

stroke, head injury, herpes encephalitis, and degenerative processes such as Alzheimer disease, but also from functional imaging studies of typical individuals and from electrical stimulation of these same areas of temporal cortex during surgery.

Areas of frontal cortex in the mesial surface of the left hemisphere, which include the supplementary motor area and the anterior cingulate region, play an important role in the initiation and continuation of speech. Damage in these areas impairs the initiation of movement (akinesia) and causes mutism, a complete absence of speech. In aphasic patients, the complete absence of speech is a rarity and is only seen during the very early stages of the condition. Patients with akinesia and mutism fail to communicate by words, gestures, or facial expression because the drive to communicate is impaired, not because the neural machinery of expression is damaged as in aphasia.

Damage to the left subcortical gray nuclei impairs grammatical processing in both speech and comprehension. The basal ganglia are closely interconnected with the frontal and parietal cortex and may have a role in assembling morphemes into words and words into sentences, just as they serve to assemble the components of a complex movement into a smooth action.

Highlights

1. Language exists at many levels, each of which has to be mastered during childhood—the elemental phonetic units (vowels and consonants) used to change the meaning of a word, the words themselves, word endings (morphemes) that change tense and pluralization, and the grammatical rules that allow words to be strung together to create sentences with meaning. By the age of 3, young children, regardless of the language(s) they are learning, have mastered all levels and can carry on a conversation with an adult. No artificially intelligent machine can yet duplicate this feat.
2. The learning strategies used by children to master language under 1 year of age are surprising. Language learning proceeds as infants (1) exploit the statistical properties of speech (distributional frequency patterns of sounds to detect relevant phonetic units and transitional probabilities between adjacent syllables to detect likely words), and (2) exploit the social context in which language occurs by following the eye movements of adults as they refer to objects and actions to learn word-object and word-action correspondences.

At early ages, natural language learning requires a social context and social interaction. Infants' strategies are not well described by Skinnerian operant conditioning or by Chomsky's innate representation and selection based on experience. Instead, powerful implicit learning mechanisms that operate in social contexts vault infants forward from the very earliest months of life.

3. Infants' speech production and speech perception skills are "universal" at birth. In speech perception, infants discriminate all sounds used to distinguish words across all languages until the age of 6 months. By 12 months, discrimination for native-language sounds has dramatically increased, whereas discrimination of foreign-language sounds decreases. Production is initially universal as well and becomes language specific by the end of the first year. By the age of 3, infants know 1,000 words. Mastery of grammatical structure in complex sentences continues until the age of 10. Future work will advance the field by linking the detailed behavioral milestones that now exist to functional and structural brain measures to show how the brain's network for language is shaped as a function of language experience.
4. A new "dual-stream" model of language has emerged based on advances in functional neural imaging and structural brain imaging over the past decade. The new model bears similarities to the dual-stream model for the visual system. The dual-stream model for language goes beyond the classic Wernicke-Geschwind model by showing that numerous brain regions and the neural pathways that connect them support sound-to-meaning (ventral) and sound-to-articulation (dorsal) pathways. Refinement in the model will continue as additional studies show relationships between behavioral and brain measures. Future studies will integrate structural and functional brain measures, genetic measures, and behavioral assessments of language processing and of learning, including second language learning in adulthood.
5. Studies on the infant brain reveal a remarkably well-developed set of brain structures and pathways by 3 to 6 months of age. Structural DTI reveals a fully formed ventral pathway at birth and a dorsal pathway that links auditory areas to premotor, but not Broca's, area at birth. EEG and MEG brain imaging studies mirror the transition in phonetic perception between 6 and 12 months of age, a "critical period" for sound learning. MEG

brain scans at this period reveal the co-activation of auditory and motor centers when infants hear speech and show changes in both sensory and motor brain areas as a function of experience. The data indicate that dorsal pathways are sufficiently well formed in the first year to support sensory-to-motor connections and imitation learning during this period.

6. Hemispheric specialization generally increases with age and language experience, with initial representation of the areas and pathways represented bilaterally and dominance emerging with language experience. There are differences in the degree of lateralization, however, for various levels of language. The dorsal stream, which mediates auditory-motor representations of speech, is more left lateralized than the ventral stream, which mediates auditory-conceptual representations of words.
7. The classical aphasia—Broca's, Wernicke's, and conduction aphasia—are well described within the context of the dual-stream model of language. Broca's aphasia, with its emphasis on the inability to produce speech but relatively good speech understanding, is seen as a dorsal stream deficit, whereas Wernicke's aphasia, with its emphasis on speech comprehension deficits, is seen as a ventral stream deficit. Conduction aphasia, like Broca's, is viewed as caused by a dorsal stream deficit, with damage that encompasses auditory and motor regions. Future research on aphasia will benefit from additional studies of functional and structural damage that can be combined with detailed behavioral protocols.
8. Future studies will allow detailed comparisons between human and nonhuman brains to reveal the structures and pathways that are uniquely human and subserve language. Future work will also focus on the degree to which language structures in humans are selectively activated by speech as opposed to other complex auditory sounds and whether adult-level selectivity is present early in development.
9. Human language represents a unique aspect of human cognitive achievement. Understanding the brain systems that allow this cognitive feat in nearly all children, and especially the discovery of biomarkers that identify children who are at risk for developmental disorders of language, will advance brain science and be beneficial for society. Behavioral studies now allow us to connect the dots with regard to how early language

experience is linked to advanced language development by the time children enter school. This may lead to language interventions that improve outcomes for all children.

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Decision-Making and Consciousness

Perceptual Discriminations Require a Decision Rule

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

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

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

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

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

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

Decisions About Preference Use Evidence About Value

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

Consciousness Can be Understood Through the Lens of Decision Making

Highlights

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 52–54). 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.

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

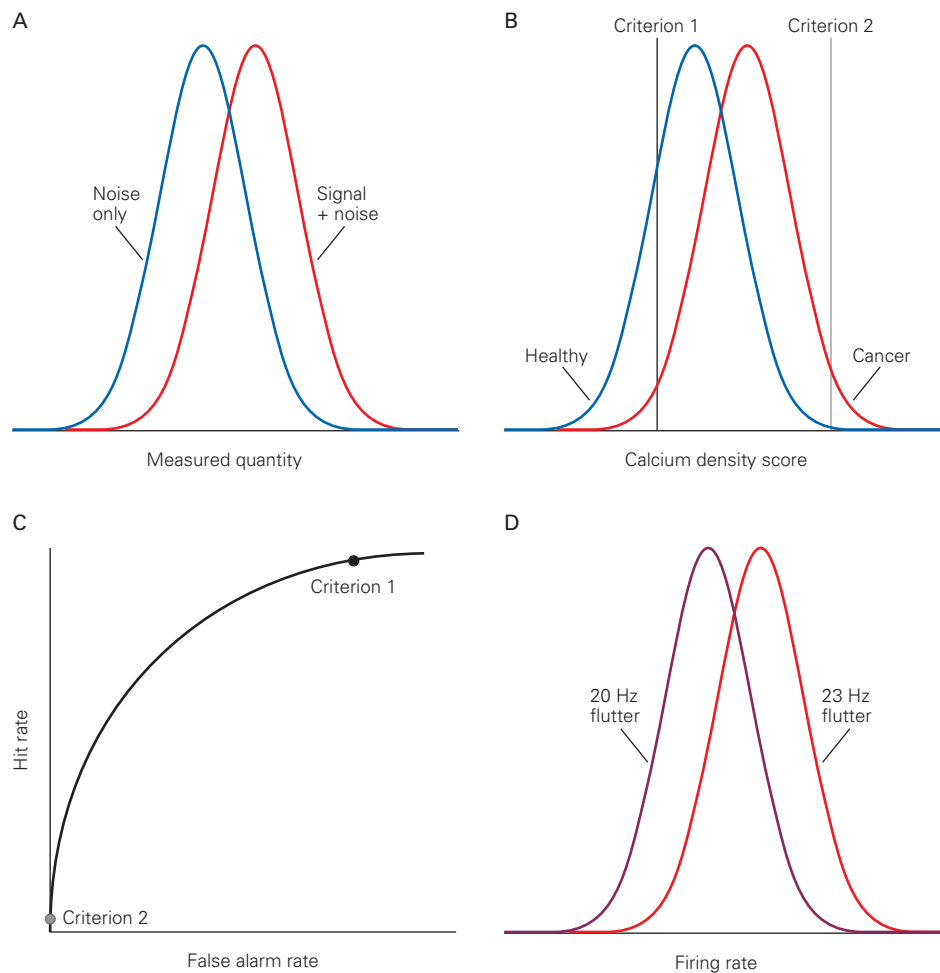


Figure 56–1 The framework of signal detection theory formalizes the relationship between evidence and decisions. In panels A through C, we consider simple yes–no decisions in which a decision-maker receives just one measurement.

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.

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

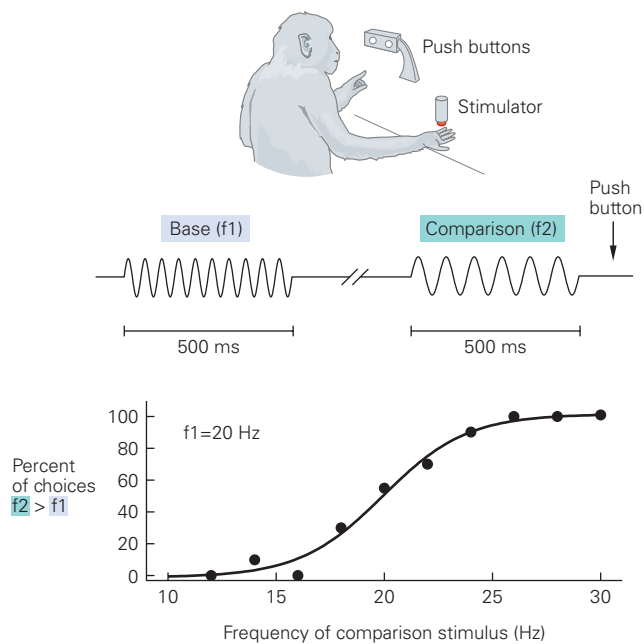


Figure 56-2 The discrimination of flutter-vibration frequency was the first perceptual decision studied in the central nervous system. A 20-Hz vibratory stimulus is applied to the finger on the right hand; following a delay period of several seconds, a second vibratory stimulus is applied. The monkey indicates whether the second vibration (f_2) was at a higher or lower frequency than that of the first stimulus (f_1) by pushing the left or right button with the other hand. The plots show that the proportion of trials in which the monkey decided that the comparison stimulus was greater than the reference depended on the magnitude and sign of the difference. With larger differences, the monkey almost always chose correctly, but when the difference was small, the choices were often incorrect. (Adapted from Romo and Salinas 2001.)

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

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

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

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

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

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