steps of nervous transmission and are dedicated for the most part to particular input–output relationships. The point of drawing these distinctions is not to establish sharp boundaries around decision-making, but to help us focus on aspects of decisions that make them a model for cognition.

For present purposes, we will use the following definition: A decision is a commitment to a proposition, action, or plan based on evidence (sensory input), prior knowledge (memory), and expected outcomes. The commitment is provisional. It does not necessitate behavior, and it can be modified. We can change our mind. The critical component is that some consideration of evidence leads to a change in the state of the organism that we liken to a provisional implementation of an action, strategy, or new mental process.

Such propositions can be represented as a plan of action: I decide to turn to the right, to leave safe shelter, to look for water, to choose a path least likely to encounter a predator, to approach a stranger, or to seek information in a book. The concept of a plan emphasizes freedom from immediacy. Moreover, not all plans come to fruition. Not all thought leads to action, but it is useful to conceive of thought as a type of plan of action. This view invites us to consider knowing as the result of directed—mostly nonconscious—interrogation, rather than an emergent property of neural representations.

Decision-making has been studied in simple organisms, notably worms, flies, bees, and leeches, as well as in mammals from mice to primates. Simpler organisms are appealing because they have smaller nervous systems, but they lack the behavioral repertory required to study decisions that entail forms of cognition. The hope is that the biological insights from these species will inform our understanding of the processes characterized in mammals, especially primates. This is a laudable goal because, to paraphrase Plato, decision-making offers our best shot at carving cognitive function at its joints—to identify the common principles that support its normal function and to elucidate their mechanisms so they may be repaired in disease.

In this chapter, we focus primarily on perceptual decisions made by primates in contrived settings. The principles extend naturally to reasoning from evidence and to value-based decisions concerning preference. In the last part of the chapter, we derive insights about broader aspects of cognition. Viewed through the lens of decision-making, brain states associated with knowing and being consciously aware may be closer to a neurobiological explanation than is commonly thought.

## Perceptual Discriminations Require a Decision Rule

Until recently, decision-making was studied primarily by economists and political scientists. However, psychologists and neuroscientists working in the field of perception have been long concerned with decisions. Indeed, the simplest type of decision involves the detection of a weak stimulus, such as a dim light or a faint sound, odor, or touch. The decision a subject must make is whether or not the stimulus is present—yes or no. In the laboratory, there is no uncertainty about where and when the stimulus is likely to be present. Such experiments were therefore used to infer the fundamental sensitivities of a sensory system from behavior, a subfield of psychology known as psychophysics. Detection experiments played a role in inferring signal-to-noise properties of sensory neurons that transduce light touch, faint sounds, and dim lights. In the last case, such experiments provided evidence that the visual system is capable of detecting the dimmest of light, a single photon, subject to background noise of photoreceptors. In other words, it is as efficient as possible, given the laws of physics.

The psychophysical investigation of perception began with Ernst Weber and Gustav Fechner in the 19th century. They were interested in measuring the smallest detectable difference in intensity between two sensory stimuli. Such measurements can reveal fundamental principles of sensory processing without ever recording from a neuron. It turns out they also lay the foundation for the neuroscience of decision-making, because every yes/no answer is a choice based on the sensory evidence.

In [Chapter 17](#), we learned how psychophysicists conceptualize the detection problem ([Box 17–1](#)). On any one trial, the state of the world is either stimulus present or stimulus absent. The decision is based on a sample of noisy evidence. 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 ([Figure 56–1A](#)). The brain does not directly perceive a stimulus but receives a neural representation of the sample. As a result, some of the noise arises from the neural activity involved in forming this representation. It is the job of the brain to decide from which distribution the sample came, using information encoded in neural firing rates. However, the brain does not have access to the distributions, just the one sample involved in each given decision. It is the separation of these distributions—the degree that they do not overlap—that determines the discriminability of a stimulus from noise. The decision rule is to say “yes” if the evidence exceeds some criterion or threshold.

Figure 56–1

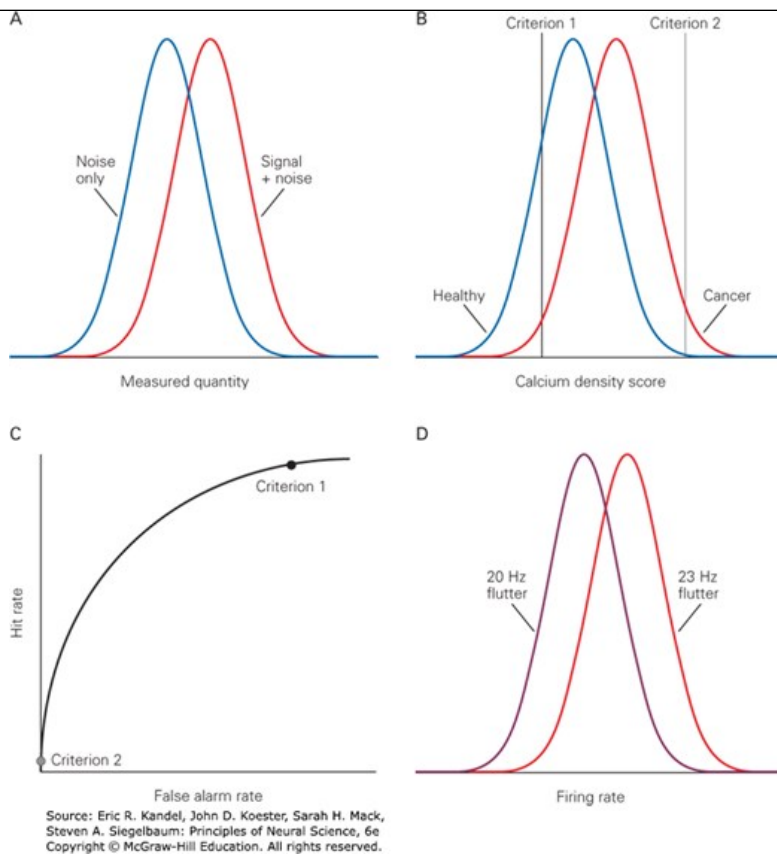
**The framework of signal detection theory formalizes the relationship between evidence and decisions.** In panels **A** through **C**, we consider simple yes–no decisions in which a decision-maker receives just one measurement.

**A.** The height of the curves represents the probability of observing a measurement on the x-axis (be it number of spikes per second, radioactive counts, or blood pressure) under two conditions: signal present or absent. In both cases, the measurement is variable, giving rise to the spread of possible values associated with the two conditions. If the signal is present, the decision-maker receives a random sample from the **Signal + noise** probability distribution (**red**). If the signal is absent, the decision-maker receives a sample from the **Noise only** probability distribution (**blue**). The decision arises by comparing the measure to a criterion, or threshold, and answering *yes* or *no*, signal is present or absent, if the value is greater or less than the criterion.

**B.** The criterion is an expression of policy, as illustrated in medical decision-making. Suppose the measure is derived from calcifications detected in a screening mammogram—a score combining number, density, and shape. The criterion 1 (**left line**) for interpreting the test as a positive or negative (breast cancer or not) is liberal. It leads to many false positives (83%), but very few women with cancer receive a negative result. Criterion 2 (**right line**) is conservative. It would miss many cases of cancer, but it would rarely render a positive result to a healthy person. That would make sense if a positive decision were rationale for a dangerous (or painful) procedure.

**C.** The receiver operating characteristic shows the combination of proportions of “yes” decisions that are correct (hit rate) and incorrect (false alarm rate) for all possible criteria. The liberal and conservative criteria are shown by the **black** and **gray** symbols, respectively.

**D.** The framework also applies to decisions between two alternatives. Here, the decision is whether a vibration applied to the index finger has a higher frequency than a vibration applied a few seconds before. The same depiction of overlapping distributions might conform to neural responses from some part of the brain that represents a sensory stimulus. For example, a neuron in the somatosensory cortex might respond over many individual trials with a higher average spike rate to vibratory stimulation of the finger at 23 Hz than stimulation at 20 Hz. However, the distributions overlap so that on any given presentation we cannot say with 100% certainty whether the vibration was at 20 Hz or 23 Hz based on the neuron’s response.



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

The criterion instantiates the decision-maker's policy or strategy. If the criterion is lax—that is, the threshold is low—the decision-maker will rarely fail to detect the stimulus, but they will often respond “yes” on the trials when there was no stimulus because the background noise exceeds the threshold. This type of error is called a *false alarm*. If the criterion is more conservative—that is, the threshold is high—the decision-maker will rarely say “yes” when the stimulus is absent but will often say “no” when the stimulus is present. This type of error is called a *miss*. The appropriate criterion depends on the relative cost of the two types of errors and also on the design of the experiment. For example, if the stimulus is present on 90% of trials, then a lax criterion might be warranted since false alarms will be rare.

The policy ought to be influenced by a value or cost associated with making correct and incorrect decisions. For example, in medical diagnosis, it is often the case that a disease affects only a small fraction of the population, but a diagnostic test does not discriminate perfectly between people with and without the disease. We can illustrate this using the distribution of mammogram calcification scores. The scores are larger in women with breast cancer than in healthy women, but the range of values overlaps to an extent, implying that the test is not perfect (Figure 56-1B).

In this situation, a lax criterion might seem problematic because it would produce a large number of false alarms: patients who are healthy but told they might have a disease based on the test. However, it may well be the case that a miss is life threatening, whereas a false alarm leads to a stressful week as the patient awaits a more decisive test. In this situation, it is actually sensible to apply a lax criterion even if it leads to many false alarms. Alternatively, a false alarm may trigger a painful or risky procedure, in which case a more stringent criterion would be more appropriate. The medical analogy allows us to appreciate the strategic roles of the criterion setting. We praise and criticize decision-makers based on their policy, not on the noisy imperfections of the measurements.

The important point is that the criterion represents a decision rule, which instantiates knowledge about the problem and an attitude about the positive value associated with making correct choices (hits and correct rejections) and the negative value of making errors (misses and false alarms). Note that the application of different criteria does not change the fundamental characteristic of the evidence samples that is responsible for the accuracy of decisions. This is reflected by the overlap between the blue and red distributions, which does not change if a decision-maker adjusts her criterion. The curve in Figure 56-1C, termed the receiver operating characteristic (ROC), shows how changing the criterion affects the accuracy of the decision

whether a stimulus (or cancer) is present or absent for all possible criteria. Each point on the curve is an ordered pair of the probability of a correct “yes” response (hits) versus an erroneous “yes” response (false alarms) associated with a given criterion (threshold). The ROC tells us something about the reliability of the measurement (ie, the separation between the two distributions) regardless of how the decision-maker uses it. The criterion tells us something about the decision-maker’s policy. It bears on why two decision-makers receiving the same evidence might reach different decisions. Indeed, it is the policy, not the noise, that the decision-maker controls and for which she may be praised or criticized, that is, held responsible. We will think about this topic again when we discuss the trade-off between speed and accuracy.

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. We will develop these connections in subsequent sections. Here, we wish to seed an important insight about the term *noise* as it pertains to the neural representations of evidence. Decision-makers do not make the same decision even when confronting repetitions of identical facts or sensory stimuli. Some variability at some stage must creep into the process. The distinction between signal and noise need not devolve into scholastic arguments about chance and determinism. Any source of variance in the representation of the evidence is effectively noise if it is responsible for errors. If the brain did not distinguish such variability from the signal and thus made a mistake, we would be justified in construing this variability as unaccounted by the decision-maker.

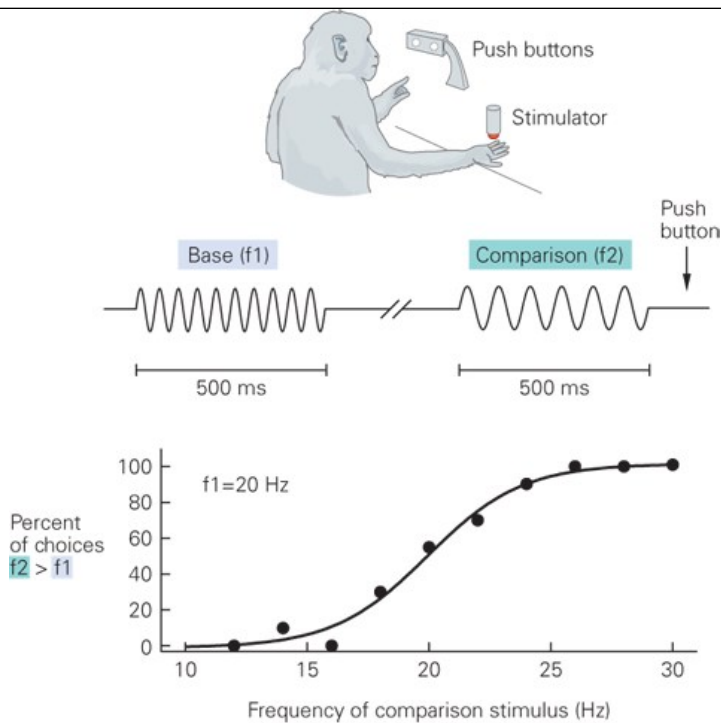
## Perceptual Decisions Involving Deliberation Mimic Aspects of Real-Life Decisions Involving Cognitive Faculties

The neural bases for more cognitive decisions have been examined by extending simple perceptual decisions in three ways: first, by moving beyond detection to a choice between two or more competing alternatives; second, by requiring the decision process to take time by involving consideration of many samples of evidence; and third, by considering decisions about matters involving values and preferences.

Vernon Mountcastle was the first to study perceptual decisions as a choice between two alternative interpretations of a sensory stimulus. He trained monkeys to make a categorical decision about the frequency of a fluttering pressure applied lightly to a fingertip (Figure 56–2). Since the *vibratory flutter* has an intensity that is easily detected, the decision is not 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.

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 (**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 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.)



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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).

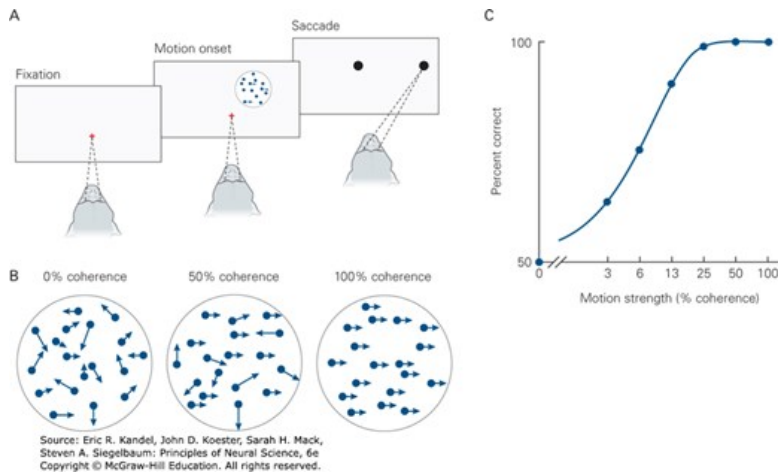
Figure 56-3

**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.



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 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.<sup>1</sup>

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.

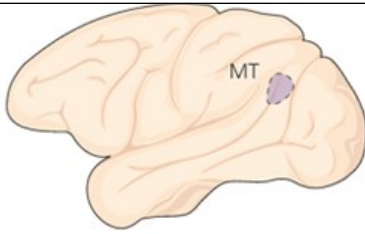
Figure 56–4

### Neurons in area MT provide noisy evidence bearing on the direction of motion.

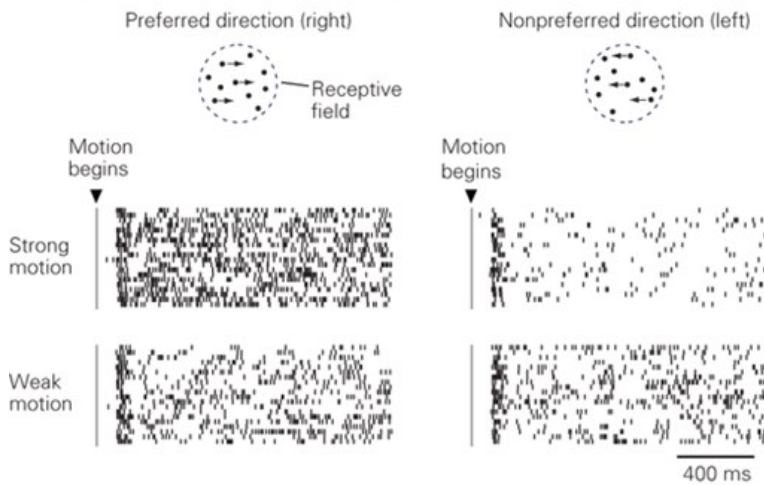
**A.** Responses from a right-preferring neuron during the discrimination task. The random dot movie is in the receptive field of the neuron. The panels in the left column of the  $2 \times 2$  panel display show the neuron's responses to motion in its preferred direction, and panels in the right column 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.

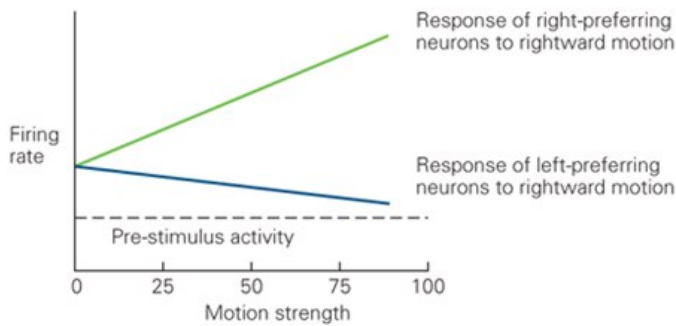
**C.** Probability distributions of the firing rates from left-preferring and right-preferring neurons to weak rightward motion. The right-preferring neuron tends to respond more, but the overlap of the distributions shows that it is possible for the left-preferring neuron to respond more than the right-preferring 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.



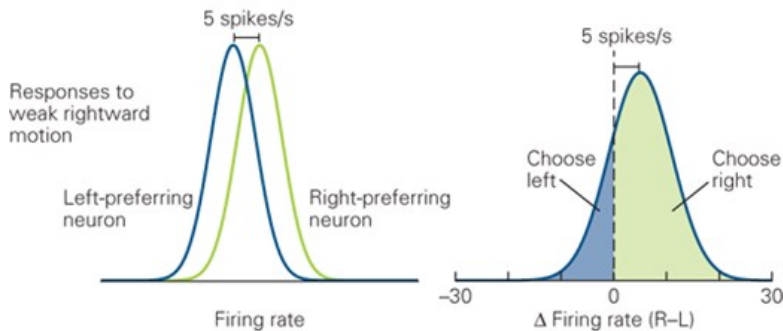
#### A Single trial responses from a right-preferring neuron



#### B Firing rate depends on motion strength and direction



#### C Noisy evidence for left and right are conceptualized as random samples from probability distributions



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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.

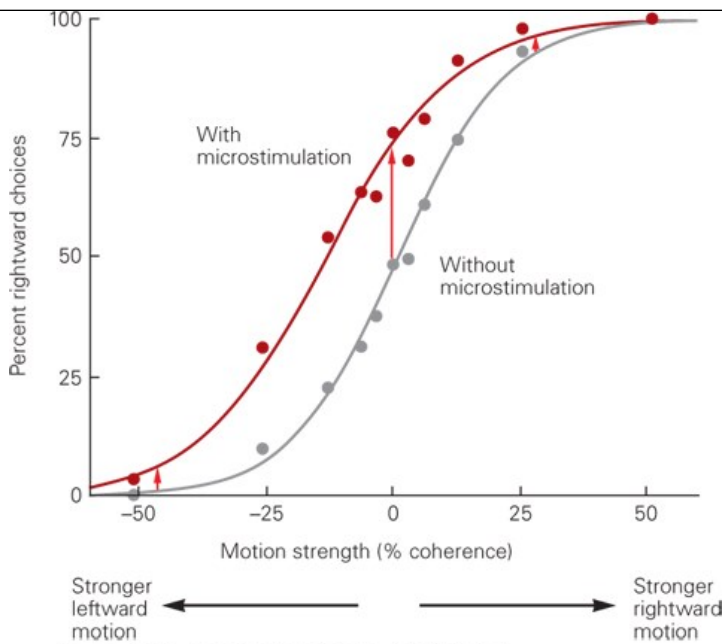
Neuroscientists have been able to use a network of small populations of neurons to model the relation between the accuracy of an animal's choice versus motion strength, known as the *psychometric function*. The success of such models gives support to the idea that the signal and noise properties of cortical 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 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](#)).

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  $\mu\text{m}$  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.)



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We now refer to such weak stimulation, designed to affect a cluster of neurons within a 50- to 100 $\mu$ 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.

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.

<sup>1</sup>The 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!

## 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.

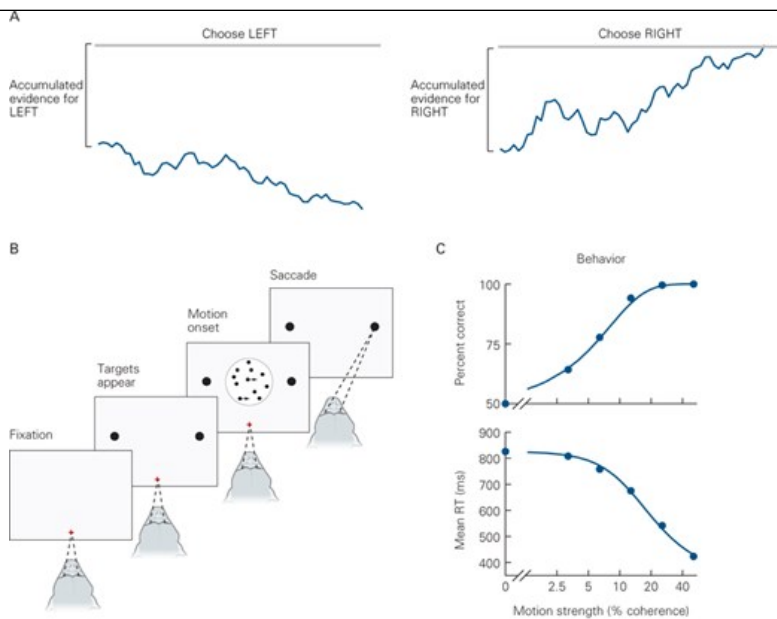
Figure 56–6

### 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.)



Source: Eric R. Kandel, John D. Koester, Sarah H. Mack, Steven A. Siegelbaum: Principles of Neural Science, 6e Copyright © McGraw-Hill Education. All rights reserved.

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).

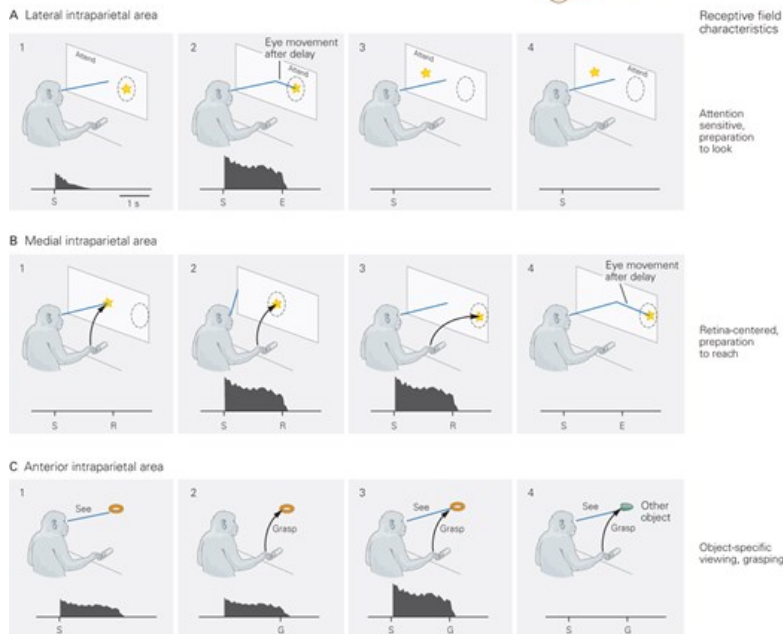
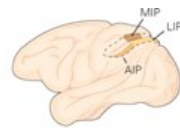
Figure 56-7

**Persistent neural activity maintains working memory, attention, and plans of action.** The monkey is asked to view a scene and respond to a visual stimulus (S) by either moving its eyes (E) or reaching (R) or grasping (G) with its hand. Each histogram represents the firing rate of a representative neuron as a function of time following presentation of the visual stimulus. The **dashed circles** show the *response fields*. This term is preferable to receptive and movement field because these neurons are neither purely sensory nor purely motor. The **blue line** shows where on the screen the monkey is asked to initially fixate its gaze.

**A.** Neurons in the lateral intraparietal area (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. Most LIP neurons are not selective for object features such as shape and color. This neuron fires when the object is presented in the neuron's response field, which lies in the circled area to the right of where the monkey is looking (1). The neuron's firing is enhanced if the object is presented while the monkey's attention is directed to this location or if the monkey is asked to plan an eye movement to the location (2). The firing can persist for several seconds after the stimulus has been removed (2), thereby providing a potential mechanism for maintaining a short-term or working memory of its location. The neuron does not fire if an object is presented outside the neuron's response field (eg, to the left) (3) even if the monkey is asked to attend to the location of the neuron's response field (4). An object must appear there even if only briefly (2).

**B.** In the medial intraparietal area (MIP), neurons fire when the monkey is preparing to reach for a visual target. This neuron starts firing shortly after the appearance of a target in the response field of the neuron, in this case, a fixed angle to the right of where the monkey is looking, whether its gaze is on the left edge (2) or the center (3) of the screen, and it continues to fire as the monkey waits to reach. The neuron does not fire when the monkey reaches for a target at the center of its gaze (1) or when the monkey plans to shift its gaze to a target in the response field, without reaching (4). The physical direction of the reach is not a factor in the neuron's firing: It is the same in 1 and 2, and yet the neuron fires only in 2.

**C.** In the anterior intraparietal area (AIP), neurons fire when the monkey is looking at or preparing to grasp an object and are selective for objects of particular shapes. This neuron fires when the monkey is viewing a ring (1) or making a memory-guided reach to it in the dark (2). It fires especially strongly when the monkey is grasping the ring under visual guidance (3). It does not fire during viewing or grasping of other objects (4).



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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.

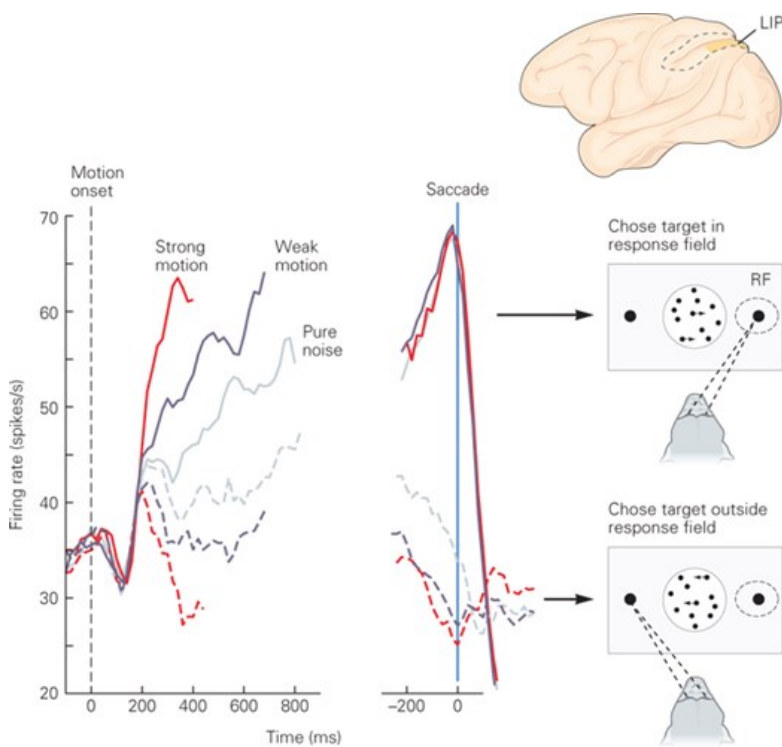
Neurons that represent the evolving decision increase their firing rates gradually as the evidence mounts for one of the choices, and they decrease gradually when the evidence favors the other option (Figure 56–8). Their firing rates, plotted as a function of time, approximate a ramp: a baseline rate 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.

Figure 56–8

**Neurons in the lateral intraparietal area (LIP) represent the accumulation of noisy evidence.** These neural recordings were obtained while a monkey performed the reaction time version of the motion task. The traces are average firing rates from 55 neurons. The neurons were of the same type shown in Figure 56–7A.

The traces show average responses to three motion strengths: strong (red), weak (purple), and zero (pure noise, gray). The **solid traces** are from trials in which the monkey chose the target in the neuron's response field (RF; right choice). The **dashed traces** are from trials in which the monkey chose the target outside the neuron's response field (left choice). For the nonzero strengths, the direction of random dot motion was the direction the monkey chose (ie, only correct choices are shown). The responses in the plot on the left, which are aligned to the start of random dot motion, exhibit a gradual buildup of activity, leading to rightward choices, and a gradual decline in activity, leading to leftward choices. The rate of this buildup and decline reflects the strength and direction of motion. The responses on the right are to the same dot motion but are now aligned to the moment the monkey makes its eye movement (**saccade**) to indicate its choice and reveal its reaction time. The responses reach a common level just before the monkey makes its choice, consistent with the idea that a threshold applied to the firing rate establishes the termination of these trials. The responses do not reach a common level before leftward choices because these decisions were terminated when a separate population of neurons, with the left choice target in their response fields, reached a threshold firing rate. (Adapted, with permission, from Roitman and Shadlen 2002. Copyright © 2002 Society for Neuroscience.)



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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 expectations derived from sources such as personal experience, books, friends, and spreadsheets. Some are based on internal (subjective) valuation or preference. Many involve reasoning from sources of evidence that may differ in reliability and that must be weighed against costs and benefits. To what extent do the neural mechanisms of perceptual decision-making apply to these other types of decisions?

Imagine the following scenario. As you leave your home in the morning, you realize that you will be outdoors from 4 to 5 pm and must decide whether to carry an umbrella. To make this interesting, assume this occurred before the age of the internet and accurate satellite weather prediction. You must decide based on yesterday's forecast of "possible chance of rain", the clear appearance of the sky at 7:00 am, a small drop in the barometric pressure compared to 1 hour before, and the observation that among a dozen pedestrians visible from your window only one seems to be carrying an umbrella. Let us assume further that you have experience with such decisions and have some sense of how reliable these indicators are. Finally, the cumbersomeness of carrying the umbrella is such that your decision boils down to a reasoned assessment of whether rain is more likely than not.

The right way to make this decision is to consider each of the indicators and ask how likely they would be if rain does or does not occur in the afternoon. These likelihoods are learned estimates of conditional probabilities, the probability of observing the indicator when it rains in the afternoon, and the probability of the same observation when it does not rain. For example, suppose through experience you have learned that the forecast, chance of rain, implies a 1 in 4 chance of rain. Then, the conditional probabilities are 1 in 4 and 3 in 4 that it will or will not rain, respectively, given the weather report. The ratio of these two probabilities is termed the likelihood ratio (LR), which is 1 in 3 in this case. If the LR is greater than 1, it

favors rain, and if the LR is less than 1, it favors no rain. There is an LR for each of the four indicators. If the product of the four LRs is greater than 1, then you should carry the umbrella.

For reasons that will be clear in a moment, it is useful take logarithms of LRs, termed the log-likelihood ratio (logLR). This provides a more natural scale for belief, and it allows us to replace multiplication with addition [recall that  $\log(xy) = \log(x) + \log(y)$ ]. To appreciate the scale, assume that the one passerby with an umbrella would be equally likely to carry the umbrella whether or not rain is a prospect. Both probabilities are 1 in 2. The LR is therefore 1, and the  $\log(1) = 0$ , which corresponds to the intuition that this observation is uninformative. LRs greater than 1 have positive logarithms, and LRs less than 1 have negative logarithms, consistent with the way they bear on the prediction of rain.

Monkeys can be trained to perform a version of this weather prediction task. In the experiment depicted in [Figure 56–9](#), a monkey had to decide whether to look at a red or a green target, only one of which would lead to a reward. Before committing to red or green, the monkey was shown four shapes. Each served as an indicator about the location of the reward. The monkey had learned to associate predictive value with a total of 10 shapes, half of which favored reward at red, the other half at green. The shapes also differed in the reliability with which they predicted the reward location. The monkey learned to rely on these shapes rationally, making its decisions by combining evidence from each shape and by giving the more informative shapes more leverage on the choices.

Figure 56–9

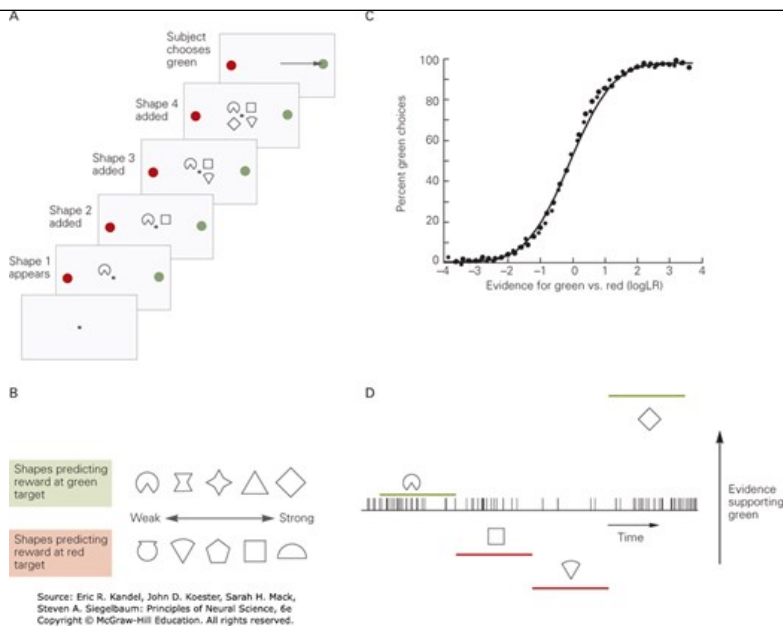
### Evidence accumulation underlies probabilistic reasoning from evidentiary symbols.

**A.** A monkey was trained to make decisions based on a sequence of four shapes, drawn randomly with replacement from a set of 10. The shapes were added to the display sequentially every one-half second.

**B.** Each shape provides a different amount of evidence that a reward is associated with a red or green choice target. Some, like the diamond and semicircle, are highly reliable predictors that a reward will occur if the choice is for green or red, respectively. Others are less reliable predictors. The degree of reliability is quantified by the likelihood ratio or its logarithm. A good decision-maker should base the decision on the product of the likelihood ratios or the sum of their logarithms (**logLR**).

**C.** The monkey's decisions were guided by the probabilistic evidence from the four shapes. On trials in which the sum of the logLR from the four shapes strongly favored green, the monkey almost always chose green. When the sum was closer to 0, the monkey had to base its decision on weak evidence and chose less consistently. The pattern of choices demonstrates that the monkey assigned greater weight to the shapes that were more reliable (strong versus weak).

**D.** The same types of parietal neurons studied in the perceptual decision-making task represent the running sum of evidence bearing on the choice target in its response field. The spikes are shown from a single decision when the green target was in the neuron's response field. The **horizontal black line** below the spikes marks the neutral level of evidence for green versus red, such that the two choice targets are equally likely to be rewarded. The vertical position of the green or red lines associated with each successive presentation of an indicated shape show the cumulative evidence conferred by the shapes that the reward was at the green target. The first shape was weak evidence for green. The second and third shapes supplied mounting evidence against green (for red). Note the reduction in firing rate. The final shape provided strong evidence for green, such that the cumulative evidence from all the shapes favored green. Note the increase in firing rate. It is an example of a single neuron in the association cortex using persistent activity to compute quantities useful for decision-making. Based on the firing rates from many trials, it was shown that neurons encode the cumulative sum of the logarithm of the probability ratios—the logLR that a reward is associated with the choice target in the neuron's response field. (Adapted, with permission, from Yang and Shadlen 2007.)



While the monkeys made their decisions, neural activity was recorded from the same parietal area studied in the motion task. As before, the neurons responded in a way that revealed the formation of the decision for or against the choice target in their response field. When the red target was in the response field, the neuron assigned positive values to the red-favoring shapes and negative values to the green-favoring shapes. When the green target was in the response field, the signs were reversed. As shown in the example, 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. In fact, the increment (or decrement) was proportional to the logLR assigned by the experimenter to the shape! The brain simply adds these logLRs to form a decision. And 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. The LIP neurons do the same thing they did in the motion decision. They produce firing rates that represent the cumulative sum of noisy increments and decrements.

By adding in units of logLR, the brain achieves reasoning from probabilistic cues in the way a statistician or actuary combines evidence from multiple sources. The experiment demonstrates that the mechanism used for perceptual decision-making is also at play in more complicated decisions that involve reasoning from more abstract sources of evidence. It speaks to the broader theme of this chapter: The study of decision-making offers insight into how the brain achieves a variety of cognitive functions.

## Decisions About Preference Use Evidence About Value

Many, if not most, decisions made by humans and animals are expressions of preference, based on an assignment of value. In some instances, the value is innate. For example, most animals experience sweet as positive and bitter as negative (Chapter 29). In the vast majority of instances, however, value is learned through experience, or it is derived from reasoning based on other preferences. Unlike a decision about the direction of motion, a medical diagnosis, or the weather, a decision about which of a pair of items one prefers is not objectively right or wrong. It can only be said to be consistent or inconsistent with one's expression of value. In fact, our knowledge of a subject's valuation of an object may only be revealed to us by observing her choices.

Yet despite the qualitative difference between subjective and objective evidence, there are parallels between the neural mechanisms that support perceptual and value-based decisions. Decision-makers take more time to choose between items of similar value than items that differ substantially in value, and their choices are less consistent. In a typical experiment, the participant is asked to indicate the value of each item that they will later make choices about. For example, they might be asked how much they are willing to pay or they are asked to indicate a rating from highly undesirable through neutral to highly desirable. This procedure is typically repeated to provide a subjective value for each item to be used in the experiment.

The participant is then asked to decide between pairs of items. The difference in the subjective values communicated before the experiment provides an index of the difficulty of the decision between the items. It is analogous to motion coherence. A similar approach works with animals. For example, a monkey might demonstrate a preference for grape juice over apple juice, and then be asked to choose between a small volume of grape juice versus a large volume of apple juice. The decision is rendered more difficult by titrating the ratio of volumes to values that lead the monkey to choose either

juice with equal tendency.

Two types of neurons associated with this type of value encoding have been identified. The first, typically located in the striatum, encodes the value associated with an action. The second, primarily in the orbitofrontal and cingulate cortex, appears to encode the value associated with specific items. Decisions about preference seem to arise from the same strategy that governs perceptual decisions. Just as a decision between left and right motion is guided by the difference in firing rates of left- and right-preferring sensory neurons, a decision between two items is based on the difference in activity of neurons encoding the values of each item. These neural representations are noisy, and this feature might explain why a decision-maker may make choices that are inconsistent with their values. It might also explain why decisions between items of similar value tend to take more time—a speed–consistency trade-off similar to the speed–accuracy trade-off discussed above.

The analogy to perceptual decision-making is appealing, but it misses the more interesting aspects of value-based decisions. As mentioned above, the value of most items is not given by biology but instead is learned. Further, there is no reason to assume that such value is monovalent. One may value an item differently, based on different qualities and considerations, and one or more of those qualities may dominate under different circumstances. Accordingly, the value of an item could appear to change simply by the occasion of its comparison to another item, which might invite emphasis on a more or less desirable aspect. Novelty, familiarity, and the value of exploration itself might also play a role in modifying a subjective valuation.

These considerations might contribute to the “noisy” representation of value that is thought to explain inconsistencies and long decision times in preference choices. This type of noise belies processes that are far more complex than variability in random dot displays and the noisy spike rates of neurons. Such evaluative processes are likely to involve prospection and memory retrieval, which are only beginning to be understood at the neural level ([Chapter 52](#)). In the end, these processes must furnish samples of evidence bearing on the relative value of the items, and this evidence is either accumulated or evaluated individually against a criterion to halt the process with a decision.

## Decision-Making Offers a Framework for Understanding Thought Processes, States of Knowing, and States of Awareness

States of knowledge have persistence. Even if they concern information derived from the senses, the knowledge of sensation generally outlasts the sensory activity itself. In this way, the state of knowledge resembles a perceptual decision—a commitment to a proposition about the object, based on sensory evidence. As we have seen, these states are often tied to possible behaviors rather than to the features of the sensory information. This is a position argued by many philosophers and the psychologist James J. Gibson.

This simple point can be made on empirical grounds. Persistent neural activity is not present in sensory areas of the brain unless a stimulus is unchanging and then only if the neurons do not adapt. Naturally, sensory neurons must change their response when the environment changes or the observer moves in the environment, whereas knowledge states persist through sensory changes and without a continuous stream of input. Indeed, persistent activity is apparent in areas of the brain that associate sources of information—from the senses and from memory—with circuits that organize behavior.

In the prefrontal cortex, persistent states represent plans of action, abstract rules, and strategies. In the parietal and temporal lobes, neural representations have the dual character of knowledge and the behavior that knowledge bears upon, such as making an eye movement or reaching, eating, or avoiding. The responses can resemble a spatial representation, as they do in area LIP, if the target of the projection is the eye movement system, but that is only because there is correspondence between space and action. A useful guide is to consider the source and target of the association. If the source is the visual cortex and the targets are premotor areas that control hand posture (eg, grip), as they do in the anterior intraparietal area ([Figure 56–7C](#)), the association area might convey knowledge about curvature, distance, convexity, and texture. One might be inclined to use terms borrowed from geometry to catalogue such knowledge, but it may be simpler to think about the repertory of hand shapes available to the organism. Importantly, the neurons in association cortex do not command an immediate action. They represent the possibility of acting in a certain way—an intention or provisional affordance ([Box 56–1](#)).

### Box 56–1 Affordances, Perception, and Knowledge

James J. Gibson, known for his ecological theory of perception, referred to *affordances* as properties of objects and the environment. The term comes from the verb *afford*. An object affords possible behaviors, such as lifting, grabbing, filling, hiding in, drawing/writing upon (eg, parchment) or with (eg, a brush), or walking upon. The affordance refers to the potential behaviors of the animal. The same object, say a stone, could afford grasping, dropping, breaking (ie, used as a tool), throwing (as a missile weapon), or pinning (as a paperweight).

Gibson was widely criticized for claiming that perceptual processes picked up these affordances directly from the optical array, what he termed “direct perception.” The term is commonly misunderstood as antithetical to computational accounts of information processing. By “direct perception,” Gibson did not mean that there were no computations on the data received through the senses. He promoted the mathematical understanding of these operations. He meant that we do not perceive the intermediates.

We do perceive the parts of objects that are accidentally occluded by something in our line of sight, and we perceive the back of an opaque object that is occluded by its front. We do not perceive the outlines, the line art, and many other details, but that is not to say that they do not register on the retina and the visual cortex. Gibson held that representation of visual information is not a sufficient condition for perception. From the perspective of the neuroscience of decision-making, one might place emphasis on the representation of potential behavior—something like a provisional commitment to a plan.

Affordance still refers to a category of actions, but it is about the organization of the action (eg, throwing) or strategy, and also—but not necessarily—a quality of the object. The modifier, “provisional,” emphasizes that the action may not actually ensue now or ever. This modifier would have been superfluous in Gibson’s use of the term *affordance*, because an affordance was a property of the object (in his ecological framework) and therefore had a permanence independent of the perceiver.

Let us defer for the moment the aspect of the knowledge state that includes conscious awareness and consider the simpler sense of knowledge as a state of possible utilization. Such preconscious ideation is probably the dominant state in which an animal interacts with the environment. It is arguably also the lion’s share of human experience, although because we are not conscious of it, we underestimate its dominance. Two important insights emerge from this perspective. The first is that the correspondence between knowledge and neuronal activity lies at a level of brain organization between sensation and behavior. Although the flow of information from sensory epithelia (eg, the retina) through the primary cortical sensory areas is essential for perception, knowledge resulting from activity in higher brain regions has temporal flexibility and persistence not seen in lower brain regions—what the philosopher Maurice Merleau-Ponty termed the *temporal thickness of the present*.

The second insight is that the computation leading to a knowledge state has the structure of a decision—a provisional commitment to something approximating a possible selection from a submenu of the behavioral repertory. We might say that the parietal association neurons interrogate the sensory areas for evidence bearing on the possibility of a behavior: look there, reach there, posture the hand this way to grasp. Of course, neurons do not ask questions. Nevertheless, we can think of the circuits as if they scan the world looking for evidence bearing on a possible behavior. The type of information they can access is limited by functional and anatomical connectivity. The type of question is framed by the target of the projection, such as regions that control gaze, reaching, and grasping.

Sir Arthur Conan Doyle endowed Sherlock Holmes with the insight that the key to discovery was knowing where to look and what to look for. We acquire knowledge by controlling the brain’s interrogation system. Some interrogations are automatic, whereas others are learned. An example of the former is a sudden change of brightness of an object in the visual field; it provides evidence bearing on the possibility of orienting the eyes or body toward it. An example of the latter draws on learning and foraging; we learn, through play and social interaction (eg, school), how to look for hidden items and how to explore in a goal-directed way.

The beautiful thing about this construction is that an answer to the question confers a kind of meaning. Even for such a mundane question like “Might I look there?” an affirmative answer—a decision to (possibly) look at an as yet undefined object in the periphery of one’s visual field—confers a spatial knowledge about the item. Before we have looked directly at it to identify what it is, we know about its *thereness*. From the perspective of decision-making, the location of an object is not perceived because there is a neural activity in a map of the visual field. Rather, the location is perceived because some aspect of the visual field—a fleck of contrast, change in brightness, appearance or disappearance—answered the question above in the affirmative.

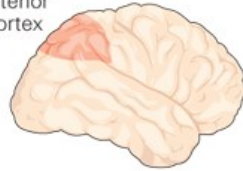
This way of thinking helps us understand the disease states known by the term *agnosia*, from the Greek word meaning “absence of knowledge.” The classic example is visual hemineglect, which is caused by damage to the parietal lobe ([Chapter 59](#)). A patient with a right parietal lesion will ignore the left side of the visual field and also the left side of objects even when the entire object is in the right visual field ([Figure 56–10](#); see also [Figure 59–1](#)). Unlike the left side blindness, called homonymous hemianopsia (or hemibland), which accompanies damage to the right visual cortex (homonymous because it is the same regardless of which eye is used), the patient with a parietal lesion does not complain of an inability to see. She is unaware of the deficit, so much so that crossing a street is a major hazard.

**Figure 56–10**

**Damage to the parietal or temporal cortices results in agnosia, or deficits in knowing.** After damage to the right parietal lobe, many patients are unaware of the left side of space or the left part of objects. The drawings on the right were made by patients with unilateral visual neglect following lesion of the right posterior parietal cortex. Agnosias can also be induced in healthy individuals by diverting attention (see [Figure 25–8](#)). (Reproduced, with permission, from Bloom F, Lazerson A. 1988. *Brain, Mind and Behavior*, 2nd ed., p. 300. New York: Freeman.)



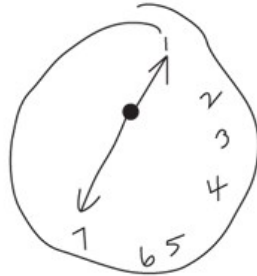
Right posterior parietal cortex



Model



Patient's copy



Source: Eric R. Kandel, John D. Koester, Sarah H. Mack, Steven A. Siegelbaum: Principles of Neural Science, 6e Copyright © McGraw-Hill Education. All rights reserved.

A hemibland patient with damage to the right visual cortex still expects to interrogate and receive information from the left visual field. When that patient receives no visual information, he knows to turn to face parallel to the street, thereby placing its contents in the intact right hemifield. In contrast, the patient with hemineglect does not interrogate the left hemifield in the first place. She does not perceive a lack of visual information because the apparatus to conduct the interrogation is not working. Like most deficits, there is enough redundancy in the brain (or the damage partial) that some visual capacities are present. In fact, when confronted with a single spot of light on a dark background, the same patient may report its presence accurately even in the affected hemifield.

There are other versions of hemineglect that involve an absence of knowledge of the body. For example, a patient with a right parietal injury may deny that her left arm is hers. She may recognize it as an arm but deny that it is hers. When asked whose arm it is, she may express ignorance bordering on disinterest (personal experience). The syndrome is usually associated with some visual neglect as well and some weakness on the same side of the body suggestive of a more rostral and superior localization. Consider that the body's position is known to us partly through the somatosensory system, partly through the predicted consequences of our motor command, and partly through vision. The arm in particular is a common feature of our lower visual field. Indeed, we are accustomed to ignoring it.

These examples are the most common of the agnosias (which are thankfully rare). Other well-known examples involve problems in face recognition (prosopagnosia) and the perception of color (achromatopsia), both associated with lesions of the temporal lobe. The different types of agnosia have loose correspondence to the anatomical specializations we learned about in [Chapter 24](#). In particular, the ventral extension of the central visual pathways into the temporal lobe is referred to as the “what” pathway, which contains circuits that are specialized for processing faces, objects, color, and semantic memory. The dorsal extension, which has been termed the “where” or “how” pathway, seems concerned with representations supporting localization.

An alternative formulation would characterize these streams in terms of associations with behaviorally relevant targets. For the dorsal stream, those are parietal areas with projections to motor systems that reach, look, or grasp. For the ventral stream, those are temporal lobe areas with projections to structures that guide foraging decisions to eat, avoid, hide, approach, mate, and communicate. The last few behaviors are social affordances conferred by color and facial identity/expression. With a small stretch of imagination, the organization of social affordances links to other functions of the temporal lobe (and temporal parietal junction) in humans. For example, these regions are associated with language comprehension and inference about what someone else is thinking. The former is associated with a devastating agnosia, known as Wernicke aphasia ([Chapters 1 and 55](#)); the latter is known as theory of mind and will be discussed below.

From the perspective of decision-making, perceiving, believing, and thinking have the character of a provisional commitment to a proposition. Brain states that correspond to a sense of knowing, be it perceiving or believing, share two important aspects with decision-making: an extended temporal profile that withstands changes in the sensory and motor streams (ie, a freedom from immediacy) and a propositional character captured by the term “affordance.” Knowing is not solely about the information but is like the outcome of a decision to embrace a proposition: Might I do something, enact something, approach someone, or retain the possibility of trying the option I am not choosing now?

Two caveats deserve mention. This framework does not replace a computational account of information processing, nor does it explain the neural mechanisms that support these computations. It mainly tells us about the level of brain organization that carries out these operations. For example, consider the search for the neurons that achieve knowledge about the color red, despite changes in the spectral content of the morning and evening light—a phenomenon known as *color constancy*. Instead of searching in sensory areas for neurons that respond selectively to red in this invariant way, one might look for neurons that guide the choice of ripe fruit. This does not obviate the computations required to recover the surface reflectance properties of the fruit’s skin, despite variation in the spectral content of the illuminating light. The raw data for such computations are supplied by sensory neurons that lack color constancy and maintain temporal fidelity with changes in the environment. The knowledge state “red,” however, is invariant to the illuminant and likely persistent. In animals that lack language, the knowledge state may not be dissociable from “ripe vegetation.”

The second caveat is that we have not distinguished knowledge states that we are consciously aware of from those that we experience unconsciously. For example, as I make my way through the forest trying to find the creek that I hear burbling, my brain might consider locations of objects I pass that are graspable, attached to vegetation, and with color suggesting ripeness. I may be unaware of this consciously. Yet that evening in my search for food, I may return to this part of the forest, guided by these unconscious encounters. I may do this without knowing why, or the memory might pierce consciousness. All that has been said up to now could apply to conscious and unconscious experience. We are now prepared to elucidate the difference.

## Consciousness Can be Understood Through the Lens of Decision Making

Clearly, we are unaware of most of the operations that transpire in our brains, and this is true even for the processes that ultimately pierce consciousness. This is why Freud famously quipped that consciousness is overrated. Every thought that enters our awareness began as neural computation preceding the conscious awareness of that thought. Indeed, the sophistication of nonconscious mental processes, including those leading to “I’ve got it!” moments and the activities we perform while occupied by a phone call, involves decisions that transpire without conscious awareness.

It is difficult to study nonconscious processing because people deny experience of the process. Indeed, the term nonconscious experience seems like an oxymoron. The experimenter must find a way to prove that information processing has occurred despite the fact that the subject is unaware of it. In recent years, it has become possible to establish conditions whereby information is provided to a human subject that has a high likelihood of going unnoticed but is nonetheless able to influence behavior, thereby permitting scientific characterization of nonconscious mental processing ([Chapter 59](#)). This has encouraged neuroscientists to ask what it is about the neural activity that gives rise to the thoughts, perceptions, and movements that do reach conscious awareness. We will not review this vast topic here but instead share a pertinent insight: Viewed through the lens of decision-making,

the problem of consciousness may be simpler than imagined.

Broadly speaking, two sets of phenomena fall under the heading consciousness. The first concerns levels of arousal. One is not conscious when one is asleep, under general anesthesia, comatose, or having a generalized seizure. One is fully conscious when awake, and there are levels of consciousness between these extremes. These states are associated with terms such as confusion, dissociation, stupor, and obtundation. Some alterations of consciousness are normal (eg, sleep), whereas others are induced by toxins (eg, [alcohol](#)), metabolic disturbances (eg, hypoglycemia), low [oxygen](#), trauma (eg, concussion), or fever (eg, delirium).

The neuroscience underlying these states—and the transitions between them—is immensely important to medicine. We might classify this group of phenomena as neurology-consciousness. However, these topics are not what most people mean when they speak of the mystery of consciousness. This is partly because they are less mysterious but also because their characterization is more objective and the phenomena can be studied in animals. That said, there is much to be learned about the mechanisms responsible for sleep, awakening, anesthesia, and so forth. Much of the neuroscience is unfolding at a rapid pace ([Chapter 44](#)).

We will not say more about neurology-consciousness here, except to seed one useful insight. Imagine a mother and father sleeping comfortably in their bedroom as a storm ensues outdoors. There are also traffic sounds and even the occasional thunder. This scene goes on for some time, until the cry of a baby awakens the parents. This common occurrence tells us that the nonconscious brain is capable of processing sounds and deciding to become conscious. It decides, nonconsciously, that some sounds afford an opportunity for more sleep while others sound a call to nurture. This decision is similar to the perceptual decisions considered earlier in this chapter. Both involve nonconscious processing of evidence. However, the commitment to awaken and parent is a decision to engage the environment consciously. This may be a touchstone between neurology-consciousness and the more intriguing consciousness that you are experiencing as you read these words (or so the authors hope).

When neuroscientists, psychologists, and philosophers ponder the mysteries of consciousness, they are referring to loftier themes than wakefulness. This loftier set of phenomena comprises awareness, imagery, volition, and agency. There is a subjective component to all conscious experience. The experience of conscious perception incorporates a sense that it is me that is beholding the content. It parallels the “me” in volition. It is not that my arm moved on its own; I made it move! We used the term deliberation earlier in this chapter to describe the thought process leading to a decision. Our use of the term was metaphorical. It describes a computation and a biological mechanism, but it does not require awareness. Actual deliberation implies conscious intention. We are aware of the steps of reasoning along the way. We could report, were we asked, about the evidence we relied upon—that is, the evidence we were consciously aware of during the decision and possibly some of the evidence we used nonconsciously were it accessible from memory to include in our report. Could the difference between conscious awareness of an item and nonconscious processing of that item be a mere matter of whether the brain has decided on the possibility of reporting? Could it be this simple?

Consider the following scenario. A psychologist concludes that a study participant has seen something nonconsciously because the item affected a subsequent behavior and the participant denies having seen it. Suppose the subsequent behavior involved reaching in the direction of the object. Based on what we know about decision-making, we would conclude that brain circuits like the ones discussed earlier received sufficient evidence to commit to the possibility of looking, reaching, and approaching, but there was insufficient evidence to commit to the possibility of reporting. Just as the brain entertains the possibility of looking, reaching, or grasping, it may also entertain the possibility of reporting. That is, reporting is also a *provisional affordance*.

Events afford the possibility of reporting, and this includes the nonconscious states of knowledge acquired through decision-making. Indeed, the event of having decided may be experienced consciously—the *aha* moment—by virtue of another decision to report. In the study scenario, the participant was not consciously aware of the item because her brain did not commit to a provisional report. The evidence did not satisfy a decision criterion like the termination bounds in the perceptual decision-making task considered earlier in the chapter.

This account provides a plausible explanation of the failure of the participant to report that she saw the item, but the mere entertaining of the possibility of reporting does not seem to explain the phenomenology of the perceptual experience itself, at least not at first glance. This explanation demands more careful consideration of the character of the report. Just as we attach states of spatial knowledge to configurations of the hand for reaching and grasping, we must consider the knowledge state that accompanies the affordance of reporting. Whether by language or gesture (eg, pointing), the report is a provisional communication with another agent or oneself (eg, in the future). It presumes knowledge about the mind of the receiver.

Cognitive scientists use the term *theory of mind* to refer to this type of knowledge or mental capacity. It can be demonstrated by asking someone to

reason about the motivation behind another agent's actions, and it can be studied in animals and preverbal children by examining their reactions to another child or puppet. In one study protocol, two children witness a desired toy placed in a left or right container (Figure 62–2). The test child then witnesses the toy's displacement to the other container while the other child is absent. When that child returns, the experimenter assesses the test child's expectation of which container the returning child will open to find the toy. Children under 3 years old do not exhibit theory of mind by this assay. They think the returning child will open the container that contains the toy, not the one it was in before the transfer. Whether animals other than humans have theory of mind is controversial. We suspect there are inchoate forms of this capacity in the animal kingdom and in children under 3. When adults perform tasks that depend on theory of mind, the right temporal-parietal junction and superior temporal sulcus are active.

Theory of mind—in concert with narrative—has profound consequences for the knowledge state associated with the reporting affordance. Imagine a woman looking at a power drill resting on a table. She experiences the location of the drill, relative to her eyes and hand, as well as its texture and shape. It has a graspable surface that is partly in her line of sight and partly occluded (eg, the back). These are the knowledge states that arise through provisional commitments to look at, reach for, and grasp the drill. They are likely to involve neural activity similar to what is illustrated in Figure 56–7, and they are the outcome of simple decisions. The drill brings to mind other affordances associated with its utility as a tool, its potential to make noise, and the potential danger posed by the sharp bit at one end. This is an elaborate, potentially rich collection of knowledge, but it could all be experienced nonconsciously. For example, if the woman were preoccupied with some other task, such as a phone conversation with her friend, she might nonetheless make use of these knowledge states.

But suppose there is a man on the other side of the table and suppose the woman—her brain, that is—has also reached a provisional commitment to report to the man about the drill between them. Consider the change to her knowledge state. The drill now has a presence not only in her visual field, relative to her gaze, her hand, and her repertory of actions, but also in the man's field of vision and his possible actions. The parts of the drill that are not in plain sight to her are known to be in the line of sight of the man. Indeed, her capacity for “theory of mind” also supplies knowledge that other parts of the drill are seen only by her and that the man could be experiencing those parts just as she experiences the parts that are not in her direct line of sight—that is, both preconsciously as occluded parts of the object and consciously as part of an object that could be seen directly from another vantage point. There is something about the drill that is at once private, public, and in the world—independent of either mind. The drill is there for the next person who enters the room, or an imagined person. The transformation of knowledge of the drill is from a collection of first-person experiences (eg, qualities and affordances) to a thing in the world that possesses an existence unto itself. It is conceivable that this state of knowledge is our conscious awareness of the world, or at least a part of it, for the knowledge state associated with a decision to report is further enriched by content of the report itself.

The report might be simple, like pointing to the location of a tool or a hiding spot, or it might involve narrative. In the case of the hiding spot, additional content might be conveyed to indicate that the enclosure affords safety from a predator or, alternatively, a predator's location. Many simple reports do not require narrative because items such as tools and enclosures persist and theory of mind presumes the affordance of a tool or a hiding place in another's mind, whereas events, which also afford the possibility of reporting, often require narrative because they are transient.

The knowledge state associated with narrative can incorporate history, simulation, prediction, etiology (eg, origin stories), purpose, and consequence. For the drill, narrative might enhance the knowledge state to include memory of the place of purchase, an episode in which it malfunctioned, and the mechanism of its detachable bit. Narrative allows us to reason in more complex environments than the scenarios considered earlier (eg, the umbrella example and the probabilistic reasoning task; Figure 56–9). We could not reason about science, medical diagnosis, and jurisprudence without origin stories, simulation, hypotheses, prospection, and counterfactuals. The evolutionary advantage of this capacity is obvious (at least for the time being, until it leads us to make the earth uninhabitable).

To summarize, the conscious awareness of an item might arise when the nonconscious brain reaches a decision to report the item to another mind. The intention is provisional in that no overt report—verbal or gesture—need occur, just as no eye movement need ensue for the parietal cortex to engage the possible intention of foveating. Just as the provisional intention to foveate corresponds to preconsciously knowledge of the location of an as yet unidentified object in the periphery, the possibility of reporting to another agent (or self), about whom we have theory of mind, corresponds to the knowledge of an item in a way that satisfies most aspects of conscious awareness.

Naturally, our journey from perceptual decision-making through affordances to consciousness is at best incomplete. For example, it does not yet provide a satisfying account of what a conscious experience feels like. But it is a start, as it supplies a coarse explanation of why sensory information acquired through the eyes is experienced differently from auditory or somatosensory experiences, and it provides insight into the private aspects of perceptual awareness as well as our experience of objects as things in the world, independent of what they afford to the perceiver. These last features

follow from the consideration of another agent's mind.

The view of consciousness from the perspective of decision-making is, if nothing else, simplifying. There is no reason to search for a special area of the brain that bestows consciousness, or a special neuron type, or a special ingredient in the representation of information (eg, an oscillation or synchronization), or a special mechanism. The mechanism might look like any other kind of provisional commitment—that is, a decision that confers a state of knowing but does not entail conscious awareness. Of course, brain activity itself is not conscious, just as the brain activity supporting a possible hand posture is not the hand posture itself. In this sense, the mechanism of consciousness is only different from other affordances because it involves reporting instead of reaching, looking toward, eating, drinking, hiding from, walking through, and mating. All are likely to involve decision formation and threshold detection.

Thus, by studying the neuroscience of decision-making, we are also studying the neuroscience of consciousness. There is still much to be learned about the mechanisms of the simplest decisions described in the first part of the chapter. For example, we do not know what sets the bounds and how thresholds are implemented in brain circuits. Nevertheless, answers to these and other fundamental questions are in the crosshairs of modern neuroscience, and therefore, so is human consciousness.

## Highlights

1. A decision is a commitment to a proposition, action, or plan—among options—based on evidence, prior knowledge, and expected outcomes. The commitment does not necessitate immediate action or any behavior, and it may be modified.
2. Decision-making provides a window on the neuroscience of cognition. It models contingent behavior and mental operations that are free from the immediate demands of sensory processing and control of the body's musculature.
3. A decision is formed by applying a rule to the state of evidence bearing on the alternatives. 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.
4. For certain perceptual decisions, the source of evidence and its neural representation are known.
5. The accuracy of many decisions is limited by considerations of the signal strength and its associated noise. 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.
6. 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). Neurons in the prefrontal and parietal cortex, which are capable of holding and updating their firing rates, represent the evolving decision variable. These neurons are also involved in planning, attention, and working memory.
7. The speed–accuracy trade-off is controlled by setting a bound or threshold on the amount of evidence required to terminate a decision. It is an example of a policy that makes one decision-maker different from another.
8. Many decisions are about propositions, items, or goals that differ in value to the organism. Such value-based decisions depend on stored associations between items and valence.
9. The source of evidence for many decisions is memory and active interrogation of the environment—information seeking. These operations come into play when animals forage and explore, and when a jazz musician improvises.
10. Decision-making invites us to consider knowledge not as an emergent property of neural representations but the result of directed, mostly nonconscious interrogation of evidence bearing on propositions, plans, and affordances. The intention is provisional in that no overt action need ensue. Just as the provisional intention to foveate corresponds to preconscious knowledge of the location of an as yet unidentified object in the periphery, the possibility of reporting to another agent (or self), about whom we have theory of mind, corresponds to the knowledge of an item in the ways we are aware of it consciously.
11. Viewed through the lens of decision-making, conscious awareness of an item might arise when the nonconscious brain reaches a decision to report

to another mind. The affordance has the quality of narrative, much like silent speech or the idea preceding its expression in language. It also imbues objects with a presence in the environment inhabited by other minds, hence independent of the mind of the perceiver. It confers private and public content to aspects of the object as perceived.

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