# SENSE AND THE SINGLE NEURON:
## Probing the Physiology of Perception

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### ABSTRACT

The newly defined field of cognitive neuroscience attempts to draw together the study of all brain mechanisms that underlie our mental life. Historically, the major sensory pathways have provided the most trustworthy insights into how the brain supports cognitive functions such as perception, attention, and short-term memory. The links between neural activity and perception, in particular, have been studied revealingly in recent decades. Here we review the striking progress in this area, giving particular emphasis to the kinds of neural events that underlie the perceptual judgments of conscious observers.

## INTRODUCTION

### Overview

The link between the activity of cells in the nervous system and sensory perception remains one of the most significant and puzzling problems in neuroscience. In many ways, the problem is central to the whole enterprise of neuroscience in its attempt to give a scientific account of the brain mechanisms underlying our mental life. The aim of this article is to develop, at a general level, a strategy for the investigation of some of the critical aspects of perceptual experience. Consistent with the generality of this aim, we draw examples from several sensory systems. The goal is not to review each sensory system in exhaustive detail, but to bring out themes and concepts that are common to all perception. In this

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article, we particularly stress the search for neurons with perceptually relevant signals, especially within the cerebral cortex. There are two components of the strategy that are critical. The first is the formulation of a clearly defined perceptual task at the behavioral level. This is essential in order to provide an objective and rigorous framework in which to study perceptual events and the neuronal signals that underlie them. The second is an emphasis on the signals provided by individual neurons, since these signals represent a fundamental medium of information transfer within the nervous system.

## Defining a Perceptual Task

The link between the brain and perception is illustrated most dramatically in cases of loss or disturbance of perceptual function consequent upon some form of damage to the brain. An examination of a patient might well begin by asking the person to describe their perceptual experience and probing for clues about the source of the dysfunction. Nonetheless, at the point of delineating a hypothesis about the problems of the patient, the doctor or scientific investigator will normally formulate one or more perceptual tasks for the person to carry out. For example, the patient might be asked to make judgments about the visibility or appearance of test stimuli. The process of formulating tasks and evaluating the patient's responses to them is essential for the objective identification of those aspects of perception that are impaired.

The same considerations apply when we wish to characterize experimentally how a specific part of the nervous system might be involved in perception. Although several clues may be obtained from the anatomical location, cellular components, and physiological properties of the brain region under study, the only direct approach is to examine the contribution of that brain region to the performance of a particular perceptual task.

## Investigating Single Neurons

Neurons form the fundamental units of information processing within the brain, and the action potentials they fire represent the major currency of information exchange. As we discuss below, there are several ways in which information might be embedded in the sequence of action potentials sent out by a neuron and several ways in which the combined activity from groups of neurons could be exploited for perceptual decisions. Nonetheless, understanding the capabilities of individual neurons is central to the strategy advanced here. To anticipate the material presented below, experimental data show that significant numbers of neurons perform at levels that compare favorably with the overall behavioral performance of the organism. Importantly, the value of combining information from many nerve cells can only be assessed effectively if the performance of the individual components has been carefully characterized.

## Approaches to Sensory Physiology

Sensory physiology currently uses several approaches for investigating how the nervous system processes sensory information. The conceptually simplest of these is to measure tuning curves as selected parameters of the sensory stimulus are varied. A neuron is considered to be "tuned" if the response is strongest to a particular value (or narrow range of values) of the stimulus and declines monotonically as stimulus values depart from this "preferred" value. For example, auditory nerve fibers are tuned for specific frequencies of sound (Kiang et al 1965); visual cortical neurons may be tuned for the orientation of line stimuli (Hubel & Wiesel 1962, Henry et al 1974), binocular disparity (Barlow et al 1967, Ferster 1981), and direction of visual motion (Hubel & Wiesel 1962, Dubner & Zeki 1971); and many somatosensory neurons are tuned for the temporal frequency of a vibrating stimulus (Talbot et al 1968, Mountcastle et al 1969). This approach has been invaluable in probing how the representation of sensory stimuli is altered as the information is passed from the sensory periphery through various stages within the central nervous system (CNS) (e.g. Van Essen et al 1981; Maunsell & Newsome 1987; Zeki 1974, 1993; Aitken et al 1984; Lamotte & Mountcastle 1975).

Stimulus selectivity (tuning) in a sensory neuron is essential for the effective analysis of sensory input, but the mere presence of selectivity does not by itself establish a specific role for that neuron in perception. A deeper level of sophistication is obtained by searching for neural transformations of sensory information that relate to well-characterized perceptual capacities or needs. For example, a two-dimensional map of auditory space is synthesized within the mid-brain of the barn owl by putting together information from two distinct cues about the location of auditory stimuli: The relative time of arrival of the sound source at the two ears and the relative loudness of the sound source measured by the two ears (Knudsen & Konishi 1978, Knudsen 1982). The auditory map in the mid-brain combines information from diverse cues into a representation that is directly useful for the owl's typical behavior of striking at prey. The synthesis of novel, behaviorally relevant representations provides much more compelling evidence that the component neurons are actually involved in controlling a particular behavior.

If the preceding styles of investigation lead to a clear hypothesis concerning the perceptual function of a set of neurons, a much more searching investigation can be initiated. Here, we wish to rigorously test the hypothesis that some neuron or set of neurons plays a critical role in the generation of a perceptual event. Much of the best evidence about this question comes from cases where both the perceptual behavior and the neuronal performance are pushed to their limits. This requires us to develop ideas about the nature of a sensory threshold. It is well established that if a human (or animal) observer is set a

difficult sensory judgment where the stimulus levels are close to threshold, then the observer makes different decisions with repeated presentations of identical sensory stimuli. A sensory threshold must be defined as the stimulus level that supports a certain probability of making a particular decision. Thus, at their limits, perceptual judgments are subject to statistical variation. A parallel variation occurs in the firing patterns of sensory neurons: Neurons give different responses to repeated presentations of identical stimuli. Both perceptual judgments and neural activity are probabilistic, so we need to develop some elementary statistical concepts to elucidate their relationship. The statistical concepts of the mean and the standard deviation of a population are familiar enough and can take us a long way. But, toward the end of this review, we have recourse to the statistical concept of covariation as well.

## Links Between Neurons and Perception

Our ultimate goal is to evaluate propositions about the relationship between neural activity and perception. We put forward here a list of idealized criteria that should be fulfilled if we are to claim that some neuron or set of neurons plays a critical role in the generation of a perceptual event. All these points are, in principle, open to experimental test, but for some criteria, no experimental test may be immediately available, owing to current technical limitations. To the extent that these criteria are fulfilled, we would feel increasingly certain about a proposed link between neural activity and perception.

1. The responses of the neurons and of the perceiving subject should be measured and analyzed in directly comparable ways.

2. The neurons in question should signal relevant information when the organism is carrying out the chosen perceptual task: Thus, the neurons should have discernable differences in their firing patterns in response to the different external stimuli that are presented to the observer during the task.

3. Differences in the firing patterns of some set of the candidate neurons to different external stimuli should be sufficiently reliable in a statistical sense to account for, and be reconciled with, the precision of the organism's responses.

4. Fluctuations in the firing of some set of the candidate neurons to the repeated presentation of identical external stimuli should be predictive of the observer's judgment on individual stimulus presentations.

5. Direct interference with the firing patterns of some set of the candidate neurons (e.g. by electrical or chemical stimulation) should lead to some

form of measurable change in the perceptual responses of the subject at the moment that the relevant external stimulus is delivered.

6. The firing patterns of the neurons in question should not be affected by the particular form of the motor response that the observer uses to indicate his or her percept.

7. Temporary or permanent removal of all or part of the candidate set of neurons should lead to a measurable perceptual deficit, however slight or transient in nature.

## *Schematic for Rest of the Review*

Although we draw examples from three major sensory systems in this article, the aim is not to provide a systematic account of any single system. Our main goals are to emphasize the similarities across sensory systems in the strategies for investigation, to review the progress in studying each system as it relates to the benchmarks identified above, and to identify those areas where ideas developed in one system could be transferred to other systems. Inevitably, our sampling of specific experimental papers (particularly in subject areas with which we are less familiar) is somewhat arbitrary, and we must apologize for the neglect of many excellent papers. We can only hope that progress toward our integrative goals compensates for our lack of comprehensive coverage.

## THE DETECTION OF SENSORY EVENTS BY NEURONS

### *Psychophysical Detection*

To begin, we consider some classic examples of the measurement of neuronal detection and discrimination functions. These examples have provided the historical groundwork for most subsequent developments in the field—and they can perform the same role for this review. Figure 1*A* shows the performance of a human observer detecting weak flashes of light against a completely dark background (Hecht et al 1942). The probability of correctly detecting the flash is plotted on the ordinate, and the log intensity of the flash is plotted on the abscissa. The detection probability rises sharply with flash intensity, but nonetheless there is a range of intensities over which the observer will sometimes detect or sometimes fail to detect flashes of the same intensity. This means that there is a source of variability in the observer's behavior, which may have its origins in the variability of the sensory neurons.

A cumulative probability curve is used to describe the behavioral (also called psychometric) detection function. This goes from 0% detection for the weakest
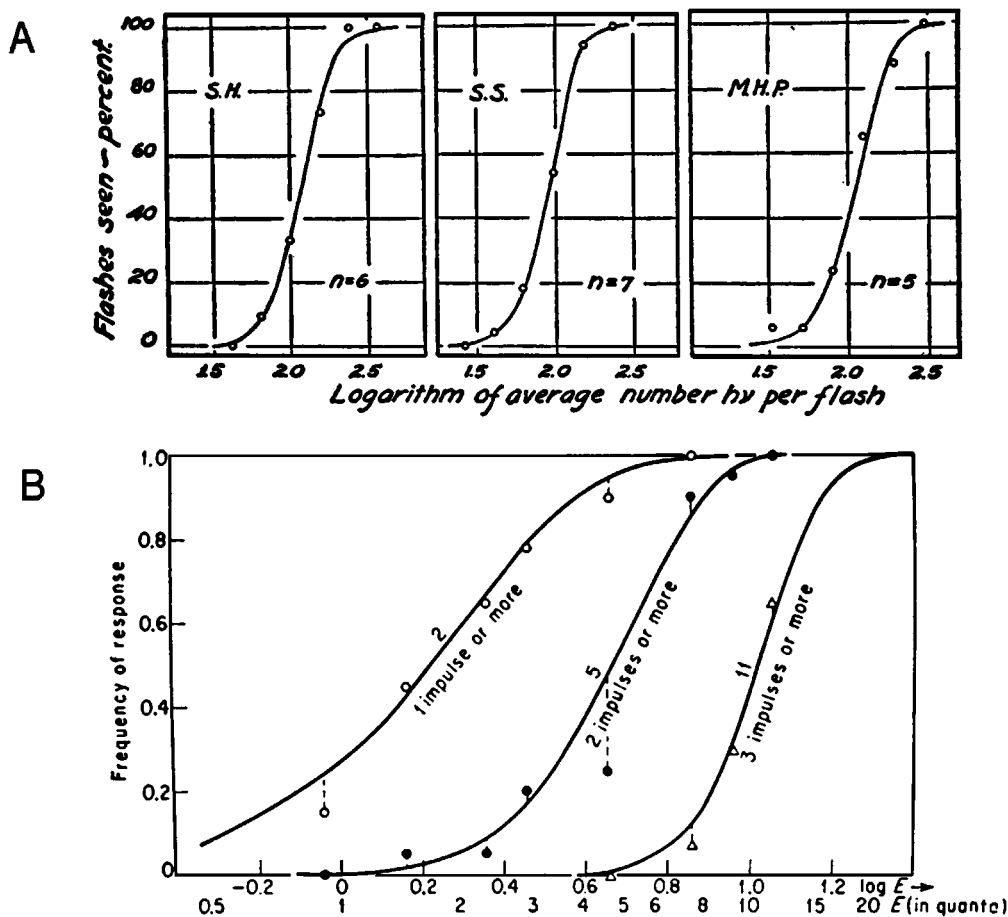
*Figure 1*    (*A*) The probability of detecting weak flashes of light by three human observers as a function of the intensity of the light [data of Hecht et al (1942)]. The flashes were designed to stimulate vision with rod photoreceptors, and each observer made 35 or 50 judgments at each intensity level. The smooth curves through the data were calculated on the (incorrect) assumption that the only source of variation in the observer's responses was the fluctuation in the number of quanta arriving at the retina. (Reproduced from *The Journal of General Physiology* by copyright permission of The Rockefeller University Press.) (*B*) The probability of detection of weak flashes of light by *Limulus* photoreceptors [data of Hartline et al (1947); see Pirenne (1967), pp. 110–18]. Each separate data set shows the probability that the neuron generated at least a certain number (1, 2, 3) of impulses on each trial that the flash was delivered. The similarity in the shapes of the neuronal and the behavioral detection functions is obvious. [From Ratliff (1962). Reproduced with permission of The McGraw-Hill Companies.]

flashes to 100% detection for the strongest flashes studied. The 50% point on this curve is the statistical mean of the cumulative probability curve and corresponds to the flash intensity at which the flashes are detected on half the trials and missed on the other half. This flash intensity is often taken as a measure of the detection threshold (although other percentage points may be chosen). A change in the detection threshold for a sensory stimulus is indicated by a shift in the position of the psychometric function along the abscissa. The slope of the psychometric function corresponds to the statistical variance of the cumulative probability curve and indicates the underlying variability in the behavior. Greater variability leads to a shallower slope. These two parameters fully describe the curves shown here. It is evident from Figure 1 that there may be interactions between the parameters, especially if a percentage value other than 50% is chosen for the threshold. For this reason, we lay greatest emphasis in this review on measurements that examine performance over the whole detection curve.

For these data, Hecht et al (1942) argued that the variability was entirely attributable to external statistical fluctuations that arise from physical variations in the actual number of quanta of light delivered in each separate weak flash. Subsequent work has also identified sources of variability in this situation that are intrinsic to the visual system. For example, Barlow (1956) hypothesized that rhodopsin molecules (the light-absorbing pigment) might isomerize spontaneously on occasion and that these events would be indistinguishable from isomerizations caused by flashes of light. This hypothesis has since received dramatic confirmation from direct electrophysiological studies (Barlow et al 1971, Lamb 1980). More generally then, noise or variability could be due to (*a*) the nature of the external stimulus, (*b*) factors at the sensory periphery, or (*c*) factors deeper within the CNS. Whatever its source, the variability shows up as variability within the psychometric detection function.

## *Visual Detection in* Limulus

A major issue in comparing neural responses to the psychometric detection function is how to devise a measure of the neural response that can be fairly compared with the probabilistic measures of behavior delivered by the psychometric function. Since neural responses are themselves variable, it is necessary to use a method that takes careful account of this variability. The first attempt to do this was modeled closely on the design of Hecht et al (1942): Hartline et al (1947) recorded from an isolated optic nerve fiber leaving the lateral eye of the horseshoe crab *Limulus* (see Pirenne 1967, pp. 110–18, for a detailed analysis of these data). They counted the number of action potentials fired by the neuron on many separate presentations as a function of different intensities of the flash of light. Then they constructed a function that relates the probability of neural

firing to the intensity of the flash. In order to decide whether the neuron had signaled the presence of the stimulus on any single trial, they required that the neuron fire $N$ action potentials on that trial, where $N$ is greater than or equal to a criterion number, $M$. For each stimulus level, the probability of neural firing is estimated from the proportion of trials when the neuron fired more than $M$ spikes. Three curves are shown in Figure 1$B$: The leftmost corresponds to the neuron firing at least one spike on a single trial and the other two correspond to the firing of at least two or at least three spikes, respectively. The shapes of these neural detection functions (neurometric functions) are remarkably similar to those of the psychometric functions. It is possible to fit a curve to the neurometric data and extract estimates of the threshold and slope for the neuron, just as for the behavioral data. But, most importantly, we now have a representation of the neural data that summarizes the trial-by-trial performance of the neuron in the same way that the psychometric function summarizes the trial-by-trial responses of a behavioral observer.

This representation of neural data is at the heart of making rigorous, quantitative comparisons between neural activity and perception. Several issues require further thought. For example, many sensory neurons have a maintained or resting discharge of action potentials in the absence of any externally applied stimulus. This background firing is variable. On any given stimulus presentation, there is a chance that the neuron might exceed the criterion $M$ simply because the background fluctuations might take the neuron's firing above the criterion just at the moment when the stimulus was presented. This probability can be estimated by measuring the statistics of the neuron's firing during blank intervals when no stimulus is presented. Subjects in behavioral detection experiments also respond incorrectly in the absence of a stimulus, and this probability is then called the false alarm rate. Moreover, there is also the question of the length of the time period over which spikes should be counted. Such a time period may need to be longer than the stimulus duration if the neural response is sluggish. Too long a time period will result in assigning spikes to the stimulus-related discharge when they actually belong to the background discharge. Too short a time period will mean that stimulus-related spikes are lost. Either of these will adversely affect the estimated sensitivity of the neuron (Fitzhugh 1958).

It is also important to consider whether the measure of the neuron's activity is appropriate. In the above example, the number of action potentials evoked by the stimulus was used, but many other possibilities exist. For example, if the perceptual task under study involves the discrimination of two temporally modulated stimuli (for example, two lights flashing on and off at different rates), it may be appropriate to use a measure of the neural discharge that is synchronized to the periodicity of the stimuli. It is clear that any measures of this

type will also be constrained by the statistical fluctuations present in neuronal firing patterns, so the same probabilistic comparisons between neuronal and behavioral performance can be achieved.

## Early Work in the Visual, Auditory, and Somatosensory Systems

More extensive and rigorous comparisons of neuronal and psychophysical performance were made in the late 1960s in classic studies on the cat retina (Barlow & Levick 1969a,b; Barlow et al 1971), the somatosensory system (Talbot et al 1968, Mountcastle et al 1972), and auditory nerve fibers (Kiang et al 1965, Siebert 1965).

Barlow et al (1971) obtained careful measures of the statistics of the neural firing of cat retinal ganglion cells by using a measure of total spike counts over a range of different counting intervals. They also carefully measured the average time course of the response of ganglion cells to weak flashes of light. They reasoned that any processor in the CNS that analyzed the output of a ganglion cell would respond most appropriately if it counted the spikes delivered on a single trial over a time period equivalent to the expected time course of the neural response. They obtained complete probability distributions for the occurrence of $0, 1, 2 \ldots N$ spikes in a 200-ms counting window for stimulus intervals that had weak flashes of light and for equivalent blank intervals. They plotted the probability that the ganglion cell fired $M$ spikes or more as a function of light level and for various values of the criterion $M$. They also analyzed the same data much more extensively using receiver-operating-characteristic (ROC) methods [see Figure 3 (below) and next section]. From these data and analyses, they estimated the absolute sensitivity of single neurons in the retina and showed that their responses were highly reliable: The variability of firing in the retinal ganglion cells could be accounted for largely by events at the photoreceptors (i.e. quantal fluctuations in the stimulus and spontaneous photon-like events probably caused by random, spontaneous isomerizations of rhodopsin). Since the ganglion cells are the output neurons of the retina, this work successfully identified the nature of the retinal signals that are delivered to the CNS during the behavioral measurement of an absolute detection threshold.

In the somatosensory system, Mountcastle and colleagues compared the psychophysical capacity for detecting a vibrating stimulus applied to the skin to the capacity of single mechanoreceptive afferents to signal the presence of such stimuli (Talbot et al 1968, Mountcastle et al 1972). The amplitude of vibration required for successful detection was measured as a function of vibration frequency for both human and monkey observers. As illustrated in Figure 2 (*bold line* and *open circles*), psychophysical thresholds decreased markedly over the range of 2–200 Hz, but rose abruptly for higher frequencies. In separate
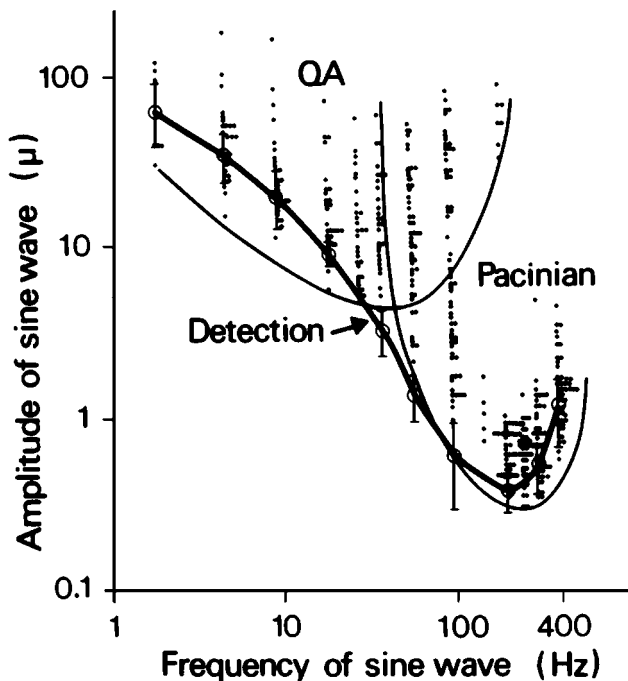
*Figure 2*    A comparison between the neuronal thresholds of primary somatosensory afferent fibers recorded from anesthetized rhesus monkeys and the psychophysical thresholds of human and monkey observers. [Data of Mountcastle et al (1972) as plotted by Darian-Smith (1984).]  The detection of these vibrating stimuli is served by two types of neuron, with the quickly adapting (QA) fibers serving the lower frequency range and the Pacinian corpuscle fibers serving the upper frequency range. The neuronal thresholds are shown as individual data points (*small filled points*) and are summarized by two bounding contours shown as *thin lines*, one for the QA fibers and the other for the Pacinian fibers. The psychophysical thresholds are shown as *open circles with error bars* and are summarized by *thick solid lines*.  The data illustrate the *lower envelope principle*, which argues that behavioral detection is supported by the most sensitive individual neurons at each point along the frequency axis. (Reproduced with permission of the American Physiological Society.)

physiological experiments, Mountcastle and colleagues measured similar detection thresholds as a function of frequency for afferent mechanoreceptive fibers (Figure 2: *thin lines* and *small filled circles*). They found that the most sensitive fibers accounted well for psychophysical performance across the range of frequencies tested. Importantly, quickly adapting (QA) fibers matched performance best in the low range of frequencies, while Pacinian fibers matched best in the high range. Psychophysical performance was therefore described best by a lower envelope of particularly sensitive fibers, with different fibers

providing the best signals at different frequencies. These observations and others (e.g. DeValois et al 1967) led to the development of a *lower envelope principle*: This proposes that the limits of psychophysical performance are set by the most sensitive individual neurons available.

Around the same time, Siebert (1965) developed models of detection and discrimination performance in the auditory domain, based on the extensive set of recordings acquired by Kiang et al (1965) in the cat auditory nerve. Siebert confined his initial analysis to the processing of high-frequency tones (for which he was able to avoid the question of periodicity coding in the auditory nerve) and used a statistic based on neural spike counts. He developed a statistical measure of the expected performance of the entire population of auditory nerve fibers during detection and discrimination tasks. The signals from the population were combined into a single sensory measure. The method of combining signals was statistically optimal, so the combination stage discarded no relevant signal from (and added no extra variance to) the signals from the individual nerve fibers. Each hypothetical neuron in the model population was given a mean firing rate and associated variability as a function of stimulus intensity and frequency; these values were derived from the measurements of Kiang et al (1965).

Even though the physiological data were from the cat auditory system, Siebert's model provided a good description of the available human psychophysical data on intensity and frequency discrimination for pure tone stimuli. It quickly became clear that the quality of signals available by pooling over the population of neurons would be easily sufficient to explain the known behavioral performance (Siebert 1970). Indeed, if the pooling were statistically optimal, as first assumed, the behavioral thresholds would be lower than found experimentally. Siebert added extra noise to the model at this point to reconcile the discrepancy. This work represents one of the first rigorous attempts to develop and evaluate a neuronal pooling model of sensory detection. We have more to say about such models in subsequent sections.

## Opening the "Black Box"

These various studies represented an enormous leap forward. Psychometric functions had been measured and discussed for 100 years. However, the true nature of the signals that underlie perceptual performance had essentially been a matter of speculation because the internal workings of the nervous system were being treated as a "black box." These studies began the process of opening the black box (e.g. Barlow 1972). The rest of this review follows the subsequent developments. The particular themes are (*a*) the influence of the lower envelope hypothesis and the neuronal pooling hypothesis, (*b*) the elimination of significant discrepancies in the earlier work, arising from the use of cross-species

comparisons and the comparison of behavioral and neurometric detection functions that were gathered under different conditions, (*c*) the importance of models of the integrative action of populations of sensory neurons, and (*d*) the measurement of trial-by-trial covariation between the firing of sensory neurons and the perceptual behavior of the organism as an important source of information about the underlying detection process. The remainder of this review, however, requires a more formal understanding of the underlying theory of decision-making in psychophysical experiments.

## STATISTICS OF DETECTION AND DISCRIMINATION

### The Decision Variable and the Observer's Criterion

In this section, we consider in more detail the factors that govern the shape of the psychometric detection function, and we link more tightly the signals that have been hypothesized at the black-box level with the signals that are actually available on single neurons. It is easiest to begin with a simple detection experiment, as shown in Figure 1*A*, in which an observer is required to indicate the arrival of a stimulus with a "Yes" response and the non-arrival of a stimulus with a "No" response. The observer sometimes makes mistakes in responding on blank trials or those with weak stimuli and thus sometimes responds "Yes" when there is no stimulus and vice versa. It is hypothesized that the observer bases these decisions on an internal signal that fluctuates over time. On average, the signal is stronger when a stronger flash is present, but this is only true on average. Occasionally, there are trials for which the signal is relatively strong, even when no stimulus has been presented. It is assumed that the observer has complete knowledge of the form of the statistical distributions of the internal signal both for trials with and for those without sensory stimuli. But all that is available to the observer on any given trial is the strength of the internal signal, which is subject to statistical fluctuation. The optimal strategy for an observer under these conditions is to set a consistent criterion level for the internal signal and to respond "No" if the signal on a given trial falls below the criterion and "Yes" if it is above the criterion (Green & Swets 1966).

The transfer of this strategy to neuronal data is illustrated in Figure 3*A*, which shows two probability distributions of the spike counts from a cat retinal ganglion cell (data of Barlow et al 1971): One of these corresponds to trials for which the stimulus was absent, and the other to trials for which a weak flash was present. Suppose that the cat relies on this neuron alone to detect the presence of the flash: It would be unable to decide reliably on any trial whether the flash was present, because of the overlap between the two distributions. As the stimulus strength is increased, however, these two distributions will move
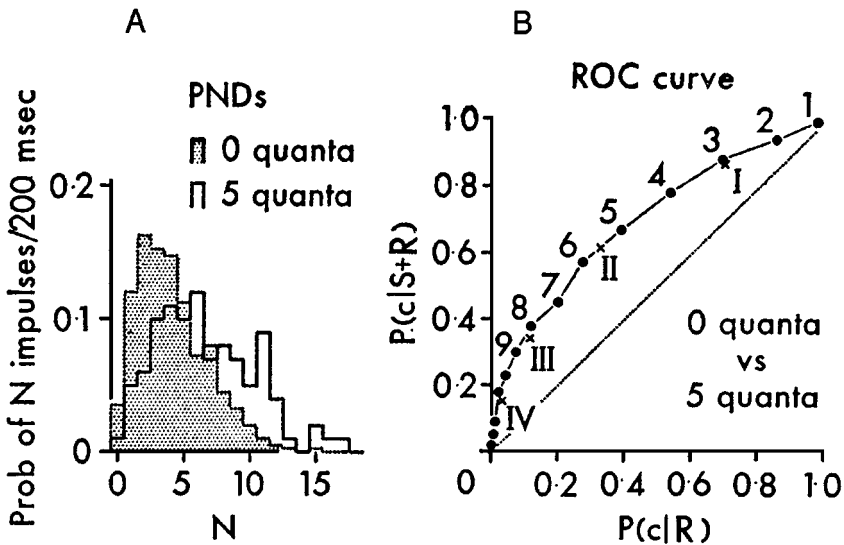
*Figure 3* (*A*) Two probability distributions [pulse number distributions (PNDs)] of neural spike counts in cat retinal ganglion cells from Barlow et al (1971): The *left-hand distribution* represents the condition where no stimulus is presented (0 quanta), the *right-hand distribution* represents the condition where a weak flash of light was presented (5 quanta on average). Owing to the overlap of the two distributions, it is inevitable that if the cat were to rely on the output of this cell to detect the flash, it would sometimes make the wrong decision. (*B*) The same probability distributions as in *A*, but transformed to a receiver-operating characteristic (ROC) curve. The probability of incorrect detections when no stimulus is presented is shown on the abscissa as $P(c \mid R)$—the probability of achieving a given count of spikes (c) from the random background firing of the neuron (R). The probability of correct detections is shown on the ordinate as $P(c \mid S+R)$—the probability of achieving a given count of spikes (c) from the firing of the neuron due to the stimulus plus the random background influence (S+R). Each point on the curve corresponds to a value of the criterion number of spike counts (c). The area under the ROC curve yields a measure of the detectability of the stimulus (see Green & Swets 1966). The *Roman numerals* and *crosses* on the curve show the performance of a theoretical ideal observer that can exploit a fixed fraction (18%) of the quanta arriving at the cornea (see Barlow et al 1971, for details). (Reproduced with permission of Elsevier Science Ltd.)

farther apart on the abscissa, and their overlap will decrease (not illustrated). The cat could adopt a criterion level that separates the two distributions more effectively, so the probability of making correct decisions would increase. These relationships define the basic sigmoid shape of the psychometric and neurometric detection functions, where the probability of detection rises smoothly with stimulus intensity, because the separation of the "stimulus" and "no stimulus" distributions steadily increases with flash intensity.

## Variation of Criterion and ROC Curves

Another common characteristic of psychophysical judgments is that the subject can attach a level of confidence to each judgment. On trials with stronger stimuli, for example, the observer may be quite confident that the stimulus was present, but the same observer will normally be less confident on trials with weak stimuli. This aspect of performance can be measured experimentally by asking observers to rate the confidence of their judgments, for example on a scale from 1 to 5 where "1" means unlikely to be present and "5" means almost certainly present. With this scale, a score of 5 is likely to be assigned only when the stronger stimuli are presented and is almost never assigned when a blank stimulus is presented. On the other hand, the lower scores will be used more readily when a weak stimulus, or even a blank, is presented. The confidence level of psychophysical judgments has a natural analog in the responses of sensory neurons. In the case of a neuron like that in Figure 3A, the number of spikes evoked by the stimulus can be regarded as a confidence rating by the neuron about the presence of the flash in the outside world.

Whether the confidence ratings are derived from verbal scoring by human observers or by treating the number of spikes from a neuron as a measure of confidence, they can conveniently be represented on a ROC diagram. This plots the probability of responses in the "stimulus present" condition on the ordinate against the probability of responses in the "stimulus absent" condition on the abscissa, for each possible confidence level (either verbal score or number of spikes). The specific example in Figure 3A uses neuronal data. Here, a low criterion number, such as the firing of a single spike, will be exceeded on virtually every trial regardless of whether the flash was presented. Thus the data point from this criterion lies in the *upper right corner* of Figure 3B (high probability for both "stimulus present" and "stimulus absent" trials, indicated by arabic numeral *1* in Figure 3B). A high criterion of nine spikes will be exceeded on only a few trials from the "stimulus present" distribution and hardly ever for the "stimulus absent" condition, so the point will fall near the *lower left corner* of Figure 3B (shown by arabic number *9* in the figure). Intermediate criterion values (arabic numerals *2* through *8*) trace out a connected curve on the ROC diagram with a convexity pointing toward the *upper left corner* of Figure 3B.

Intuitively, one can see that the area under the ROC curve will vary monotonically with the separation of response distributions like those in Figure 3A. If the two distributions are identical, the probability of a response from either distribution exceeding criterion will be the same for all possible criteria. The ROC curve will then lie along the positive diagonal, and the area under the curve will

be 0.5. As the separation of the two distributions increases (which will occur in this example with increasing number of quanta in the flash), the convexity of the ROC curve pushes further toward the *top left corner* of the graph, and the area under the curve approaches unity. If the area under the ROC curve is plotted as a function of flash strength, the data points form a sigmoid curve, varying from 0.5 to 1.0, that characterizes the sensitivity of this particular neuron to the flash stimulus. Neurometric functions computed in this manner offer several critical advantages for examining the relationship between neural signals and perceptual judgments:

1. The area under the ROC curve provides an index of discriminability that is faithful to the probabilistic nature of neural responses: It takes into account both the mean and trial-to-trial variability of the signal.

2. The area under the ROC curve corresponds theoretically, and in practice, to the probability of psychophysical detection in a two-alternative forced-choice (2AFC) task, where an observer indicates detection by choosing which of two intervals or spatial locations contains the stimulus (Green & Swets 1966). Thus neurometric functions based on ROC measurements can be compared directly to psychometric functions obtained from human or animal observers, both in terms of threshold and slope.

3. The area under the ROC curve is a nonparametric measure: It does not rely on any assumption about the shape of the underlying distributions of responses. This property gives a useful general validity to the analysis, since the distribution of neural responses is sometimes not Gaussian (as in Figure 3*A*) and is sometimes not known for certain.

## Neuronal Signals

These tools allow us to be faithful to the probabilistic nature of both neuronal and perceptual data. Since we can now treat neural signals as potential decision variables, we can ask how well the physiological responses could account for the perceptual performance. Thus, we are poised to open the black box. We would like to know just how the actions of neurons cause the psychophysical observer to shift from one conscious judgment to another. We would like to know the locations of the neurons involved, how many of them need to be active, and how their combined action leads to the formation of a behavioral decision. We will frame much of our discussion in terms of two influential ideas introduced above for relating neuronal activity to perceptual judgments: the lower envelope principle and pooling models.

# THE LOWER ENVELOPE PRINCIPLE
# AND POOLING MODELS

## *Lower Envelope*

Barlow (1995) recently restated the lower envelope principle as follows: "Sensory thresholds are set by the class of sensory unit that has the lowest threshold for the particular stimulus used and are little influenced by the presence or absence of responses in the enormous number of other neurons that are less sensitive to that stimulus." The application of this formulation to the results of Talbot et al (1968) in Figure 2 is clear enough: At each temporal frequency of vibration, the psychophysical threshold is thought to be reached when the neuron with greatest sensitivity to that frequency begins to detect the stimulus. Barlow formulated the principle in terms of a "class of sensory unit." Thus, in Figure 2, at vibration frequencies where both the quickly adapting (QA) and Pacinian corpuscle (PC) afferents are activated by high amplitudes of vibration, the detection threshold is set by whichever class of afferent is more sensitive to the stimulation frequency.

In its pure form, the lower envelope principle means literally that a single neuron governs the behavioral threshold. The development of the lower envelope principle has been very much a reaction by neurophysiologists to the formerly prevalent notion that single neurons are inherently unreliable devices. This is why such emphasis has been placed on the comparison of behavioral and neuronal thresholds and the search for cases where individual neurons perform as well as the entire observer. Clearly, it is unreasonable to expect to find an individual neuron that can match behavioral performance for every task that we might conceivably ask observers to carry out. It is important to understand how the lower envelope principle applies with more complex stimuli.

Suppose that the neurons from Talbot et al (1968), whose thresholds are illustrated in Figure 2, were stimulated with a vibration that contains many different temporal frequencies. In this case, the detection of the high-frequency components in the vibration would be supported by the PC afferents and the detection of lower frequencies would be supported by the QA afferents. Therefore, when a multifrequency stimulus is presented on a single trial, it may be detected by the PC afferents only or by the QA afferents only or by both. The lower envelope principle asserts that any of these three neuronal detection conditions is sufficient to satisfy psychophysical threshold. If the same multifrequency stimulus is presented several times at the same amplitude level in a sequence of trials, the psychophysical detection can be fulfilled with a different neuronal afferent (QA or PC) on different trials because of fluctuations in the response of each afferent from trial to trial. Thus, the lower envelope principle asserts that

psychophysical detection is fulfilled by a single neuronal detection, but it does not guarantee that the same neuron is responsible for detection on every trial. The consequences of this point are developed in more detail when we examine data that compare neuronal and psychophysical thresholds.

## Pooling Models

The essence of a pooling model is the combination of signals from several sensory neurons. The most concrete way to conceive of how this might be arranged is to imagine several sensory neurons converging anatomically on a target neuron. Suppose that several of these sensory neurons begin to fire action potentials: If the appropriate synaptic connections are in place, the target neuron can summate the signals arriving, and its output will reflect the pooled activity of the incoming neurons. To return to the detection of the multifrequency vibratory stimulus introduced above, a pooling model begins by adding together the signals from different afferents. The strength of the pooled signal determines the psychophysical response. The claim is that this neuronal signal is the decision variable hypothesized on the basis of psychophysical experiments. On any single trial, suppose that there is a signal in the QA afferents that is not strong enough by itself to exceed the criterion for psychophysical detection. If there is also a signal in the PC afferents that is not strong enough to exceed the criterion by itself, this will add to the signal from the QA afferents. The combined signal may then be strong enough to exceed the criterion. In a lower envelope model, this secondary information is lost, since the psychophysical detection is fulfilled only when the signal in some single neuron is sufficient to exceed the criterion by itself. Pooling models allow for a combination of signals both across classes of neuron and within members of one class.

It is sometimes thought that the essential distinction between the lower envelope principle and pooling models resides simply in the total number of neurons that potentially contribute to the perceptual decision. This is incorrect. The distinction really lies in how the signals from neurons are combined. The lower envelope principle allows for many neurons to be involved in a decision, provided that the critical event on each individual trial occurs in just one of the neurons involved. On the other hand, in the limiting case, a pooling model with just one neuron in the pool is identical to the lower envelope hypothesis.

Pooling has been introduced here as if it were a simple anatomical convergence. Such a picture illustrates one form of pooling model in which the action potentials of neurons are added together directly. We refer to this as response pooling. This is a reasonable strategy when each neuron in the pool provides a similar quality of signal. However, some neurons may have more variability in their firing than others, resulting in a lower quality signal in these highly

variable neurons. A more efficient form of pooling would take this reality into account by giving a low weight to poor-quality signals and a stronger weight to high-quality signals. In the extreme, if everything possible were known about the statistical quality of each signal in the pool, the weights could be selected in an optimal way so that no useful information would be wasted (Green 1958). This defines a theoretical upper bound on the performance of the pooling model, which is sometimes called an ideal observer model, after its use in analyzing human performance. Real models or systems can perform up to this limit but not beyond it.

Both response pooling (Shadlen et al 1996) and the ideal observer approach (Siebert 1965, Geisler & Albrecht 1997) have been used to model central pooling processes, and some papers have specifically compared the two approaches (Delgutte 1996; Johnston et al 1973, 1979; Lachs et al 1984; Viemeister 1988). The two types of model differ in one important aspect. Consider adding an extra insensitive neuron to the pool. If action potentials are pooled, as in the response pooling model, the addition of an insensitive neuron dilutes the useful signal from any sensitive neurons already in the pool. For the ideal observer model, on the other hand, the addition of an insensitive neuron is negligible because its firing receives a low weight, on the grounds that it can contribute little that is worthwhile.

Pooling across neurons is potentially very powerful. Suppose that the observer can add together the signals from a pool of $N$ neurons whose thresholds for a stimulus are all the same and whose firing patterns are statistically independent. Then simple statistical arguments predict that the psychophysical threshold based on a pool of those $N$ neurons will show a factor of $\sqrt{N}$ improvement over a single neuron's threshold. In this case, we might expect that psychophysical thresholds would be much lower than thresholds for single neurons in the CNS, simply because there are so many neurons available. As we demonstrate below, however, this conjecture is not supported by the data: Thresholds of single neurons in the cortex frequently match psychophysical thresholds—and at least some cortical neurons have thresholds lower than the psychophysical threshold. In the next section, we document the exquisite sensitivity of cortical neurons in comparison with psychophysical sensitivity. In the subsequent section, we critically examine the issue of statistical independence among cortical neurons.

## THE COMPARISON OF THRESHOLDS

Since its formulation in the late 1960s, the lower envelope hypothesis has received considerable support from studies in several laboratories, most extensively in the sensory periphery. Results established for the periphery may

not transfer readily to the CNS because of the much greater number of neurons within the CNS. The peripheral components of the visual and somatosensory systems are characterized by spatially extended surfaces (retina and skin) that are sampled efficiently by the anatomical distribution of sensory neurons. Within the cortical representations, there are many more neurons serving the same patch of the skin or retina. This would provide an opportunity for pooling that does not exist in the periphery. The following examples illustrate ways in which processing at the cortical level can be reconciled with the lower envelope principle, though, as noted below, these examples do not rule out the possibility that pooling processes are at work.

## Cortical Detection of Spatial Contrast Patterns

The visual detection of spatial contrast patterns (lines, bars, sinusoidal gratings, and other variants) has been studied intensively, both psychophysically and neurophysiologically, in the primary visual cortex. Tolhurst et al (1983) recorded single neurons from cortical area V1 in anesthetized cats and monkeys. The visual stimuli were drifting patterns of luminance contrast with a spatial sinusoidal form (gratings), whose orientation, spatial frequency, and drift rate were adjusted to match the stimulus preferences of the single neuron under study. Tolhurst et al generated neurometric functions for the detection of spatial contrast by single cortical neurons. They found that the general shape of the neuronal detection functions was similar to previous measurements of the behavioral detection functions of monkey and human observers, but there were significant discrepancies in the thresholds and slopes of the neuronal and behavioral data. Neuronal thresholds were higher and slopes were shallower than their behavioral counterparts.

The attempt to resolve these discrepancies illustrates an important aspect of the lower envelope principle: The receptive field of the neuron itself is a temporal and spatial window through which the neuron receives information from the external environment. In a real sense, therefore, a visual neuron is blind to events outside its receptive field. Hawken & Parker (1990) argued that a significant part of the discrepancies between behavioral and neuronal contrast thresholds was attributable to this cause. Portions of a spatially extended grating target must fall outside the receptive field of a cortical cell but would be visible to a psychophysical observer. Hawken & Parker therefore measured human psychophysical thresholds for targets that were designed to approximate the receptive field structure of V1 neurons. They also remeasured the neuronal detection functions, with a concentration on monkey visual cortex as a model for human vision and with particular attention to measuring the receptive field characteristics of the neurons (eccentricity, spatial frequency, width, height, etc). Matching of the psychophysical task to the spatial structure of the receptive

field provided a considerable reconciliation of the discrepancy in thresholds. Hawken & Parker (1990) also found that the slopes of the neuronal detection functions were on average close in value to the slopes of the psychophysical detection functions measured in a forced-choice task. Thus, they proposed that the detection of spatial contrast patterns by V1 neurons could indeed be understood in terms of the lower envelope principle.

It is important to be clear about how the lower envelope model would account for the improved detection thresholds that are found for spatially extended stimuli that extend beyond the receptive field of a single cortical neuron. The psychophysical observer could potentially improve detectability by combining signals from receptive fields at several locations in space. A pooling model would suggest that the signals are actually added together to form a pooled decision variable, a process that is sometimes called physiological summation. The lower envelope models differ from pooling models in attributing the improved detectability-to-probability summation, in which behavioral detection threshold is reached when any one of a number of sensitive detecting mechanisms exceeds its individual threshold [as described for the somatosensory example above and discussed by Tolhurst et al (1983), Relkin & Pelli (1987), and Hawken & Parker (1990)]. In probability summation models, detection thresholds improve with a spatially extended stimulus because more neurons are potentially excited. Thus, there is an increased probability that the response of a single neuron will exceed criterion. The concept of probability summation has been highly influential in the psychophysical literature (Watson 1979, Pelli 1985, Graham 1989) and preserves the spirit of the lower envelope principle, since the detection on any single trial is attributable to the additional activity in some single neural element.

## Visual Pattern Discriminations

Parker & Hawken (1985) also examined a number of spatial discrimination tasks at the neuronal level in the primate visual cortex. The common feature of these tasks is that the spatial discriminations that can be achieved behaviorally are more precise than the inter-cone spacing at the retina: For this reason, these discriminations have been termed hyperacuity (Westheimer 1981). Again, consistent with the lower envelope principle, Parker & Hawken found that the most sensitive neurons in V1 could discriminate reliably within the hyperacuity range. Other work has examined different aspects of spatial discrimination performance. Notably, in the visual cortex of anesthetized cats, Bradley et al (1987) found that the best discrimination thresholds for orientation were as good as 2–3°, comparable with the known psychophysical performance of cats. One important observation was that the most sensitive regions of the tuning curve are its flanks, where the relationship between neural firing and changes

in orientation is steepest. Vogels & Orban (1990) reported similar results in a comparison of neuronal and psychophysical capacities for orientation discrimination in alert rhesus monkeys. In each case, the findings can be reconciled with the lower envelope principle, provided that due account is taken of the structure and size of the receptive field of the cortical neurons.

## Somatosensory Frequency Discrimination

Following their groundbreaking studies in the somatosensory periphery, Mountcastle and colleagues extended their investigations to the primary somatosensory cortex, SI (Mountcastle et al 1969, 1990; Lamotte & Mountcastle 1975). In a particularly elegant analysis, these investigators examined the relationship between perceptual frequency discrimination and the underlying activity of SI neurons. In psychophysical experiments, observers were required to state whether the second of two vibrating stimuli applied to the skin was higher or lower in frequency than the first. Psychophysical thresholds were characterized using the methods of signal detection theory described above.

Employing the same stimuli used in the psychophysical studies, Mountcastle and colleagues recorded the responses of primary somatosensory afferents and of single neurons in primary somatosensory cortex. Figure 4 illustrates several responses of a cortical neuron to repeated presentations of a sinusoidally vibrating stimulus. The neuron fired brief bursts of spikes that were entrained to the period of the vibrating stimulus, and Mountcastle and colleagues hypothesized that the period of this spike discharge comprised the critical neural signal underlying the subjects' frequency discrimination ability, at least for temporal frequencies below 100 Hz. Plainly, however, the entrainment of neural discharge to the vibrating stimulus is somewhat variable between repetitions, and this variability should limit the fidelity of the observers' psychophysical judgments. Taking into account the variability of the periodic discharge, Mountcastle and colleagues estimated the frequency discrimination capabilities of single SI neurons. Consistent with the lower envelope hypothesis, they found that the information in the most sensitive SI neurons could in principle support the observed levels of behavioral discrimination. Importantly, this work shows that the perceptually relevant aspect of the neural spike train could in principle be a temporal pattern of activity, a point that is emphasized again in more recent work on somatosensory frequency discrimination by Recanzone and colleagues (Recanzone et al 1992). Nonetheless, the signal detection framework for comparing neurons and behavior can still be applied.

## Summary

This work has established that at least some cortical neurons can detect and discriminate sensory stimuli with performance levels matching those of the
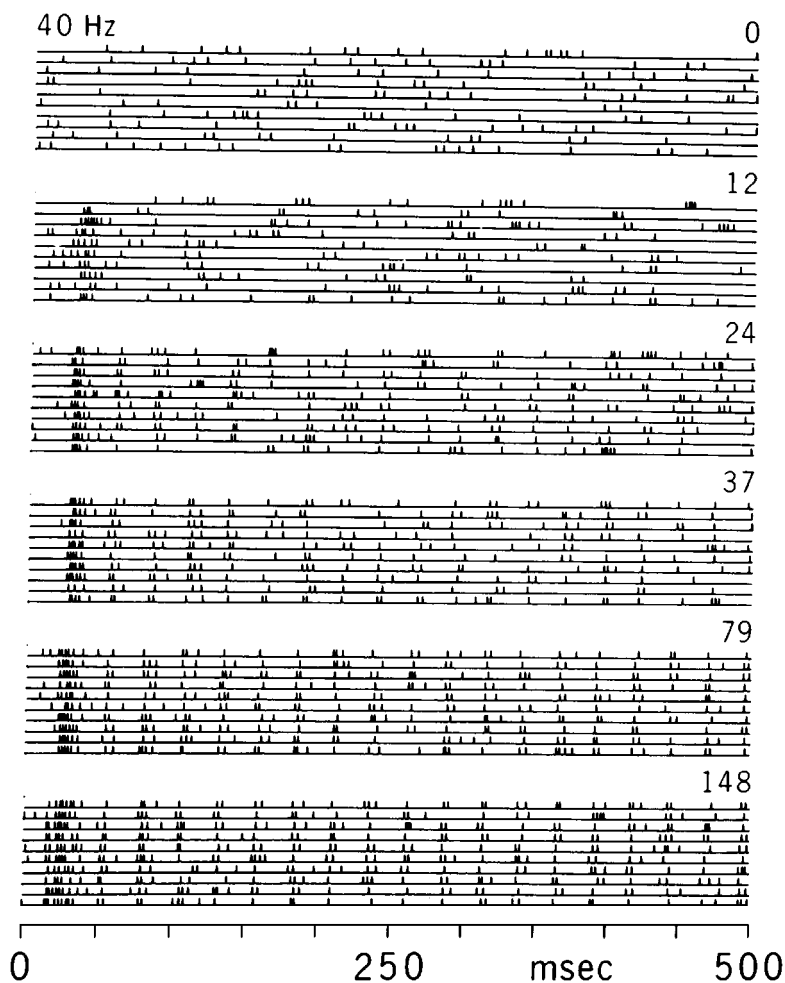
*Figure 4*   The responses of a single cortical neuron from the primary somatosensory area of rhesus monkey, when the skin was stimulated with a sinusoidally vibrating probe that gently indented the skin over a range of different amplitudes of vibration [data from Mountcastle et al (1969)]. The periodic form gradually becomes apparent as the amplitude of the vibration is increased (vibration amplitudes are indicated in micrometers to the *right* of each set of rasters).  It is evident that the periodic component of the response is statistically unreliable at low amplitudes and increases in reliability as amplitude increases.  Mountcastle et al (1969) extracted this periodic component and studied how its variability would limit the frequency discrimination capabilities of behavioral judgments. (Reproduced with permission of the American Physiological Society.)

entire organism. This illustrates the high quality of sensory signals that are available from single neurons at all levels of the system. Obviously, these results conform well to the expectations of a lower envelope model. However, a more detailed look at pooling models shows, ironically, that they are also equally capable of delivering a consistent interpretation of these results.

Geisler & Albrecht (1997) highlight this difficulty neatly in a recent comparison of neural and psychophysical sensitivity for contrast and spatial frequency in the visual system. They employed signal detection theory to compute the minimal detectable increment in contrast or spatial frequency that could be signaled reliably by V1 neurons across a range of base contrasts and spatial frequencies. These increment thresholds were then compared to the increment thresholds of human and monkey observers measured psychophysically across the same ranges of contrasts and spatial frequencies. Their plots showed that the best V1 neurons matched psychophysical performance closely, consistent with the lower envelope principle for relating neural activity to behavior. Geisler & Albrecht went on to show, however, that the performance could be equally well predicted by an optimal pooling model that combined data across their entire sample of V1 neurons, provided that predicted thresholds could be scaled upward by a factor that represents noise or inefficiences in the central pooling process. (The optimal pooling procedure actually yielded psychophysical thresholds considerably lower than those observed experimentally, but the general shape of the contrast threshold vs spatial frequency curve was similar to that observed experimentally. Consequently, a simple scaling procedure could correct the mismatch in absolute thresholds. Below, we discuss a physiological interpretation of central inefficiencies.) Even when the analysis was extended to include a comparison of the slopes of predicted and actual psychometric functions, the essential ambiguity remained (W Geisler & D Albrecht, personal communication): Data sets of this type simply do not provide enough experimental constraints to distinguish between alternative possibilities.

The next three sections are devoted largely to the presentation of new theoretical insights and experimental data that provide additional constraints for testing the two hypotheses. These experimental data also go substantially further toward meeting the criteria developed at the beginning of this review for demonstrating a compelling link between neuronal activity and perception.

## POOL SIZE AND THE PROBLEM OF RESPONSE COVARIANCE

The simplest forms of pooling propose that the signals from individual neurons are statistically independent. This is a critical assumption for the prediction of behavioral thresholds from neuronal data and for estimating the size of any

neuronal pool that contributes to a perceptual judgment. This section explores the consequence of response covariance for these predictions.

## The Detection of Temperature Changes

The psychophysical detection of temperature increments and decrements has been examined in terms of the neural activity in peripheral warming and cooling fibers (Darian-Smith et al 1973, 1979a,b; Johnson et al 1973, 1979). The mean and variance of the firing of temperature-sensitive fibers was measured in anesthetized monkeys when small changes in temperature were applied with a thermal probe. Human psychophysical thresholds for detection of small temperature changes were measured using the same probe. The sensitivity of single thermally sensitive fibers was substantially worse, on average, than the psychophysical sensitivity of human subjects, as might be expected, since the thermal probe covered the receptive fields of many afferent fibers.

The difference in neuronal and psychophysical thresholds could be reconciled if the noisy signals from a pool of afferent fibers were averaged at some central location. Darian-Smith et al (1973) modeled such a scheme to determine how many fibers would be required to account for the observed psychophysical sensitivity. Figure 5A shows the computed performance as a function of the duration of the cooling interval. The family of curves illustrates the performance expected for pools of increasing size: Increasing the number of fibers from 1 to 64 reduced the expected discrimination threshold by roughly an order of magnitude. The *horizontal dashed line* in the figure shows the discrimination threshold of the human observers, and the *dashed vertical line* shows their integration time: The intersection of these two lines represents the performance level of human observers that should be matched by the model. The best match occurs when decisions are based on a pool of 16 fibers.

From a knowledge of innervation density of thermally sensitive fibers at the skin surface and the size of their thermal probe, Darian-Smith et al (1973) calculated that roughly 50–70 fibers are potentially available to carry thermal information to the CNS during the performance of this task. Why, then, is psychophysical performance matched best by a pool of only 16 fibers? Importantly, these investigators realized that the sensitivity gained by averaging across fibers is necessarily limited by the amount of common variability within the afferent pool. For any single presentation of a sensory stimulus, averaging can decrease noise in the afferent pool only to the extent that the noise carried by individual fibers is independent. By contrast, variability that is common to all of the afferent fibers cannot be averaged out. The calculations in Figure 5A assumed statistical independence, but additional calculations (Figure 5B) explored the effect of trial-to-trial correlation ($\rho$) in the spike counts generated by neighboring nerve fibers in response to an individual stimulus presentation. This second set of calculations was performed for a neuronal pool size of 50,
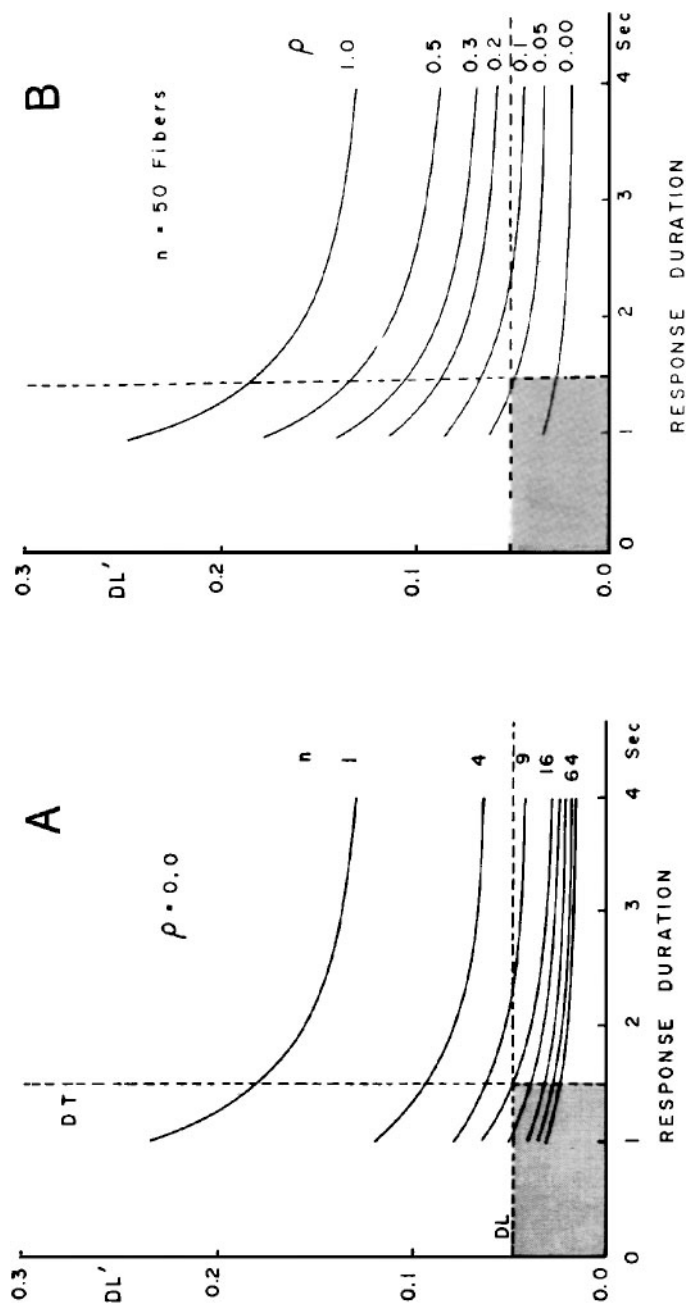
*Figure 5*   (*A*) The calculation of the detection threshold for a change in the temperature of a cooling probe applied to the skin of an anesthetized monkey as a function of the duration of the neural response. [From Johnston et al (1973).] The model included a simple decision rule to predict the performance of an ideal observer whose decisions were based solely on the centrally pooled neural signals. The ideal observer's performance, which reflects the fidelity of the pooled neural signals, is given as a difference limen (DL'), which is simply the minimum temperature difference (in °C) that the observer would discriminate correctly on 75% of the trials. (Both the actual and modeled psychophysical tasks employed two-alternative, forced-choice procedures, so random performance is 50% correct.) The curves show the predictions arising from pooling different numbers of neurons (*n*) with properties equivalent to the ones recorded experimentally on the basis that the responses in the pool of primary somatosensory afferents are statistically independent ($\rho = 0.0$). (*B*) The predicted thresholds based on pooling responses from 50 neurons as a function of the duration of the neuronal response. Each curve shows the predicted thresholds from pooling the same 50 ($n = 50$) neurons with a different assumption about the degree of correlation ($\rho$) between the signals in the pool of neurons. (Reproduced with permission of the American Physiological Society.)

as hypothesized on the basis of innervation density. In the extreme case, of course, 50 fibers are no better than 1 if trial-to-trial variation in afferent fiber discharge is perfectly correlated across the pool ($\rho = 1.0$, compare Figures 5A and 5B). The activity averaged across 50 afferent fibers can account nicely for human psychophysical performance if there is a small amount of correlated noise within the afferent pool ($\rho = 0.05$).

These investigators supposed that the correlations might be induced by factors external to the peripheral neurons, such as fluctuations in the regional blood flow through the skin. There were no experimental measures of the actual amount of correlated noise present within the afferent pool, nor were these studies pursued at a central level where it might be possible to identify a neuron that actually receives input from the expected 50 or so afferents. Nevertheless, these studies established some of the fundamental principles about how pooling of neuronal signals could be implemented. Rather similar theoretical conclusions were reached with respect to auditory neurons (Winslow & Sachs 1988).

## Visual Cortical Areas

Given the theoretical and practical importance of this issue, it is remarkable that few groups have attempted to quantify the common noise in populations of cortical neurons. We are aware of four such studies in the visual system: in striate cortex of the anesthetized cat (van Kan, Scobey & Gabor 1985), in striate cortex and inferotemporal cortex of alert monkeys (Gawne & Richmond 1993, Gawne et al 1996), and in extrastriate visual area MT of alert monkeys (Zohary et al 1994). Somewhat surprisingly, the measurements obtained in these four studies agree closely despite substantial differences in preparation, cortical area, and visual stimuli. Responses (in the form of spike counts or a closely related measure) to repeated presentations of the same stimulus tend to be weakly correlated, with correlation coefficients generally falling between 0.05 and 0.20. Even this small amount of covariance severely limits the improvement in sensitivity that results from averaging signals across a pool of neurons: Predicted behavioral sensitivity fails to improve significantly for pool sizes greater than 100 neurons (Zohary et al 1994, Shadlen et al 1996). Both van Kan et al (1985) and Zohary et al (1994) found that common noise is higher for pairs of neurons with similar physiological properties. We suspect that correlation coefficients would also prove higher for neurons with overlapping receptive fields (as in the retina: see Mastronarde 1989, Meister et al 1995), although none of these four studies addressed this question directly.

## Auditory Pathways

In contrast to the above observations, Johnston & Kiang (1976) reported that the firing of pairs of auditory nerve fibers was statistically independent, even

when they served closely similar regions of the frequency range. As this is such a critical experimental observation, it would bear repetition, particularly in view of the fact that one inner hair cell contacts up to 10 auditory nerve fibers, thereby creating the conditions in which correlated activity may be present. At more central sites in the auditory pathways, there is evidence of correlated activity in the form of temporal synchrony (Voigt & Young 1980, Eggermont 1993, DeCharms & Merzenich 1996), but it is not yet clear whether temporal synchrony translates into correlated spike counts of the sort described above, or whether temporal synchrony bears any other relationship to behavior (Delgutte 1996).

## Summary

Covariance in the responses of neurons significantly affects the performance of a pooling model. The gain in threshold from the pooling of $N$ neuronal responses falls short of the expected $\sqrt{N}$ gain in threshold performance. If the covariance is caused by a source of noise that is common to all the neurons in the pool, it should be possible to estimate the common source of noise by averaging and then to subtract it from the other signals in the pool to create a new pool of statistically independent neurons. At the present, this proposal is entirely hypothetical. More study is clearly needed on this issue in all sensory systems, but models of central pooling processes would be greatly simplified if the amount of response covariance within pools of physiologically similar neurons is relatively constant across the cerebral cortex.

Below, we consider another form of covariation, in which fluctuations in the responses of neurons are correlated with the perceptual judgments of the observer. First, however, we concentrate on eliminating several factors that have made the comparisons of neural and psychophysical data problematic. Once these problems have been cleared up, we can address the question of covariations and their consequences more precisely.

# SIMULTANEOUS ACQUISITION OF NEURAL AND PSYCHOPHYSICAL DATA

The clearest answers about the relationship between neural activity and perception are achieved by recording from appropriate sensory neurons while a psychophysical subject performs a rigorously controlled detection or discrimination task. This type of experiment can eliminate confounding species and intersubject differences, as well as worrisome differences in the stimulus and anesthetic conditions between many psychophysical and physiological studies. Simultaneous assessment of neural and psychophysical thresholds has been attempted only rarely because of the considerable technical difficulties involved.
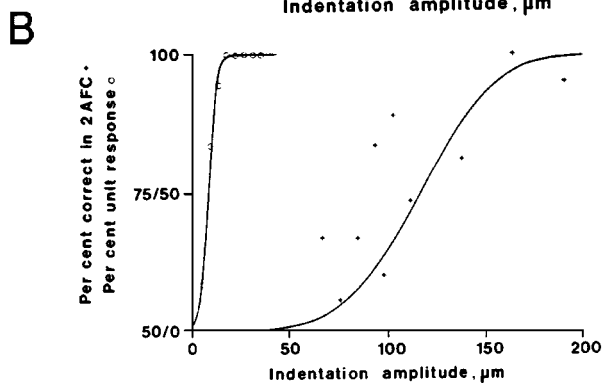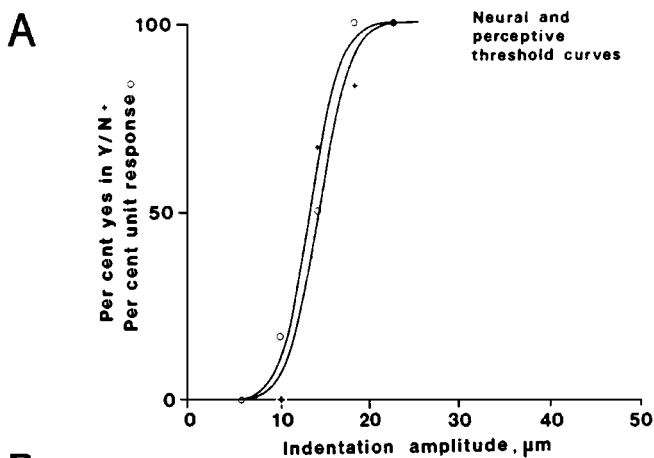
Two approaches to this problem have been adopted. The first is to obtain physiological recordings from peripheral somatic afferents of behaving human subjects—a field that has been dubbed microneurography. The second is to obtain physiological data from experimental animals (typically rhesus monkeys) that have been trained to perform threshold detection and discrimination tasks. Physiological data are more readily obtained with the latter preparation, but progress is slower because of the extensive time involved in training monkeys to perform threshold discriminations under controlled stimulus conditions.

## Microneurography in Humans

Vallbo & Hagbarth (1968) pioneered the microneurography technique for recording the activity of single units in human peripheral nerve. Vallbo and his colleagues used this approach to assess quantitatively the neural and psychophysical sensitivity to brief indentations of the glabrous (smooth) skin of the hand (reviewed by Vallbo 1995). In a typical experiment (Johansson & Vallbo 1976, 1979b), a microelectrode is inserted transcutaneously into the median nerve of a volunteer subject. Receptive fields of single peripheral fibers are mapped and physiological properties are assessed by conventional qualitative methods. A small, rounded glass probe (0.45 mm in diameter) is then positioned over the most sensitive region of the receptive field, and neural responses are recorded during repeated skin indentations over a range of indentation amplitudes. Peripheral mechanoreceptive fibers typically have little or no spontaneous firing, so a neural response may be reasonably defined as the occurrence of a single action potential in response to skin indentation on any given trial. As illustrated in Figure 6A (*open symbols*), the probability of eliciting a spike is zero for indentations of 5 $\mu$m or less but rises to unity for amplitudes of 20 $\mu$m or more. Neural threshold, defined as the stimulus that elicits a spike on 50% of the trials, is approximately 13 $\mu$m for this fiber.
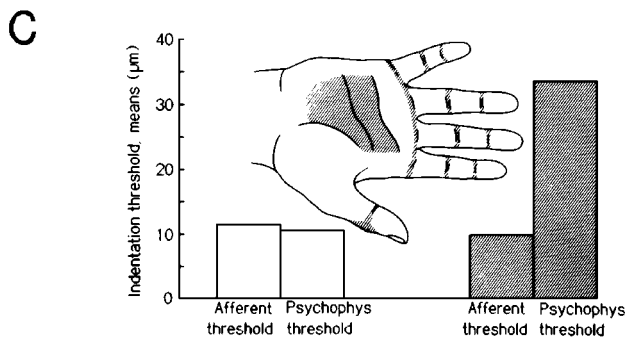
$\longrightarrow$

*Figure 6* (*A*) A comparison of behavioral detection (*crosses*) by a human observer and neuronal detection (*open circles*) by a primary somatosensory afferent fiber recorded from the same conscious human observer [data of Vallbo & Johansson (1976)]. The behavioral threshold was measured at exactly the same point on the skin that was served by the receptive field of the afferent fiber. At this point on the finger pad of the hand, the behavioral and neural detection functions agree closely. (*B*) The same comparison for the crease of the palm. Here the high sensitivity of the neuron is maintained, but the threshold for the behavior is about 10 times higher than that of the neuron. The human observer is somehow unable to access the signals from the neurons serving this region of the hand. (*C*) Provides a summary of the thresholds of single afferent fibers and human psychophysical judgments for two regions of the hand. At the finger tip, neuronal and behavioral thresholds are in good agreement, but at the crease of the palm the neuronal thresholds are considerably better than the behavioral thresholds. (Reproduced with permission of the authors.)

**A**

Neural and
perceptive
threshold curves

Per cent yes in Y/N +
Per cent unit response o

Indentation amplitude, μm

**B**

Per cent correct in 2 AFC +
Per cent unit response o

Indentation amplitude, μm

DETECTION THRESHOLD

Contrast between skin regions with regard to
psychophysical and afferent unit thresholds

**C**

Indentation threshold, means (μm)

Afferent    Psychophys
threshold   threshold

Afferent   Psychophys
threshold   threshold

After obtaining such physiological data, Johansson & Vallbo acquired psychophysical data using the same set of stimuli applied to the same location on the skin surface. In the psychophysical task, subjects reported on each trial whether or not a skin indentation occurred within a brief, specified interval of time (yes/no task). Figure 6A (*crosses*) depicts a psychometric function obtained in this manner at the same skin location from which the illustrated neurometric data were recorded. Plainly, the neural data provide an excellent match to the psychophysical data, both in sensitivity (threshold) and in the slope of the functions.

This correspondence between neural and psychophysical sensitivity was typical of rapidly adapting mechanoreceptive fibers recorded from the most sensitive regions of the hand, particularly the volar surfaces of the finger tips. Interestingly, psychophysical thresholds increased substantially in less sensitive regions such as the palm and creased areas of the hand, but the thresholds of rapidly adapting fibers in these regions remained low. Figure 6B, for example, illustrates an experiment in which the neuronal threshold was roughly an order of magnitude lower than the psychophysical threshold. The summary histograms in Figure 6C show that this contrast held true, on average, over the entire data set.

This comparison of neural and psychophysical data leads to two compelling conclusions. First, psychophysical detection thresholds appear to be determined by the thresholds of rapidly adapting afferents in the most sensitive regions of the skin surface, consistent with the lower envelope principle. Second, single neurons are considerably more sensitive than the observer in certain regions of the skin surface. Surprisingly, human subjects appear unable to access the very sensitive information present in these mechanoreceptive fibers. In such cases performance would appear to be limited by noise sources or processing inefficiencies within the CNS. This is an awkward observation for the lower envelope principle.

## Experiments in Nonhuman Primates

VISUAL MOTION PERCEPTION    Several groups have carried out simultaneous acquisition of neural and psychophysical data in rhesus monkeys trained to perform threshold detection or discrimination tasks. Newsome and colleagues have performed an extensive study of the analysis of motion signals in extrastriate visual cortex (Newsome et al 1990, 1995). These investigators set out to determine whether the activity of directionally selective neurons in the visual cortex could account for the psychophysical performance on a forced-choice direction discrimination task. The experiments concentrated on two closely related areas of the extrastriate visual cortex, the middle temporal visual area (MT, or V5) and the medial superior temporal visual area (MST). For two reasons,

these areas are ideal for a rigorous comparison of neural and psychophysical performance. First, roughly 90% of MT and MST neurons are directionally selective, in that they respond optimally to stimulus motion in their preferred direction but little (or not at all) to the opposite or null direction (Dubner & Zeki 1971, Zeki 1974). These neurons appear to encode information appropriate for mediating perceptual judgments of motion direction (Movshon et al 1985, Rodman & Albright 1989). Secondly, lesion studies have confirmed that MT and MST play a prominent role in processing signals underlying motion perception (Newsome & Paré 1988, Marcar & Cowey 1992, Pasternak & Merigan 1994, Orban et al 1995).

Newsome and colleagues employed a direction discrimination task, in which performance depends in large measure upon information of the sort supplied by MT and MST neurons. The monkeys viewed a dynamic random dot display, in which a specified fraction of the dots moved coherently in a single direction while the remaining dots moved in random directions. On each trial the monkey reported whether the coherent dots moved in one direction or in the direction 180° opposite (up vs down, right vs left, etc). The ease or difficulty of the discrimination was determined by the proportion of dots in coherent motion. Psychometric functions were constructed by plotting the percentage of correct choices as a function of motion coherence level. These plots provided quantitative estimates of the sensitivity (threshold) and the slope of the psychometric function.

Each experiment began by determining the receptive field boundaries of a single neuron and its preferred direction and speed. The psychophysical task was then modified to match the visual stimuli to the physiological properties of the neuron, as illustrated in Figure 7. Stimuli were presented within the receptive field of the neuron, and the axis of the direction discrimination was aligned with the preferred-null axis of the neuron. In each experiment, therefore, the investigators arranged conditions so that the neuron under study was most likely to contribute to the perceptual judgments being made.

The responses of single neurons were then recorded while the monkey performed the discrimination task. MT and MST neurons were highly sensitive to the directional information in these displays, even for weak motion coherences. The neuronal responses were transformed into neurometric functions that express the performance expected of an ideal observer (in percent correct choices) that discriminates the direction of motion in the display based only on the responses of the neuron under study. Neural performance measured in this manner matched psychophysical performance remarkably well, both in sensitivity and in the slopes of the neurometric and psychometric functions. Figure 8A is a frequency histogram of the ratio of neural threshold to psychophysical threshold for 216 MT experiments performed in three monkeys.
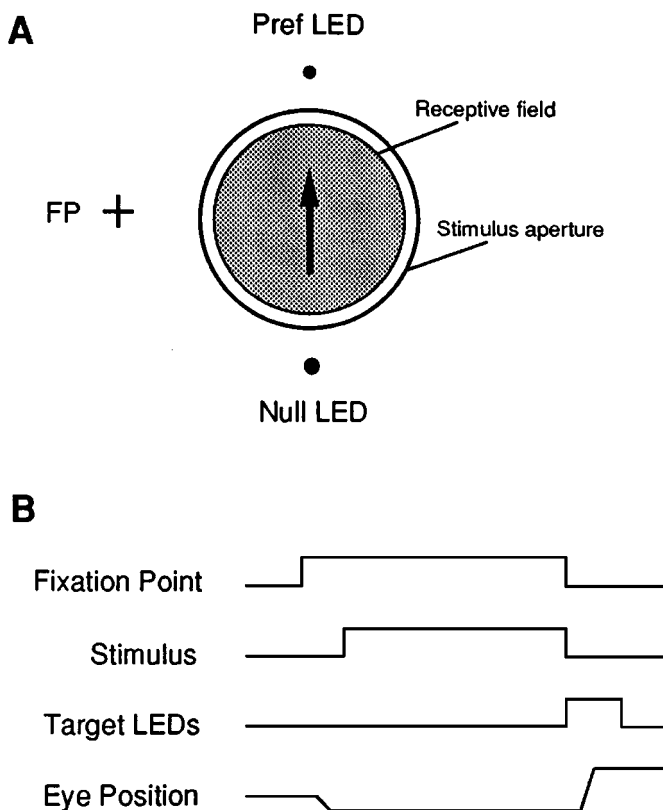
*Figure 7*   (*A*) The experimental procedure adopted by Britten et al (1992) for studying the directional thresholds of cortical neurons in middle temporal visual area (MT, or V5). The motion stimulus is aligned over the receptive field and its spatial properties match the receptive field size and eccentricity. The direction of coherent motion in the visual stimulus was either in the neuron's preferred direction (*arrow*) or in the direction 180° opposite. The monkey indicates its decisions about the direction of motion by making a saccadic eye movement to one of the two light-emitting diodes (LEDs) on either side of the motion stimulus. (*B*) The course of events in time during a single trial. A fixation point appears, and the monkey directs its gaze toward this point. The random dot stimulus appears for two seconds, after which the fixation point and visual stimulus disappear. Simultaneously, two LEDs appear, and the monkey indicates its decision by making a saccadic eye movement to the LED corresponding to the perceived direction of motion. (Reproduced with permission of the Society for Neuroscience.)
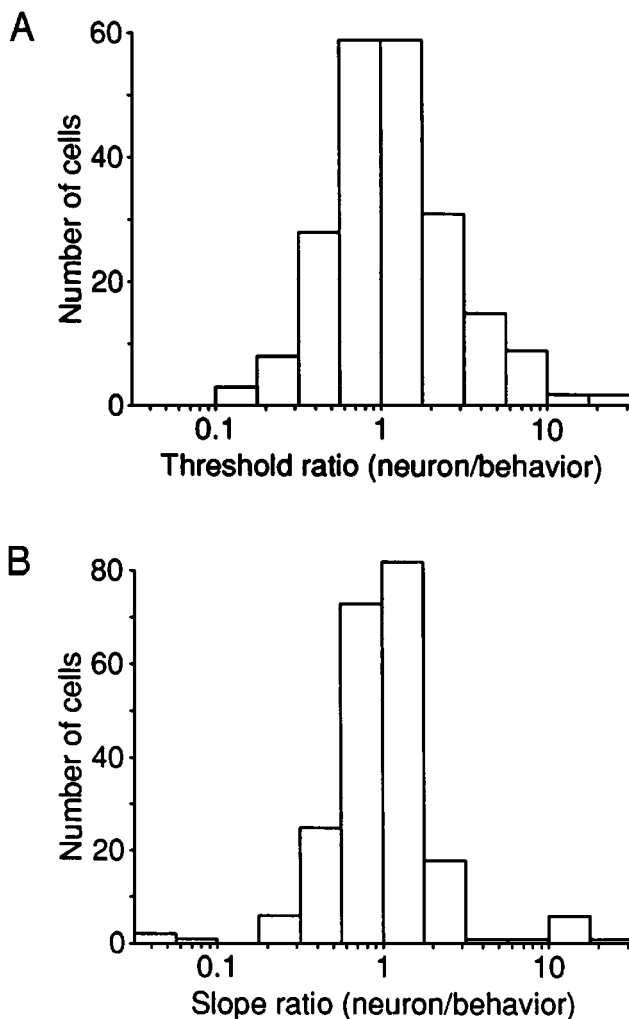
*Figure 8*   (*A*) A comparison of thresholds of 216 neurons in visual cortical area MT(V5) and simultaneously acquired behavioral thresholds from the monkey observers.  The neuronal thresholds are plotted relative to the behavioral threshold for a motion stimulus that just filled the receptive field and matched the neuron's preferred direction of movement.  (*B*) A similar comparison for the slopes of the neuronal and behavioral decision functions.  [Data of Britten et al (1992).]  (Reproduced with permission of the Society for Neuroscience.)

Figure 8*B* is a similar frequency histogram of slope ratios. The mean of both distributions is centered near unity, confirming the general congruence of neural and psychophysical data across the entire set of experiments (Newsome et al 1989, Britten et al 1992, Celebrini & Newsome 1994).

Plainly, however, considerable variability exists even for this data set collected under near optimal conditions. Note that neurons with relatively poor sensitivity (values lying to the right in Figure 8*A*) are not unexpected: Many such data points could be generated simply by recording from marginally directional cells. The more surprising outcome, as in the experiments of Vallbo and colleagues, is that many MT neurons appear to contain information that is not accessible perceptually to the observer. Again, central sources of noise or processing inefficiencies need to be invoked to account for these observations.

NOCICEPTION    There are some intriguing data from recordings of single nociceptive neurons in the trigemino-thalamic system of monkeys during the performance of a temperature increment detection task in the mildly nociceptive range. The experimental strategy was to use reaction time measurements as an indication of subjective pain intensity, and examine how mean reaction time covaried with mean neuronal response under a number of manipulations of the thermal stimuli. A specific subset of thermally sensitive neurons in the trigeminal nucleus (wide dynamic range 1, or WDR1, neurons) yielded mean responses that covaried with reaction time (Maixner et al 1986, 1989; Kenshalo et al 1989; Bushnell et al 1993).

Using the same paradigm, Bushnell et al (1993) characterized the responses of thermally sensitive neurons in VPM, a region of the thalamus that receives a direct input from the trigemino-thalamic tract. In contrast to the reaction time metric of subjective intensity, psychophysical thresholds were measured for the detection of small increments in temperature. The mean responses of thermally sensitive thalamic neurons rose monotonically with larger temperature increments, in parallel with the monkeys' performance.

SOMATOSENSORY DISCRIMINATION TASKS    Two new studies have appeared in which investigators recorded from neurons in the somatosensory cortex while monkeys discriminated various aspects of threshold mechanical stimuli: speed of movement (Romo et al 1996) and the texture of gratings (Sinclair & Burton 1991). As in the nociceptive studies above, each study identified neural signals that covaried monotonically with the monkeys' performance.

AUDITION    Remarkably, we have been unable to identify studies of the auditory pathways in which neural signals have been measured at the same time as the subject is performing at near-threshold levels in a detection or discrimination task. Although the activity of auditory nerve fibers has received considerable

experimental and theoretical attention (CD Geisler et al 1985, Young & Barta 1986), insight into the neural substrates of auditory perception will ultimately require investigation of the central auditory pathways in the context of specific psychophysical tasks.

### Summary

There are few studies that have measured the responses of neurons during the performance of a well-controlled psychophysical task. Of those studies, even fewer have seized the opportunity to assess neuronal sensitivity in a manner that can be compared directly to performance. As emphasized above, the tightest links between neuronal and behavioral performance can only be established by methods that take account of the reliability of both neural and psychophysical responses on a trial-by-trial basis. The establishment of a potential monotonic decision variable for a sensory judgment (as in the recent nociceptive and somatosensory studies of the CNS) is an important step, but it should be considered a prelude to more rigorous analysis.

Nonetheless, invaluable information has been gained from those studies that have acquired closely matched neuronal and behavioral data. Many of the conclusions from earlier studies survive, despite the worries about anesthetic state, etc. More significantly, these newer studies identify the presence of neurons whose performance exceeds that of the behavior generated by the observer. Realistic versions of both the lower envelope principle and pooling models allow for some central inefficiencies or sources of noise in central decision mechanisms. This additional variance can often be exploited in the models to help to bring the neuronal and the behavioral data into agreement. In the next section, we introduce a different experimental constraint that the models also need to match.

## TRIAL-TO-TRIAL COVARIATION BETWEEN NEURAL RESPONSE AND BEHAVIORAL CHOICE

### Interpretation of Covariation

Combined physiological and psychophysical experiments provide an important new constraint for evaluating the relationship between neural activity and perceptual performance. The essential insight underlying the new analysis is that both neuronal responses and psychophysical performance are noisy near threshold. A given neuron may or may not yield a spike (or may yield a variable number of spikes) in response to repeated presentations of a particular stimulus. Similarly, a psychophysical subject may detect (or correctly discriminate) such a stimulus on some trials while failing on others. Do the fluctuations of neural responses predict the probabilistic psychophysical decisions on a trial-to-trial

basis? A positive answer to this question adds powerfully to the case that a particular set of neurons is contributing to a perceptual judgment.

Neural responses and psychophysical decisions will covary trivially if the stimulus strength changes from trial to trial, possibly due to fluctuations in extraneous factors, as noted above in the case of thermal discrimination judgments. The more revealing case occurs when internal neural noise accounts for observed psychophysical variability upon successive presentations of externally identical stimuli. This sort of covariation cannot be driven by the environmental stimulus, but must arise from causal relationships within the nervous system.

Covariation of this type is not an exclusive prediction of either the lower envelope hypothesis or pooling models: The expected size of the covariation between neurons and observer depends essentially on the number of neurons being monitored to form the perceptual decision and the extent of any correlations between the signals on the neurons involved. For example, in the extreme where a single neuron is used for the psychophysical judgment, there should be a 100% correlation between fluctuations in the firing of the neuron and the behavioral choices of the observer. With a very large pool of uncorrelated neurons, the link between the behavioral choice and any particular neuron in the pool will be weak, regardless of whether the signals from the pool are combined by physiological summation (pooling models) or probability summation (lower envelope): If the pool contains correlated signals, this will strengthen the link between behavioral choice and neuronal firing.

## Signals in Mechanoreceptive Afferents

Clear results first emerged from microneurography experiments performed by Vallbo & Johansson (1976). They recorded from single mechanoreceptive fibers in humans while the subject attempted to detect brief indentations of the skin at the most sensitive point of the fiber's receptive field. For indentation amplitudes near neural threshold, a mechanoreceptive fiber typically responds with a single spike on some trials and fails to respond on others. Figure 9 illustrates results from a experiment in which the threshold of the mechanoreceptive fiber was near psychophysical threshold for the human subject. The subject detected the 10-$\mu$m skin indentation on 16 of 30 trials, while the fiber fired a spike on 17 of 30 trials. Remarkably, the occurrence of a spike on a given trial predicted psychophysical detection almost perfectly. The two differed on only one trial, in which a spike occurred but the subject failed to detect the stimulus. The firing of a single action potential by this fiber could account almost perfectly for the perceptual decisions of the human subject!

These observations strongly support an inference of causality between the neural response and the psychophysical decisions. They imply the existence of remarkably secure synaptic links between the somatosensory periphery and the
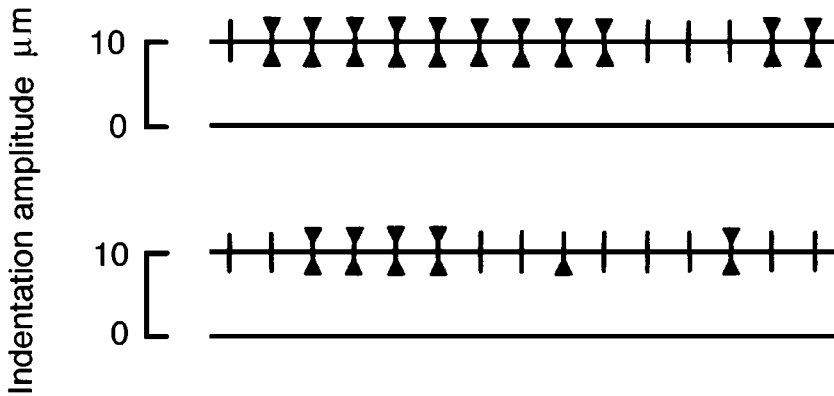
*Figure 9*   Two sets of dual trial-by-trial records (from Vallbo & Johansson 1976) of the correspondence between neuronal and behavioral responses. A single nerve fiber serving the hand of a conscious human observer was stimulated with a 10-$\mu$m indentation of the skin. Each stimulus presentation is marked by a *vertical line* crossing a *horizontal line*. A *filled triangle* attached to the vertical line below the horizontal line indicates the firing of a single action potential by a mechanoreceptive afferent fiber, and the absence of such a triangle indicates no neural response. A *filled (inverted) triangle* attached to the *vertical line* above the *horizontal line* indicates that the human observer reported the conscious detection of the skin indentation, and the absence of such a triangle indicates no detection by the observer. The high congruence of neural firing and action potentials implies that the subject is capable of consciously registering the presence or absence of a single action potential in this peripheral fiber. (Reproduced with permission of the authors.)

central sites where perceptual decisions are formed. Vallbo & Johansson argue, in fact, that a single action potential in the periphery can elicit a subjective percept in the human subject (Vallbo & Johansson 1976, Johansson & Vallbo 1979b, Vallbo 1995). They support this argument with calculations based on innervation densities, which suggest that only a single rapidly adapting fiber is likely to be activated by the threshold skin indentations used in their study (Johansson & Vallbo 1976, 1979a). Strong conclusions of this nature would be warranted, however, only if the results in Figure 9 can be reproduced and analyzed systematically. To our knowledge, this figure is the only example of a tight covariation between neural response and psychophysical decision anywhere in the microneurography literature. Given their undeniable importance, further experiments of this nature should be pursued aggressively.

## The Central Nervous System

TEMPERATURE DETECTION    Dubner et al (1989) appear to have been the first to report a trial-to-trial covariation between perceptual judgments and the activity of sensory neurons in the CNS. While a trained monkey attempted to detect

a temperature increment in a thermode applied to the glabrous skin of the face, the responses of thermally sensitive neurons were recorded in the nucleus of the trigeminal nerve. For a near-threshold temperature increment of 0.2°C (from a base of 46°C), the responses of WDR1 neurons were significantly greater on trials in which the monkey correctly detected the stimulus than on trials in which the monkey failed. Regrettably, the number of trials obtained was too few to quantify the covariation between neuronal and behavioral responses, but inspection of the available data suggests that the covariation was less perfect than for the mechanoreceptive fiber illustrated in Figure 9. Smaller covariances would be expected if many neurons in the trigeminal nucleus contributed to the psychophysical decision: The response variance of any single neuron would then account for only a small proportion of the total decision variance.

VISUAL MOTION DISCRIMINATION    Britten et al (1996) have performed the most extensive analysis to date of covariance between neural responses and perceptual judgments. Many trials were gathered during a direction-discrimination task (see above) for each of several motion coherence levels near or below psychophysical threshold; the monkey made errors on a substantial fraction of these trials. Quantitative analysis revealed a small, but significant, association between the responses of MT neurons and the behavioral choices: For repeated presentations of a given stimulus, the monkey tended to choose the preferred direction of a particular neuron more often when that neuron yielded a larger than average number of spikes. Britten and colleagues used a signal detection–based metric, which they termed the choice probability, to compute the proportion of trials on which an ideal observer could predict the animal's choice based on the responses of the MT neuron under study, given prior knowledge of the direction and coherence of the motion stimulus. The most impressive neurons permitted reliable prediction for roughly 70% of the trials, but the average value was a substantially more modest 56% (recall that random performance would be 50% correct). Celebrini & Newsome (1994) obtained very similar values for neurons in visual area MST, a closely related area of the motion pathway, and Thiele & Hoffman (1996) have reported a related phenomenon in MST and the superior temporal polysensory area (STPp).

## Potential Problems

Trial-to-trial covariation between neuronal response and psychophysical choices provides a potentially powerful tool for establishing the involvement of a particular pool of neurons in a perceptual judgment. Measurement of this covariation is, however, fraught with pitfalls (see Britten et al 1996, for a more extended discussion). Foremost among these is that misleading results can be obtained if the repeated stimulus presentations selected for analysis are not actually identical.

Somatosensory stimuli, for example, are notoriously difficult to deliver with great precision because of minute skin movements associated with respiration, pulse, etc. Visual stimuli in awake animals can vary from trial to trial because of small fixational eye movements (Gur et al 1997). Inherent stimulus variance of this nature, if sufficiently large, can drive both neuronal variance and decision variance, creating an illusion of neural and psychophysical covariation for stimuli that are erroneously assumed to be identical. A second difficulty is that many trials are required in order to obtain precise measurements if the covariation is subtle. For the average MT neuron, for example, 100–200 trials are required for reliable measurement. If, on the other hand, the trial-to-trial covariation is substantial, as in the microneurography data of Figure 9, fewer trials are necessary.

## LOWER ENVELOPE PRINCIPLE OR POOLING?

### The Significance of Stimulus-Independent Choices

Trial-to-trial covariation of neural response and behavioral choice provides an additional constraint for models that link neural activity to performance: They should predict psychophysical threshold and the slope of the psychometric function as before, but they must also account for the observed amplitude of the choice probability. For example, choice probabilities as large as those implied by Figure 9 would provide nearly incontrovertible support for the lower envelope principle or a pool with very small numbers of neurons. Nearly all the variance in the decision process would then be attributable to the response variance of a single sensory neuron.

Based on the very few studies currently available, choice probabilities are substantially weaker in the CNS. Nonetheless, even modest choice probabilities are remarkable in view of the many neurons potentially available to provide input to the psychophysical decision process. If these decisions were to depend upon the activity of a large pool of neurons whose response fluctuations are statistically independent, covariance between the psychophysical decision and a particular neuron's response would be vanishingly small because any single neuron would have little impact on the decision. However, many of the responses of adjacent cortical neurons are not independent but covary to a small but important extent (as reviewed above). Conceivably, then, correlated noise carried within large pools of sensory neurons could generate a measurable covariation with behavioral choices for each neuron in the pool.

### Pooling Models in MT

To test this possibility, Shadlen et al (1996) developed a response pooling model in which entire psychophysical experiments could be simulated (using Monte

Carlo techniques) together with the underlying neural responses on each trial. Importantly, the model (*a*) accepted experimentally measured MT responses as inputs, being faithful to both the mean and variance of the neurophysiological data, (*b*) incorporated measured levels of correlated noise among the MT inputs, (*c*) combined the MT inputs according to a simple additive response-pooling procedure, and (*d*) produced psychophysical decisions by a simple comparison of pooled MT signals of opposite preferred direction (e.g. up vs down). Benchmarks for the performance of the model were good matches between simulated and experimental values for (*a*) psychophysical threshold, (*b*) slopes of the psychometric functions, and (*c*) size of the choice probability. Major free parameters in the model were the number of input neurons (simulated pool sizes ranged from 1 to 1,024 neurons), the average sensitivity of the pool of input neurons (Is the input pool dominated by the best MT neurons, or does it include less sensitive ones?), and the amount of noise added by the central decision mechanism.

The experimentally determined benchmarks were fulfilled by a model in which the input pools were composed of at least 70–100 neurons; the performance of the model was essentially identical for all larger pool sizes because of the common noise carried by the input neurons. In addition, the input pools in the favored model contained large numbers of relatively insensitive MT neurons. Finally, the model incorporated noise associated with the central decision process. The nature of this decision noise and its implications for psychophysical performance are a matter of active investigation (MN Shadlen & WT Newsome, in preparation).

In the context of the model, the inclusion of relatively insensitive neurons in the pool and central decision noise addresses the problem created by the presence of some neurons whose performance considerably exceeds observed behavioral performance. The difficulty of this observation for the lower envelope principle has already been mentioned. Decision noise also contributed crucially to reconciling simulated with experimentally measured choice probabilities. Many specific aspects of this pooling model are open to debate and will undoubtedly require revision in the light of better experimental data and new theoretical insights. Nevertheless, the principles incorporated into the model have wide applicability and urgently need study in systems other than visual motion perception.

In addition to their pooling model, Shadlen et al (1996) also implemented a probability summation model, similar in some respects to the lower envelope principle: In order to have any degree of success, this model needed to draw information from neurons with a broad range of sensitivities, rather than selecting out just the most sensitive neurons in the pool, as the lower envelope principle would demand. The authors concluded that this small-numbers model was substantially less successful in accounting for the experimental data.

## Uncertainty

Both the lower envelope principle and pooling models require knowledge about which neurons should be monitored in order to extract information relevant to a particular perceptual task. For example, in its simplest form, the lower envelope principle asserts that observers can unerringly tap into a group of sensitive neurons that deliver the best available information for a particular sensory task. Pooling models also require rather specific knowledge about the nature of neuronal signals. In the example of the discrimination of motion direction (Shadlen et al 1996), the available neurons must be segregated rather carefully to form two pools so that a decision variable can be formed from the relative strengths of the signals for leftward vs rightward motion, or up vs down, and so on. Whichever model is favored, in order to get the best performance from its available sensory neurons, an organism needs to have information about how those neurons are most effectively applied to the perceptual task that currently confronts the organism. At the behavioral level, there is evidence that observers often respond as if they are to some degree uncertain about which of the available psychophysical detecting mechanisms are most appropriate (Tanner 1961, Pelli 1985, Graham 1989). This important aspect of perceptual behavior has not yet been addressed at the neuronal level.

## Models of Intensive Perceptual Judgments

The main topics of this review are simple detection and discrimination tasks and their neural underpinnings. We should point out, however, that much interesting work on the central pooling of neural signals has studied a rather different sort of psychophysical task: namely, subjective estimates of the intensity of a sensory stimulus. In general, psychophysical subjects can estimate intensity over a larger range of stimulus amplitudes than is coded by single neurons, whose responses tend to saturate (e.g. Kiang et al 1965, Barlow et al 1987). By pooling signals over a population of sensory neurons with different thresholds and different receptive field locations, however, neural metrics can be derived that correspond nicely to psychophysical performance. A classic analysis of this kind concerns the neural coding of the amplitude of vibratory somatosensory stimuli (Johnson 1974). This area of investigation is beyond the scope of the current review, but we refer the reader to other recent reviews for additional information (Johnson & Hsiao 1992, Burton & Sinclair 1996, Johnson et al 1996, Handwerker & Kobal 1993).

## Summary

Only two research projects have evaluated the lower envelope principle and pooling models in a way that analyzes choice probabilities as well as comparisons of neuronal and behavioral detection functions. These two projects have come to markedly different conclusions. In the somatosensory periphery,

considerable support has been gained for the lower envelope principle (Vallbo 1995), whereas for motion processing in cortical area MT(V5), the results favor a pooling approach (Shadlen et al 1996). Whether this situation reflects a fundamental difference between the periphery and the cortex will only be resolved with more work at both levels in behaving subjects.

## ELECTRICAL MICROSTIMULATION

### Interfering in the Causal Sequence

We have thus far reviewed increasingly sophisticated physiological, psychophysical, and computational data concerning the relationship between neural activity and perception. When applied in concert, in the context of well-controlled behavioral tasks, these approaches can build a compelling case for the involvement of specific sets of neurons in particular aspects of perception. Is it possible to build an even more certain case for causal relationships between neural activity and perception? With this question we turn to a consideration of electrical microstimulation experiments.

Since the pioneering studies of Penfield, Brindley, and others, sensory physiologists have been aware of the potential of electrical stimulation experiments for intervening in the causal relationship between the activity at specific loci in the nervous system and subjective perceptual experience (e.g. Penfield & Perot 1963, Brindley & Lewin 1968). Unfortunately, electrical stimulation techniques are sufficiently crude with respect to the intricate organization of cortical circuitry that the utility of this technique has generally been limited to the association of major cortical regions with gross visual, auditory, or somatosensory percepts. (Notable exceptions can occur at some stimulation sites in the superior temporal lobe—see Penfield & Perot 1963.)

### Microneurography

More recent studies, however, indicate that electrical microstimulation, employed in appropriately designed experiments, can provide important insights. The first provocative example arose from microneurography experiments in which the investigators attempted to stimulate a particular mechanoreceptive fiber electrically after determining its receptive field location and physiological properties using standard neurographic recording procedures (Ochoa & Torebjörk 1983, Vallbo et al 1984). In general, the human subjects experienced a subjective sensation after the intensity of the stimulation current reached a particular threshold value, which varied somewhat from experiment to experiment [typically 0.5–2.0 $\mu$A in the experiments of Vallbo et al (1984)]. The electrically evoked sensation was usually described as a light indentation at a specific location on the skin surface, although its quality sometimes seemed "odd" or

"exotic" (Vallbo 1995). In roughly 50% of their stimulation experiments, the projective field of the electrically evoked sensation (i.e. the region of skin surface where the sensation occurred) coincided with the receptive field of the fiber mapped during the recording phase of the experiment. This elementary sensation usually remained stable as the experimenters raised the amplitude of the stimulating current until a second threshold point was reached and a second sensation occurred, simultaneously with the first, but at a different point on the skin surface. The simplest interpretation of these data is that a second fiber was recruited at higher stimulation amplitudes, giving rise to a separate elementary sensation.

Whether the microneurographers have actually succeeded in recording from and stimulating single mechanoreceptive fibers has proved controversial (Wall & McMahon 1985, Torebjörk et al 1987, Calancie & Stein 1988). The issues at stake are substantial. For example, the subjective quality of the electrically evoked sensation appears to correspond to the specific type of mechanoreceptive fiber stimulated if the trains of electrical pulses are sufficiently long. Thus electrical stimulation of rapidly adapting fibers tends to be associated with sensations of vibration or movement, while stimulation of slowly adapting fibers is more typically associated with sensations of light touch or sustained pressure (Ochoa & Torebjörk 1983). Observations of this nature, while necessarily subjective and somewhat anecdotal, strongly support "labelled line" theories of sensory encoding, in which the activity of specific peripheral receptors gives rise to specific elementary sensations. Vallbo (1995) also employs the microstimulation results to add to the case that a single action potential in a single peripheral fiber can elicit a subjective sensation. No stronger claim could be made for the significance of single action potentials. The data do currently point in this direction, but our own judgment would be influenced strongly by more detailed and systematic studies of trial-to-trial covariation between the neural response and behavioral choice.

## Visual Motion Perception

To date, electrical microstimulation has rarely proven to be an incisive experimental tool in sensory regions of the CNS. Recently, however, microstimulation has been used to probe whether there is a causal link between directionally selective neurons in the visual cortex and performance on a direction discrimination task (Salzman et al 1990, 1992; Murasugi et al 1993; Celebrini & Newsome 1994; Salzman & Newsome 1994). Neurons in extrastriate areas MT and MST of the rhesus monkey are organized in columns such that neurons in a given column tend to have a common preferred direction and receptive field location (Albright et al 1984, Malonek et al 1994). By electrically stimulating a single column, the experimenters attempted to insert into the cortical circuitry

an artificial signal representing a particular direction of stimulus motion. The key experimental question was whether this artificial signal, when applied simultaneously with an ambiguous visual motion stimulus, would influence a monkey's perceptual judgments.

Remarkably, microstimulation at a single location in MT or MST could exert striking effects on the monkeys' perceptual choices that were predictable from the physiological properties of the stimulated column. In one experiment, for example, stimulation of a column encoding upward motion induced a bias in the monkey's choices toward the upward direction. In the same experiment, the microelectrode was then advanced 300 $\mu$m into a "down" column, and the same stimulation protocol produced an excess of downward judgments (Salzman et al 1992). Such experiments establish conclusively that activity in directionally specific circuits of the monkey's visual cortex underlies judgments of motion direction in the psychophysical task used by these investigators.

## Summary

These recent experiments that use microstimulation are exciting but should be interpreted carefully. First, they do not indicate that a complex visual stimulus is completely encoded by the neurons at a single location in the cortex. Obviously, the random-dot motion stimuli excite vast numbers of neurons in many regions of the cortex, and this pattern of excitation is not recreated by stimulation of a single site in MT or MST. Rather, the experiments suggest that stimulation of an appropriate site in the cortex can add a single fundamental quality or attribute to a stimulus already present in the environment and encoded in a complex pattern of activity across the visual cortex. Thus, if the animal were looking at a natural object, such as a banana, we envisage that the onset of microstimulation would tend to induce the animal to report the object as moving in the direction corresponding to the direction preferences of neurons at the site of the stimulating electrode. This all implies that the computation of motion within the cortex is, to some extent, distinct: Motion appears to be computed separately and assigned as an attribute of a particular stimulus in the environment.

Second, there is no definitive evidence about the subjective experience of the animal during microstimulation. A number of indirect arguments suggest that the microstimulation indeed elicits a sensation of motion (Salzman et al 1992), but ultimately, our only sure knowledge concerns the animal's reports, not the sensations. We suspect that this issue can only be settled by experiments in human subjects. Finally, microstimulation experiments by themselves are no substitute for a careful analysis of signals at the single unit level. Even with a positive result in hand from microstimulation, how the system actually works would remain a mystery without knowledge of the sensitivity and covariance of signals carried by single sensory neurons, the effects of central

pooling, and the extent of trial-to-trial covariation between neural and behavioral responses. Microstimulation, even when successful, is one piece of a very complex puzzle.

## CONCLUDING REMARKS

We have traced the development of ideas linking neural activity to perception—from the straightforward comparison of statistically defined neural and behavioral thresholds through to attempts to intervene directly in the perceptual process by electrical stimulation. Throughout this development, analytical and experimental approaches have become increasingly sophisticated, with profound consequences for conceptual thinking about the relationship between neural firing and perception. Each development (measurement of signals carried by single neurons, effects of pooling, effects of covariation in the neuronal population, covariation between neural responses and behavior, microstimulation) has individually brought new insights but also now contributes to a concerted approach that can be applied to different systems and perceptual tasks.

We have dealt almost exclusively with neural codes based on spike rate or spike counts, with considerable success in many cases. Alternative codes have been proposed based on the temporal pattern of spikes from individual neurons or on the temporal interrelationships between spikes in different neurons (e.g. Abeles 1991, Richmond & Optican 1992, Singer & Gray 1995, deCharms & Merzenich 1996). Obviously, temporally based codes in sensory systems are likely to be particularly relevant when the perceptual judgment requires a discrimination of some temporal component of the stimulus. The evidence for temporal codes in nontemporal tasks, however, is substantially weaker. If such proposals are to be taken seriously, the candidate neural code should fulfill the kinds of criteria that we have advanced here. Thus, the coded signal must be evaluated statistically for comparison with the behavioral thresholds, slopes of psychometric functions, effects of pooling and trial-to-trial covariance with behavior, and so on. It is also reasonable to propose that where a neuron appears to be capable of delivering two possible codes, the preference for one code over another should be judged in the light of how well the codes meet the criteria advanced at the beginning of this review.

If we refer back to this list of criteria, it is evident that no set of measurements has completed a basic set of critical experiments, even for just one perceptual task, one set of candidate neurons, and one type of neural code. Nonetheless, there is now substantial agreement on what those sets of measurements should contain, and this must be counted one of the successes of the past 30–40 years. There is far less agreement about the number of neurons that are involved in particular perceptual tasks. Here the study of different systems and different tasks has led to widely diverse conclusions: In the peripheral axons of the human

somatosensory system, a single action potential is thought to be a perceptually significant event, whereas in the central visual area MT(V5), perceptual judgments of motion direction are thought to depend on the pooled activity of at least 100 neurons, and possibly more. Two conclusions can be drawn here. First and simply, it would be invaluable to have new studies in other regions of the sensory systems with different perceptual tasks in order to bring out the generality of any conclusions. Second and more subtly, the nature of the cognitive decision processes proves to be highly influential on the interpretation of the basic sensory data. Studies comparing the neural and psychological processes during simple decision making are timely, feasible, and of the greatest interest.

The work considered here has done much to open the black box, by directly examining the neural signals involved in psychological processes that had previously been hypothetical entities. Even so, many mysteries remain. Consider the entire sequence of neural events that is initiated by the arrival of a simple stimulus during a perceptual task. Sensory signals must be accumulated over an appropriate time interval as evidence builds toward the formation of a decision; an internal sensory criterion must be maintained by the observer; a decision must be formed and held in short-term memory until the time for response arrives; and the decision must be mapped flexibly onto appropriate motor response systems. The neural mechanisms underlying most of these stages are as yet unobserved and unanalyzed, yet they shape perceptual performance no less significantly than the initial sensory transduction events. Arguably, the attempt to understand perceptual performance from input to output is the neuroscientist's surest route to an experimentally based "cognitive neuroscience" that examines the neural mechanisms underlying mental phenomena, such as short-term memory and decision-making. The accomplishments of the past 30 years have brought these previously abstract processes within the scope of physiological investigation.

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