Chapter One

Cross-Talk Between Psychophysics and Physiology in the Study of Perception[1]

E. Bruce Goldstein

All perception is neural activity.

Casagrande & Norton, 1991, p. 42

You can observe a lot by watching.

Yogi Berra

The illusion that perception is a simple process follows from the ease with which we perceive. The reality, however, is that perception is the outcome of an extraordinary process that is accomplished by mechanisms which, in their exquisite complexity, work so well that the outcome – our awareness of the environment and our ability to navigate through it – occurs effortlessly under most conditions.

This *Handbook* is a record of the progress we have made towards uncovering the complexities of perception. This progress has been achieved by research that has approached the study of perception psychophysically (studying the relationship between the stimulus and perception) and physiologically (studying the relationship between physiological events and perception). The purpose of this chapter is to show that the psychophysical and physiological approaches not only make their individual contributions to understanding perception, but also that they often function in collaboration with one another. The message of this chapter is that this collaboration, or "cross-talk," has been and will continue to be a crucial component of perceptual research.

Psychophysical, Physiological and Linking Relationships in Perceptual Research

The basic relationships of perceptual research are diagramed in Figure 1.1. The three relationships are (a) relationship ϕ, between stimuli and the physiological response; (b) relationship ψ, between stimuli and the perceptual response; and (c) relationship L, between the physiological response and the perceptual response.

Relationship ϕ, the physiological relationship, is the dominant method for studying the physiological workings of perceptual mechanisms. Emblematic of this approach is classic research such as Hubel and Wiesel's (1959, 1962) specification of the response and organization of neurons in the cat and monkey visual system; Kiang's (1965) measurement of frequency tuning curves in the cochlear nucleus of the cat; and Mountcastle and Powell's (1959) research on the relationship between tactile stimulation and the response of neurons in the monkey's somatosensory cortex.

Relationship ψ is studied by what are usually called the psychophysical methods. These methods include the classic Fechnerian methods used to determine thresholds (Fechner, 1860), and Stevens' (1961) magnitude estimation techniques for scaling above-threshold experience. For the purposes of this chapter, we will also include as psychophysics any technique that measures the relationship between stimuli and response, including phenomenological observations (cf. Katz, 1935) and measures such as identification, recognition, and reaction time.
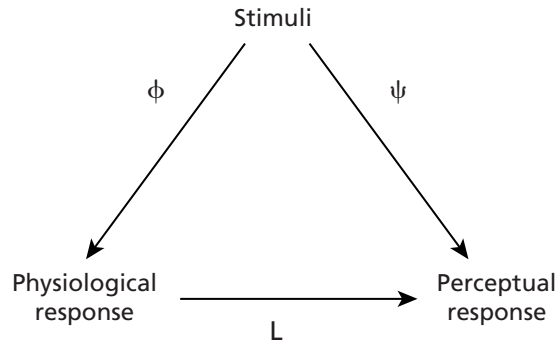
Figure 1.1. The basic relationships of perceptual research. See text for details.

Relationship L is the linking relationship between physiology and perception. Determining this relationship is often the ultimate goal for those concerned with determining the physiological basis of perception, but it is the most problematic to measure. The core problem is that it is difficult to measure both physiological responding and perceptual response in the same subject (although, as we will see, not impossible). Because of the difficulty in simultaneously measuring physiological and perceptual responding, relationship L has often been inferred from independent measurements of relationships ψ and ϕ, often with relationship ψ determined in humans, and relationship ϕ in animals. When relationship L is determined by inference from relationships ψ and ϕ, it is called a linking hypothesis (see Teller, 1984, who considers in some detail the factors involved in making this inference; also see Teller & Pugh, 1983).

One goal of this chapter is to show how these three relationships are interrelated. This may seem like a modest goal, because these relationships must, of necessity, be related, as they are all components of the same system. However, our interest extends beyond simply identifying relationships, to considering the *processes* by which these relationships have been discovered. Approached from this perspective, it becomes clear that the discovery of one relationship has often been dependent on or facilitated by knowledge gained from another of the relationships, with the physiological and psychophysical approaches being engaged in "cross-talk," which directs, informs, and enhances the creation of knowledge on both sides of the methodological divide. We begin by considering how psychophysics provides the foundation for physiological research on perception, and will then consider examples of how cross-talk between psychophysics and physiology has helped determine (a) the mechanisms, and (b) the locus of operation of these mechanisms.

Before beginning the discussion, a few caveats are in order. The highlighting of instances of cross-talk between psychophysics and physiology does not mean that the psychophysical and physiological approaches cannot be profitably pursued independently of one another. There is a vast physiological literature that is concerned primarily with determining basic physiological mechanisms of sensory systems (although even these experiments are often motivated by a desire to link physiological functioning and perceptual

outcomes). Conversely, some psychologists have taken a purely psychophysical approach, with the idea being to explain perception by focusing solely on psychophysically defined relationships (cf. Gibson, 1950, 1979; Sedgwick, Chapter 5 for visual examples; Yost, Chapter 14 and Dowling, Chapter 15 for auditory examples)[2]. This "pure psychophysics" approach is reminiscent of Skinner's (1953) behaviorism, which is based on determination of stimulus-response contingencies, without any reference to what is happening inside the "black box."

Psychophysics as Guiding Physiological Research

One of the primary outcomes of psychophysical research is determination of the stimulus parameters that are relevant for perception. Knowing that there is a relationship between wavelength and hue, frequency and pitch, binocular disparity and depth perception, and the temporal relationship between two flashing lights and the movement that is perceived between them, not only defines the phenomena of perception, but focuses attention on the stimulus information that is relevant to perception.

Consider, for example, the discovery that binocular disparity can provide sufficient information for depth perception (Julesz, 1964; Wheatstone, 1838). This finding not only formed the basis of psychophysical research on binocular depth perception, but guided physiological research as well. Imagine what the search for the neural signal for depth perception would have been like had disparity been unknown. Physiologists might still have discovered neurons that respond best to objects located at different distances, but to understand the nature of the stimulus information driving these neurons, the role that binocular disparity plays in depth perception would eventually have had to be discovered as well. Luckily, the psychophysicists had made this discovery long before the physiologists recorded from neurons that respond to binocular disparity in the striate cortex (Barlow, Blakemore, & Pettigrew, 1967).

In addition to identifying relevant stimulus parameters, psychophysics has often determined ψ relationships that have provided "system specifications" for physiology to explain. The classic example of this "system specification" is Hecht, Shlaer, and Pirenne's (1942) conclusion, based on psychophysical measurements, that the absolute threshold for rod vision is about 7 quanta, and that these quanta are absorbed by 7 visual pigment molecules, each located in a different receptor. From this conclusion it follows that isomerization of a single visual pigment molecule is adequate to excite a receptor.

This conclusion that isomerizing only one visual pigment molecule can excite a receptor threw down the gauntlet to researchers who were searching for the molecular mechanism of visual transduction, by requiring that this mechanism explain how isomerization of only one out of the 100 million molecules in a receptor (cf. Wandell, 1995) can cause such a large effect. Researchers realized that the answer probably involved some type of amplification mechanism (Wald, 1968; Wald, Brown, & Gibbons, 1963) but it wasn't until over 40 years after Hecht et al.'s psychophysical observation that the "enzyme cascade" responsible for this amplification was described (Baylor, 1992; Ranganathan, Harris, & Zuker, 1991; Stryer, 1986).

What is notable about the role of psychophysics in the Hecht et al. example is that a psychophysical result led to a physiological prediction at the molecular level. Not all psychophysical research has achieved specification at that level, but there are numerous examples of situations in which psychophysical data have helped guide further physiological research. Consider, for example, the ψ finding in the auditory system that listeners can detect frequency differences of just a few Hz (depending on the frequency range being tested). However, Bekesy's (1942, 1960) determination of the ϕ relationship between frequency and basilar membrane vibration indicated tuning too broad to explain this frequency selectivity, especially at low frequencies. This mismatch between the ϕ and ψ relationships motivated a search for a physiological mechanism that would discriminate between nearby frequencies. Eventually, more accurate measurement of basilar membrane vibration using Mossbauer techniques in living animals revealed that the tuning of basilar membrane vibration was much sharper than indicated by Bekesy's original measurements (Johnstone & Boyle, 1967; Johnstone, Patuzzi, & Yates, 1986). (See Moore, Chapter 12, p. 389.)

Specifying Physiological Mechanisms

The two examples above describe situations in which psychophysical results motivated further physiological research. In both cases, the psychophysical results furnished physiological researchers with specific goals: identification of the molecular amplification mechanism in the visual example, and identification of physiological responses that can signal small frequency differences in the auditory example. But psychophysical results can go beyond simply posing questions for physiologists to answer. They can suggest theories regarding physiological mechanisms. The rationale behind this inference of physiological mechanisms from psychophysics is illustrated in Figure 1.2.

Figure 1.2a shows a mechanical device consisting of two rods protruding from a black box. The rod at A represents the *stimulus* in a psychophysical relationship, and the rod at B represents the *response*. Our goal is to determine what is happening inside the black box, by determining the relationship between the stimulus at A and the response at B. In our first "psychophysical" experiment, we move the rod at A to the right and observe a corresponding rightward movement at B. Based on this stimulus-response relationship, we can venture a guess as to what is happening inside the black box. One possibility is that the rods at A and B are connected, or are part of the same rod (Figure 1.2b). To check the validity of this hypothesis we do another experiment, pulling rod A to the left. When we do this, rod B remains motionless, a result that invalidates our original hypothesis, and leads to a new one, shown in Figure 1.2c. To determine whether this is the correct hypothesis, we can do further psychophysical experiments, or we can move to the physiological approach and look inside the black box. What we see may confirm our psychophysically based hypothesis, may partially confirm it (the physiology and psychophysics match, but not exactly), or may disconfirm it altogether. All of these outcomes have occurred in perceptual research. We now consider color vision, which provides an example of a situation in which psychophysical results led to predictions of physiological mechanisms long before physiological measurements were available.
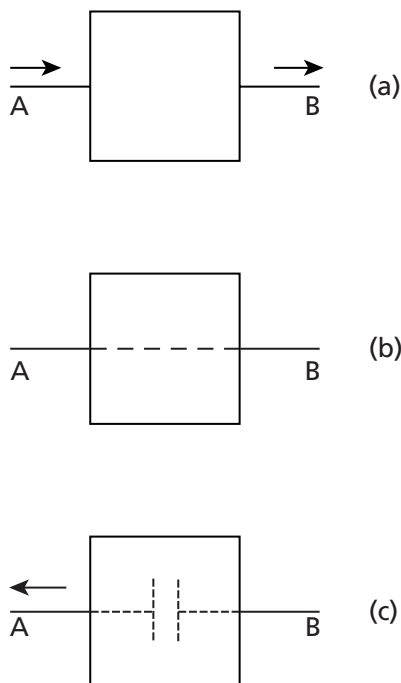
Figure 1.2. Mechanical analogue illustrating the process of inferring mechanisms within the black box, based on relationships observed between stimulus at A and response at B. (a) Moving the rod to the right at A causes rightward movement at B. (b) Hypothesized internal mechanism: The rod is continuous from A to B. (c) Moving the rod to the left at A causes no response at B, so a new mechanism, shown by the dashed line, replaces the old hypothesis.

Theories of Color Vision

Color vision provides the classic example of psychophysics predicting physiology, because color vision research and theorizing stretches from the 19th century, when psychophysics stood alone because the necessary physiological technology was unavailable, to the present, when psychophysical and physiological research often occur side by side. Adding to the interest in color vision is the proposal of two competing theories, the trichromatic (Helmholtz, 1852; Young, 1802) and opponent-process (Hering, 1878, 1964) theories of color vision. Trichromatic theory has its roots in the following assertion, by Young (1802):

> Now as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles . . . . it becomes necessary to suppose the number limited; for instance to the three principal colours, red, yellow, and blue . . . . each sensitive filament of the nerve may consist of three portions, one for each principal colour.

This statement is derived mainly from psychophysics but assumes some physiology. On

the physiological side is the mention of the retina, which was known to be the light-sensitive surface upon which images were formed and vision began. On the psychophysical side are color-matching experiments, which indicate that people with normal color vision can match any wavelength by mixing a minimum of three other wavelengths. This psychophysical fact was the evidence behind the idea of "three principal colours."

Another important psychophysical fact that followed from the color-matching experiments was the phenomenon of metamerism. When subjects match one wavelength by mixing the correct proportions of two other wavelengths, they have created two fields that are physically different, but perceptually identical. The fact that physically different stimuli can lead to the same perception implies that the physiology underlying these perceptual responses may be identical (see Teller, 1984), a property which is a key feature of trichromatic theory's assertions (a) that the basis of color vision is the pattern of firing of three mechanisms, and (b) that two physically different wavelength distributions can result in the same patterns of firing.

In the years following the proposal of trichromatic theory, various functions were proposed for the three mechanisms (e.g., Stiles, 1953), but accurate specification of these mechanisms had to await physiological measurement of cone absorption spectra (Bowmaker & Darntall, 1980; Brown & Wald, 1964). Thus, the general form of the physiology (three mechanisms) was correctly predicted by psychophysics, but it was necessary to look into the black box to determine the details (pigment absorption spectra).

Opponent-process theory, as described by Hering, postulated that color vision was the result of three opposing processes, red-green, blue-yellow, and black-white, with white, yellow, and red causing a chemical reaction that results in the buildup of a chemical and black, blue, and green causing a reaction that results in a breakdown of the chemical. These physiological predictions were based on phenomenological observations, such as the fact that it is difficult to imagine a bluish-yellow or a reddish-green.

Years after Hering's proposal, modern physiological research revealed opponent S-potentials in the fish retina (Svaetichin, 1956) and opponent single unit responding in the monkey lateral geniculate nucleus (DeValois, 1965; DeValois, Jacobs, & Jones, 1963), thus confirming Hering's predicted opponency and replacing his proposed chemical reactions with neural excitation and inhibition. Around the same time that these opponent physiological mechanisms were being revealed, Jameson and Hurvich (1955; also Hurvich & Jameson, 1957) were using a quantitatively precise psychophysical cancellation procedure to specify the strengths of the opponent mechanisms. Cross-talk, if it existed, between physiology and psychophysics is not obvious from journal citations (e.g., the Hurvich and Jameson papers were not liberally cited in physiological papers of the time), although Hurvich and Jameson's papers are now considered classics.

Whatever the nature of the interaction between opponent psychophysics and color vision physiology, the physiological research was necessary not only to confirm Hering's prediction of opponency, but to gain the theory's acceptance by color vision researchers. A contest pitting Helmholtz's prestige and the quantitative nature of color-matching data against an unlikely physiological mechanism derived from Hering's phenomenological observations translated into color vision research of the 1950s being a largely trichromatic world. As late as the 1960s, Hering's theory was mentioned only briefly or not at all in the discussions of color vision in prominent texts, even after publication of the Hurvich and

Jameson papers (Brindley, 1960; LeGrand, 1957; Pirenne, 1967; but see Graham, 1959 for an early acknowledgement of the Hurvich and Jameson work). Eventually, opponent physiology, with DeValois' single-unit work being especially important, gained acceptance for opponent theory, and the "contest" was over, with trichromatic responding being recognized as the outcome of receptor physiology, and opponent responding as the outcome of subsequent neural wiring.

The story of color vision does not, however, end with the physiological confirmation of trichromatic and opponent-process theories, because what the physiologists saw inside the black box matched the psychophysics on a general level only. There is not a one-to-one match, for example, between many of the electrophysiologically determined opponent functions and Hurvich and Jameson's psychophysically determined functions. Also psychophysical experiments in which parameters such as spot size and illumination are varied have revealed complexities that demand further physiological investigation (Hood & Finkelstein, 1983), and we are far from understanding the physiology of color vision at the cortical level (Lennie, 2000; Chapter 4, this volume).

In summary, color vision provides an instructive story of continuing cross-talk between psychophysics and physiology. Early psychophysics led to the proposal of physiological theories, later physiological research confirmed the general outlines of these theories, and then further psychophysical research raised new questions to be answered by additional physiological research. This is similar in some respects to the example, described above, of auditory frequency discrimination, in which the absence of a match between physiologically and psychophysically determined capacities led to further physiological research.

Lateral Interactions in the Retina

Another example of psychophysics predicting physiology is provided by Mach bands, the illusory light and dark bands seen at the borders of contours. Ernst Mach (1865) carried out a mathematical analysis of these bands, and concluded that the bands "can only be explained on the basis of a reciprocal action of neighboring areas of the retina" (Ratliff, 1965, p. 98). Mach further described this reciprocal interaction in terms of excitatory and inhibitory influences. Although Mach's conclusions were correct, they were largely ignored, because the necessary physiological techniques were not available for confirmation (Ratliff, 1965). This situation, which is reminiscent of the fate of Hering's opponent-process theory, was finally rectified almost 100 years later by electrophysiological demonstrations of lateral inhibition in the Limulus (Barlow, 1953; Hartline, 1949; Hartline, Wagner, & Ratliff, 1956; Ratliff & Hartline, 1959). Again, physiology resurrected a psychophysically based physiological theory. However, as was the case for color vision, numerous discrepancies between the psychophysics and physiology remained to be worked out (Ratliff, 1965).

Mechanisms of Pitch Perception

The auditory system provides a number of examples of cross-talk between psychophysics and physiology. We note the following three psychophysical findings, which have had

physiological repercussions: (a) the ability to "hear out" components of a chord; (b) periodicity pitch, the constancy of pitch perception when a complex tone's fundamental frequency is removed (periodicity pitch); and (c) the effects of auditory masking (see Moore, Chapters 12 and 13).

Hearing Out Components of a Chord

In the early 19th century, Ohm proposed his acoustic law, which stated that the ear analyzes a complex tone into its components (Bekesy, 1960). Ohm's acoustic law, plus observations by Helmholtz and others that when a number of tones are combined to create a chord, it is possible for trained listeners to "hear out" the individual notes that make up the chord (see Plomp & Mimpen, 1968), indicated that pitch perception operates in an analytic fashion. This contrasts with vision, which operates in a synthetic fashion, so when two colors are mixed (say red and green) to create a third (yellow), the components of the mixture are not perceived.

The phenomenologically observed analytic nature of pitch perception was the basis of Helmholtz's (1865) resonance-place theory of pitch, which stated that a particular frequency was signaled by the vibration of individual fibers, arranged along the basilar membrane in a tonotopic fashion, like the strings inside a piano. This conception provided a system in which components of a complex tone stimulate different receptors and are processed in separate channels, thus enabling listeners to hear out the components of a chord.

Helmholtz's proposal provides an example of a psychophysically inspired physiological theory, but this time (in contrast with his proposal of trichromatic theory), the proposed physiology was wrong. After almost a century of dominating auditory theory, the resonance-place theory fell victim to Bekesy's (1942, 1943) observation that the basilar membrane vibrates in a traveling wave. Licklider's (1959) commentary that "Almost overnight, the problem that everyone had been theorizing about, was empirically solved" (p. 44) acknowledges the power of looking inside the Black Box. This observation of the actual physiology kept the place concept, but replaced resonating fibers with a wave traveling down the membrane. As noted above, Bekesy's measurement of the basilar membrane's vibration did not, however, put the problem of frequency discrimination to rest. More accurate specification of the basilar membrane vibration was needed to explain the precision of psychophysically measured frequency discrimination.

Periodicity Pitch

The psychophysical observation of excellent frequency discrimination was eventually explained physiologically. However, another psychophysical observation, that the pitch of a complex tone remains constant, even when its fundamental frequency is eliminated (Fletcher, 1929), has posed more difficult problems. This effect, which is called *periodicity pitch* or *the effect of the missing fundamental*, has had a large influence on auditory research and theorizing. Periodicity pitch is difficult for a strict place theory to explain, it provides evidence favoring a temporal approach to frequency coding, and it has caused some theorists to focus more centrally in the auditory system in their search for an explanation for auditory pitch coding (Meddis & Hewitt, 1991; Srulovicz & Goldstein, 1983).

The Effect of Masking

The auditory masking experiments of Fletcher (1938) and others provided psychophysical evidence for the localization of frequencies along the basilar membrane, and led to the concept of the critical band – channels that independently analyze a narrow band of frequencies. The cochlea's analysis of frequency occurs, according to this psychophysically based idea, through the action of filters tuned to small frequency ranges. (Also see Schafer, Gales, Shewmaker, and Thompson (1950), who explicitly equated the critical band with tuned filters.) These tuned filters were subsequently demonstrated physiologically by single unit recordings of frequency tuning curves from neurons in the cat's auditory nerve (Galambos & Davis, 1943) and cochlear nucleus (Kiang, 1965). (Also see Zwicker, 1974, who demonstrated a correspondence between Kiang's neural tuning curves and psychophysical tuning curves, determined using a different masking procedure.)

It could be argued that perhaps the electrophysiologists might have discovered the neural tuning curves on their own, without any prior knowledge of psychophysics. If, however, history had turned out that way, it would still have been necessary for the psychophysicists to give perceptual reality to the physiologists' neural filters. In fact, discovery of the neural filters for visual features provides an example of such a sequence of discovery, with the physiological discovery of visual feature detectors just preceding the psychophysical measurement of these detectors.

Detectors for Orientation, Size and Spatial Frequency

In the previous examples, psychophysical observations predated the relevant physiology by many years. In these situations, it is appropriate to call the relationship between psychophysics and physiology a predictive relationship. However, sometimes parallel developments in psychophysics and physiology have coexisted closely in time, a situation which might be called a synergistic relationship. This appears to be the case for research on neurons in the visual system that respond selectively to stimuli with specific orientations, directions of motion, or sizes. (Note that in the literature size has been discussed mainly in terms of spatial frequency, where small sizes correspond to high spatial frequencies, large sizes to low spatial frequencies.) We will focus on orientation and spatial frequency.

One of the earliest references to such neurons was Hubel and Wiesel's (1959) pioneering paper describing receptive fields of neurons in the cat striate cortex. In that paper they state that "the particular arrangements within receptive fields of excitatory and inhibitory regions seem to determine the form, size and orientation of the most effective stimuli . . ." (p. 588). Thus began a series of papers describing the properties of receptive fields of single neurons in the cat cortex (Hubel & Wiesel, 1962, 1965, 1968). These papers, plus others such as Lettvin, Maturana, McCulloch, and Pitts' (1959) cleverly titled paper, "What the frog's eye tells the frog's brain," led to the concept of specialized neural detectors in the visual system (see Frishman, Chapter 3; Levine, Chapter 2).

Campbell and Kulikowski (1966), in one of the first papers to look for psychophysical evidence of feature detectors, began their paper with a reference to Hubel and Wiesel,

followed by a question: "Hubel and Wiesel (1959, 1962) have shown that many of the cells in the visual cortex of the cat respond only to lines with a certain orientation . . . Is it possible to demonstrate in man psychophysically a similar orientational selectivity?" (pp. 437–438). Campbell and Kulikowski's affirmative answer to their question was followed by a flurry of experiments demonstrating the existence of orientation, size, and spatial frequency channels in humans (Blakemore & Campbell, 1969; Blakemore & Sutton, 1969; Campbell & Kulikowski, 1966; Campbell & Robson, 1968; Gilinski, 1968; Pantle & Sekuler, 1968). The primary psychophysical procedure in most of these experiments was selective adaptation, in which the effect of an adapting exposure to a particular orientation, size, or spatial frequency on subsequent sensitivity to that feature was determined. The resulting decrease in sensitivity, which usually occurred across a narrow band of orientations or frequencies, was taken as an indication of the tuning of the relevant detector.

The synergy between psychophysics and physiology is symbolized in a number of ways. In summarizing the results of an electrophysiological study of the response of neurons in the cat striate cortex to spatial frequency, Campbell, Cooper, and Enroth-Cugell (1969) state that "these neurophysiological results support psychophysical evidence for the existence in the visual system of channels, each selectively sensitive to a narrow band of spatial frequencies." So Hubel and Wiesel's physiological results inspired the search for psychophysical channels, and now, just a decade later, new physiological results are supporting the psychophysical evidence!

To make the marriage between psychophysics and physiology complete, another paper from Campbell's laboratory is titled "On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images" (Blakemore & Campbell, 1969), even though the research reported in the paper is psychophysical, not neural. Similarly, in Thomas' (1970) paper titled "Model of the function of receptive fields in human vision," he describes a number of psychophysical procedures that can be used to study "the receptive fields of various detector systems," and provides a model of receptive field functioning, based solely on psychophysical results. A more recent example of a paper with a physiological title that reports psychophysical research is Yang and Blake's (1994) paper "Broad tuning for spatial frequency of neural mechanisms underlying visual perception of coherent motion." Thus, from the seed planted by electrophysiological research on feature detectors in the late 1950s and early 1960s grew a vast literature of interlocking physiological and psychophysical research. (See Graham, 1989, for an impressive compendium of psychophysical research on pattern analyzers.)

Object Recognition and the Binding Problem

We have seen how physiological research on feature detectors in animals inspired psychophysical research which established the existence of these detectors in humans. Physiological feature detectors have also inspired other psychophysically based research and theories. For example, a number of theories of object recognition have taken the lead from physiological feature detectors to propose basic perceptual units called "primitives" (Biederman, 1987; Julesz, 1984; Peterson, Chapter 6; Treisman & Gelade, 1980). One way to think about these primitives is that they are perceptual manifestations of neural feature detectors.

However, these primitives are not necessarily isomorphic with the neural detectors, as noted by Nakayama and Joseph's (1998) statement that

> Although Treisman and Gelade's and Julesz's theories were inspired by neurophysiological findings, they maintained a certain distance from these results, preferring to define the characteristics of these units a priori or to let them be characterized by the search experiments themselves. (p. 280)

Thus, while these psychophysically based theories of object recognition may have been inspired by physiological feature detectors, the detectors, as defined by the results of psychophysical search experiments, do not necessarily represent a one-to-one mapping of psychophysics onto physiology. This is not surprising, given the complexity of object recognition. This complexity is highlighted by one of the more challenging problems in object recognition – the binding problem.

The binding problem has been defined both perceptually and physiologically. From a perceptual perspective the binding problem asks how we generate a unitary perceptual experience of an object that combines object qualities such as color, shape, location, and orientation (Roskies, 1999; Treisman, 1999). Psychophysical experiments done in conjunction with Treisman's feature integration theory of object recognition have provided evidence for "illusory conjunctions" – misperceptions that are created when features are incorrectly combined during a brief period of preattentive processing (Treisman, 1986; Wolfe & Cave, 1999). These illusory conjunctions, which represent a case of incorrect feature binding, provide a psychophysical entree to the study of stimulus parameters that may be relevant to the binding process.

On the physiological side, the binding problem is represented by the fact that information about various visual features is processed in different areas (or modules, see Nakayama, Chapter 23) in the cortex. A large literature hypothesizing mechanisms such as temporal synchronization of neural firing represents current attempts to determine the physiological mechanism responsible for the unification of this spatially separated feature information (Gray, 1999; Singer, 1999). The relationship between psychophysical and physiological approaches to the binding problem is, like the relationship between psychophysically and physiologically defined feature detectors, not necessarily one-to-one, but it is not unreasonable to expect a coming together of these two perspectives as our knowledge of both the psychophysical and physiological aspects of object recognition increases.

Locating Physiological Mechanisms

Our discussion has been focused on how the collaboration between psychophysical and physiological research has helped determine physiological mechanisms. However, as Blake (1995) points out, it is possible to use what he calls "psychoanatomical strategies" to determine the location or relative ordering of these mechanisms. The examples below speak to how psychophysics and physiology have provided information both about the ordering of processing and the sites of physiological mechanisms.

The Locus of Orientation Perception

An example of how psychophysical measurements, combined with a knowledge of anatomy, can locate the site of a perceptual effect is provided by the tilt aftereffect, which occurs after a person is adapted to a grating with a particular orientation. When the vertical grating on the right of Figure 1.3 is viewed just after adaptation to the tilted grating on the left, the vertical grating appears to be tilted slightly to the right. The psychophysical evidence that one of the sites of this effect is beyond the lateral geniculate nucleus is that it transfers interocularly, so the effect occurs when the adapting grating is viewed with the left eye and the test grating is viewed with the right eye. This transfer indicates that binocular neurons in the cortex are involved, because the signals from the left and right eyes do not meet until they reach the striate cortex (Banks, Aslin, & Letson, 1975) (see Maffei, Fiorentini, & Bisti (1973) for interocular transfer measured in single neurons).

Early vs. Late Selective Attention

The event related potential (ERP), an electrophysiological response recorded using scalp electrodes, has been used to provide evidence relevant to a long-standing controversy in the field of attention: Does the selection that occurs when attention is focused on one stimulus occur early in processing or late in processing? Chun and Wolfe (Chapter 9, p. 291) refer to Hillyard, Hink, Schwent, and Picton's (1973) research, which showed that when subjects attend to information presented to one ear, ERP components that occur within 100 msec are enhanced for the attended stimuli. Similar results also occur for visual stimuli (see Mangun, Hillyard, & Luck, 1993), indicating that attentional modulation occurs very early in visual processing. Chun and Wolfe present similar arguments, based
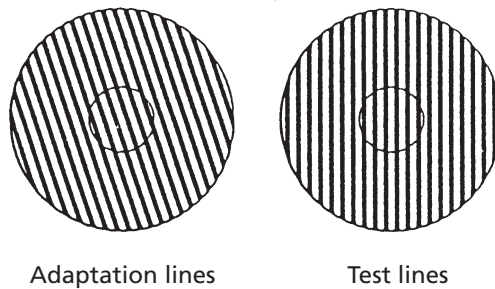

Adaptation lines   Test lines

Figure 1.3. Stimuli for achieving the tilt aftereffect. Cover the test pattern on the right, and stare at the pattern on the left for about 60 seconds, moving your eyes around the circle in the middle. Then cover the left-hand pattern, and transfer your gaze to the test lines on the right. If you see the test lines as tilted to the right, you are experiencing the tilt aftereffect. To achieve interocular transfer, repeat this procedure viewing the left grating with the left eye, and the right with the right eye. This effect is usually weaker than the one that occurs when the adaptation and test lines are viewed with the same eye.

on the presence of specific components of the ERP, that words that are "blinked" during a Rapid Serial Visual Presentation (RSVP) procedure are semantically processed, even though they are not consciously perceived (Shapiro & Luck, 1999).

Linking Structures with Function

Linking structures with their functions has long been a goal of sensory neurophysiology. This has been accomplished in a number of ways, all of which necessarily involve correlating physiological and perceptual responses.

Perceptual Effects of Lesioning and Brain Damage

One of the major discoveries of the 1990s has been the identification of two processing streams in the visual cortex, the ventral stream from the striate cortex to the temporal lobe, and the dorsal stream from the striate cortex to the parietal lobe. The determination of the functions served by these streams has been achieved by assessing the behavioral effects of brain damage caused by (a) lesioning in animals and (b) accidental brain damage in humans.

The technique of lesioning a specific brain area, followed by assessment of the resulting behavioral deficits, is a time-honored way of localizing the functions of specific areas. This technique involves measuring the ψ relationship of Figure 1.1 with and without a specific structure present. Using this technique in monkeys, Ungerleider and Mishkin (1982) concluded that the ventral stream was responsible for providing information relevant to "what" an object is, and the dorsal stream provides information about "where" it is. These experiments are significant not only because they were the first to identify the functions of the dorsal and ventral streams, but also because they established an anatomical schema for future researchers.

Milner and Goodale (1995; also see Goodale & Humphrey, Chapter 10), came to a different conclusion, by assessing the behavior of brain-damaged human subjects (also see Humphreys & Riddoch, Chapter 7). They argue that the ventral stream is best characterized as being responsible for "perception" (roughly equivalent to "what"), whereas the dorsal stream is best characterized as being responsible for "action" – the sensory-motor coordination of movement with relation to an object. The main import of both the Ungerleider and Mishkin and the Milner and Goodale research for our purposes is that the conclusions from both lesion and neuropsychological studies involve a collaborative effort between physiology and psychophysics, with a physiological manipulation leading to a psychophysically measured outcome.

Comparing Animal Electrophysiology and Human Psychophysics

The most common way of determining the function of a particular structure is by measuring ϕ relationships, with the goal being to identify a neuron's preferred stimulus (cf. Hubel & Wiesel, 1959). Although these experiments typically have not included measurement of the ψ relationship, stimuli are used which have known perceptual effects. Thus, oriented

or moving lines, and lights with different wavelength distributions, are used because they are known to be perceived as oriented, moving, or colored by humans.

The ψ relationship in these studies is often not determined because of the difficulty of training animals to make psychophysical judgments (but this has been done, see Stebbins (1971) and more recent examples described below), so the relationship between physiology and perception is usually a qualitative one. A further disadvantage of this method is that it requires generalizing from animals to humans, something electrophysiologists have never been shy about doing (see Adrian (1928) for some of the earliest examples of this, involving the eel) but which should be done with a sensitivity to interspecies differences. If comparisons between human psychophysics and animal physiology are to be made, it is clearly preferable that human psychophysics be compared to monkey physiology. A recent paper by Kapadia, Ito, Gilbert, and Westheimer (1995) which determines parallels between human contrast sensitivity and the response of monkey V1 neurons provides a good example of this approach.

Despite the disadvantages of only measuring neural responding in animals, localizing function by determining what stimuli neurons prefer has yielded a wealth of data, including identification of neurons in the monkey's IT cortex that respond selectively to complex objects (Tanaka, 1993) and faces (Rolls & Tovee, 1995), cells in area V4 that respond to color (Felleman & Van Essen, 1991), and cells in area MT that respond predominantly to the direction of movement (Felleman & Van Essen, 1987). These results provide suggestions, but not proof, of the functions of neurons in a particular brain area. For example, Gordon and Abramov (Chapter 4) discuss problems with assuming area V4 is the locus for color perception, even though it contains many neurons that respond selectively to specific wavelengths. More certain conclusions can be derived from experiments in which the ϕ and ψ relationships are determined in the same animal, as described in the next section.

Correlating Electrophysiology and Psychophysics in the Same Animal

Recent research from a number of laboratories has begun combining simultaneous measurement of electrophysiological and behavioral responding in the same animal. Newsome (see Movshon & Newsome, 1992; Newsome & Pare, 1988; Newsome, Britten, & Movshon, 1989; Newsome, Shadlen, Zohary, Britten, & Movshon, 1995) measured the firing of MT neurons as the monkey makes a discrimination of the direction of movement of "dynamic random dot" stimuli that vary in correlation between 0 percent (all dots moving randomly) to 100 percent (all dots moving in the same direction). The result, plots of "neurometric" and "psychometric" functions (proportion correct vs. correlation) for both neurons and behavior, revealed a close connection between the neural responding and perception. Newsome has also shown that electrical stimulation of MT neurons during behavior increases the monkey's ability to discriminate the direction of movement (see Shiffrar, Chapter 8, p. 242).

Leopold and Logothetis (1996) also achieved simultaneous measurement of behavior and electrical responding in monkeys. The stimulus, a vertical grating presented to one eye and a horizontal grating presented to the other, is designed to create binocular rivalry, so the monkey's perception flips from one perception to the other. The monkey indicates, by a key press, which stimulus it is seeing, while electrical activity is simultaneously recorded

from neurons in area V4 of extrastriate cortex. The link between perception and physiology is established by changes in firing that are time-locked to changes in the monkey's perception of the gratings (also see Logothetis & Schall, 1989). Note that in this experiment the physical stimulus remains constant, but perceptual changes occur that are associated with changes in neural firing. We now describe a similar procedure, which has recently been applied to humans using cortical imaging techniques to measure the physiological response.

Correlating Cortical Imaging and Perception in Humans

Moore and Engel (1999) devised a procedure in which perceptual changes elicited to a constant stimulus are correlated with neural activity in the lateral occipital region (LO) of cortex. They first measured the fMRI response of an area in LO that had previously been shown to respond well to three-dimensional stimuli. They measure the fMRI response to a high-contrast stimulus, which is initially perceived as a two-dimensional black and white pattern (Figure 1.4a) and then presented a gray-scale image of the same object (Figure 1.4b). This gray-scale image biases the subject to see the high-contrast stimulus as a three-dimensional volumetric object, and when the fMRI response to the high-contrast stimulus (Figure 1.4c) is remeasured, the response in LO increases, even though the stimulus pattern has not changed. This result is particularly interesting because it demonstrates a link between electrical responding and *interpretation* of a stimulus.

It is fitting to end this chapter with this experiment, because this collaboration between psychophysics and physiology reflects recent increases in interest in (a) cognitive contributions to perception (cf. Ballesteros, 1994; Rock, 1983), and (b) the role of inferential processes built into our nervous system, which provide heuristics that help us decode ambiguous information in the environment (cf. Goldstein, 1998; Ramachandran, 1990; Shepard, 1984). As with the other research discussed in this chapter, the operation of these aspects of perception will eventually be elucidated through cross-talk between psychophysical and physiological research.

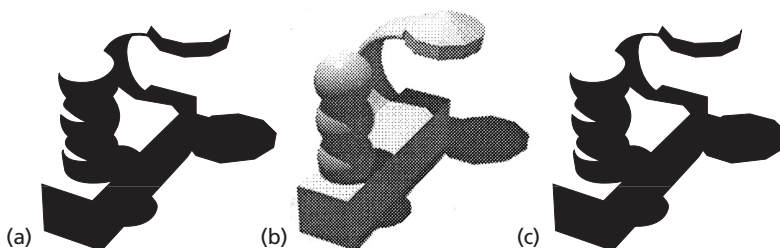

(a)   (b)   (c)

Figure 1.4. Stimuli used by Morre and Engel (1999). (a) High contrast object, which is initially perceived as two-dimensional. (b) Gray-scale image of the same object. (c) Same object as (a), which appears three-dimensional after viewing (b).

Conclusion

The various examples above make a case for the idea that a full understanding of perception demands using both psychophysical and physiological approaches and that the issue is not simply one of measurement at different levels of analysis, but of a true cross-fertilization between the information derived from one level and the information derived from the other level.

This type of cross-talk between behavior and physiology has been noted by Schacter (1986) as applied to research on memory. Schacter distinguishes three kinds of relations between cognitive psychology and neuroscience:

1. Collateral relations, in which an issue pursued in one field can't be mapped onto the other field. Schacter cites the issues of whether memory occurs presynaptically or postsynaptically as having little to say about the mnemonic facilities that interest many cognitive psychologists.
2. Complementary relations, in which description of a phenomenon in one discipline can supplement description of similar phenomena in the other discipline. Localization of function, in which the mental mechanisms hypothesized by memory researchers can sometimes be mapped onto neuroanatomical structures, is an example of such a complementary relation.
3. Convergent relations, in which cognitive psychologists and neuroscientists "coordinate their agenda to bring to bear the various conceptual and experimental tools of their respective disciplines to analyze it." When this happens, according to Schacter, findings at the cognitive level may help neuroscientists understand phenomena at the physiological level, and vice versa.

Schacter concludes that convergent relations are difficult to achieve for much of memory research (or at least they were in 1986. Recent human event related potential and neuroimaging research, such as that of Fernandez et al. (1999) and Smith and Jonides (1999), have brought the achievement of convergent relationships in cognition closer to reality). It is clear, however, that in the field of perception, convergent relations are common, and, in fact, that this convergence has evolved to the point that many perceptual researchers do not consider the psychophysical and physiological approaches to be coming from different disciplines. Instead, they see psychophysics and physiology as simply two different ways of understanding the three relationships of Figure 1.1, with special emphasis on determining linking relationships between physiology and perception. The various chapters in this Handbook illustrate how research in perception has progressed along both psychophysical and physiological lines, with the relation between them being at least complementary, and often convergent.

Notes

1. I thank Norma Graham, Donald Hood, Donald McBurney, Davida Teller, and William Yost for their comments on an early draft of the manuscript.
2. References to "Chapters," such as occurs here, refer to Chapters in this Handbook.

Suggested Readings

Brindley, G. S. (1960). *Physiology of the retina and the visual pathway*. London: Edward Arnold.
Teller, D. Y. (1984). Linking propositions. *Vision Research*, *24*, 1233–1246.
Teller, D. Y. (1990). The domain of visual science. In L. Spillman and J. S. Werner (Eds.), *Visual perception: The neurophysiological foundations*. San Diego, CA: Academic Press.

Additional Topics

Basic Taste Qualities
The psychophysically derived idea of basic taste qualities has been supported by physiological research demonstrating different molecular transduction mechanisms for each of the basic qualities (Kinnamon, 1988; McBurney, 1988; Schiffman & Erickson, 1993).

Experiential Effects on Physiology and Perception
There is a large literature showing that changes in an organism's experience both during early development and in adulthood can cause parallel physiological and perceptual changes (Blake & Hirsch, 1975; Merzenich, Recanzone, Jenkins, Allard, & Nudo, 1988; Rauschecker, 1995; Wiesel, 1982).

Developmental Effects
Corresponding changes in psychophysical sensory functioning and physiological functioning occur during development, beginning in early infancy (Gwiazda & Birch, Chapter 20 (for vision); Werner & Bernstein, Chapter 21 (for auditory, somatosensory, and chemical)).

References

Adrian, E. D. (1928). *The basis of sensation*. London: Christophers.
Ballesteros, S. (1994). *Cognitive approaches to human perception*. Hillsdale, NJ: Erlbaum.
Banks, M. S., Aslin, R. N., & Letson, R. D. (1975). Sensitive period for the development of human binocular vision. *Science*, *190*, 675–677.
Barlow, H. B., Blakemore, C., & Pettigrew, J. D. (1967). The neural mechanism of binocular depth discrimination. *Journal of Physiology*, *193*, 327–342.
Baylor, D. (1992). Transduction in retinal photoreceptor cells. In P. Corey & S. D. Roper (Eds.), *Sensory transduction* (pp. 151–174). New York: The Rockefeller University Press.
Bekesy, G. von (1943). Über die Resonanzkurve und die Abklingzeit der verschiedenen Stellen der Schneckentrennwand. *Akust. Z.*, *8*, 66–76. (On the resonance curve and the decay period at various points on the cochlear partition. *Journal of the Acoustical Society of America*, *21*, 245–254, 1949.)
Bekesy, G. von (1960). *Experiments in hearing*. New York: McGraw-Hill.

Bekesy, G. von. (1942). Über die Schwingungen der Schneckentrennwand beim Präparat und Ohrenmodell. *Akust. Z.*, *7*, 173–186. (The vibration of the cochlear partition in anatomical preparations and in models of the inner ear. *Journal of the Acoustical Society of America*, *21*, 233–245, 1949.)

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*,115–147.

Blake, R. (1995). Psychoanatomical strategies of studying human visual perception. In T. Papathomas (Ed.), *Early vision and beyond* (pp. 17–25). Cambridge, MA: MIT Press.

Blake, R., & Hirsch, H. V. B. (1975). Deficits in binocular depth perception in cats after alternating monocular deprivation. *Science*, *190*, 1114–1116.

Blakemore, C. B., & Sutton, P. (1969). Size adaptation: A new aftereffect. *Science*, *166*, 245–247.

Blakemore, C., & Campbell, F. (1969). On the existence of neurons in the human visual system selectively responsive to the orientation and size of retinal images. *Journal of Physiology*, *203*, 237–260.

Bowmaker, J. K., & Dartnall, H. J. A. (1980). Visual pigments of rods and cones in a human retina. *Journal of Physiology*, *298*, 501–511.

Brindley, G. S. (1960). *Physiology of the retina and the visual pathway*. London: Edward Arnold.

Brown, P. K., & Wald, G. (1964). Visual pigments in single rods and cones of the human retina. *Science*, *144*, 45–52.

Campbell, F. W., & Kulikowski, J. J. (1966). Orientational selectivity of the human visual system. *Journal of Physiology*, *187*, 437–445.

Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, *197*, 551–566.

Campbell, F. W., Cooper, G. F., & Enroth-Cugell, C. (1969). The spatial selectivity of the visual cells of the cat. *Journal of Physiology*, *203*, 223–235.

Casagrande, V. A., & Norton, T. T. (1991). Lateral geniculate nucleus: A review of its physiology and function. In J. R. Coonley-Dillon & A. G. Leventhal (Eds.), *Vision and visual dysfunction: The neural basis of visual function* (Volume 4, pp. 41–84). London: Macmillan.

DeValois, R. L. (1965). Analysis and coding of color vision in the primate visual system. *Cold Spring Harbor Symposia on Quantitative Biology*, *30*, 567–579.

DeValois, R. L., Jacobs, G. G., & Jones, A. E. (1963). Responses of single cells in primate red-green color vision system. *Optik*, *20*, 87–98.

Fechner, G. (1860). *Elements of psychophysics* (H. E. Adler, Trans.). New York: Holt, Rinehart and Winston.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1–47.

Fernandez, G., Effern, A., Grunwald, T., Pezer, N., Lehnertz, K., Dumpelmann, M., Van Roost, D., & Elger, C. E. (1999). Real-time tracking of memory formation in the human rhinal cortex and hippocampus. *Science*, *285*, 1582–1585.

Fletcher, H. (1929). *Speech and hearing*. New York: Van Nostrand.

Fletcher, H. (1938). The mechanism of hearing as revealed through an experiment on the masking effect of thermal noise. *Proceedings of the National Academy of Sciences*, *24*, 265–274.

Galambos, R., & Davis, H. (1943). The response of single auditory-nerve fibers to acoustic stimulation. *Journal of Neurophysiology*, *7*, 287–304.

Gibson, J. J. (1950). *The perception of the visual world*. Boston: Houghton Mifflin.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.

Gilinski, A. S. (1968). Orientation-specific effects of patterns of adapting light on visual acuity. *Journal of the Optical Society of America*, *58*, 13–18.

Goldstein, E. B. (1998). When does visual processing become cognitive? *Contemporary Psychology*, *43*, 127–129.

Graham, C. H. (1959). Color theory. In S. Koch (Ed.), *Psychology: A study of a science. Volume 1* (pp. 145–285). New York: McGraw-Hill.

Graham, N. (1989). *Visual pattern analyzers*. New York: Oxford University Press.

Gray, C. M. (1999). The temporal correlation hypothesis of visual feature integration: Still alive and well. *Neuron*, *24*, 31–47.

Hartline, H. K. (1949). Inhibition of activity of visual receptors by illuminating nearby retinal elements in the *Limulus* eye. *Federation Proceedings*, *8*, 69.

Hartline, H. K., Wagner, H. G., & Ratliff, F. (1956). Inhibition in the eye of *Limulus*. *Journal of General Physiology*, *39*, 651–673.

Hecht, S., Shlaer, S., & Pirenne, M. H. (1942). Energy, quanta, and vision. *Journal of General Physiology*, *25*, 819–840.

Helmholtz, H. L. F. von (1865). *Die Lehre von den Tonempfindungen als physiologische Grundlage für die Theorie der Musik*, (2nd ed.). Braunschweig: Viewig & Sohn. (*On the sensations of tone*. New York: Dover, 1954. Reprint of the 2nd English edition, 1885.)

Helmholtz, H. von (1852). On the theory of compound colors. *Philosophical Magazine*, *4*, 519–534.

Hering, E. (1878). *Zur Lehre vom Lichtsinn*. Vienna: Gerold.

Hering, E. (1964). *Outlines of a theory of the light sense* (L. M. Hurvich & D. Jameson, Trans.). Cambridge: Harvard University Press.

Hillyard, S. A., Hink, R. F., Schwent, V. L., & Picton, T. W. (1973). Electrical signs of selective attention in the human brain. *Science*, 177–180.

Hood, D. C., & Finkelstein, M. A. (1983). A case for the revision of textbook models of color vision: The detection and appearance of small brief lights. In J. D. Mollon & L.T. Sharpe (Eds.), *Color vision: Physiology and psychophysics* (pp. 385–398). New York: Academic Press.

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology*, *148*, 574–591.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, *160*, 106–154.

Hubel, D. H., & Wiesel, T. N. (1965). Receptive fields and functional architecture in two non-striate visual areas (18 & 19) of the cat. *Journal of Neurophysiology*, *28*, 229–289.

Hurvich, L. M., & Jameson, D. (1957). An opponent-process theory of color vision. *Psychological Review*, *64*, 384–404.

Jameson, D., & Hurvich. L. M. (1955). Some quantitative aspects of an opponent-colors theory: I. Chromatic responses and spectral saturation. *Journal of the Optical Society of America*, *45*, 546–552.

Johnstone, B. M., & Boyle, A. J. F. (1967). Basilar membrane vibrations examined with the Mossbauer technique. *Science*, *158*, 390–391.

Johnstone, B. M., Patuzzi, R., & Yates, G. K. (1986). Basilar membrane measurements and the traveling wave. *Hearing Research*, *22*, 147–153.

Julesz, B. (1964). Binocular depth perception without familiarity cues. *Science*, *145*, 356–362.

Julesz, B. (1984). A brief outline of the texton theory of human vision. *Trends in Neuroscience*, *7*, 41–45.

Kapadia, M. K., Ito, M., Gilbert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys. *Neuron*, *15*, 843–856.

Katz, D. (1935). *The world of colour*. London: Kegan Paul, Trench, Trubner.

Kiang, N. (1965). *Discharge patterns of single fibers in the cat's auditory nerve*. Cambridge, MA: MIT Press.

Kinnamon, S. C. (1988). Taste transduction: A diversity of mechanisms. *Trends in Neurosciences*, *11*, 491–496.

LeGrand, Y. (1957). *Light, color and vision*. London: Chapman & Hall.

Lennie, P. (2000). Color vision. In E. R. Kandel, J. H. Schwartz, & T. M. Jessell (Eds.), Principles of neural science, 4th edn. (pp. 572–589). New York: McGraw-Hill.

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, *379*, 549–553.

Lettvin, J. Y., Maturana, H. R., McCulloch, W. S., & Pitts, W. H. (1959). What the frog's eye tells

the frog's brain. *Proceedings of the Institute of Radio Engineers*, *47*, 1940–1951.

Licklider, J. C. R. (1959). Three auditory theories. In S. Koch (Ed.), *Psychology: A study of a science. Volume 1* (pp. 41–144). New York: McGraw-Hill.

Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, *245*, 761–763.

Mach, E. (1959). *The analysis of sensations*. New York: Dover. (Original work published 1914.)

Maffei, L., Fiorentini, A., & Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science*, *182*, 1036–1038.

Mangun, G. R., Hillyard, S. A., & Luck, S. J. (1993). Electrocortical substrates of visual selective attention. In D. Meyer and S. Kornblum (Eds.), *Attention and performance XIV* (pp. 219–243). Cambridge, MA: MIT Press.

McBurney, D. H. (1969). Effects of adaptation on human taste function. In C. Pfaffmann (Ed.), *Olfaction and taste* (pp. 407–419). New York: Rockefeller University Press.

Meddis, R., & Hewitt, M. J. (1991). Virtual pitch and phase sensitivity of a computer model of the auditory periphery: I. Pitch identification. *Journal of the Acoustical Society of America*, *89*, 2866–2882.

Merzenich, M. M., Recanzone, G., Jenkins, W. M., Allard, T. T., & Nudo, R. J. (1988). Cortical representational plasticity. In P. Rakic & W. Singer (Eds.), *Neurobiology of neocortex* (pp. 42–67). Berlin: Wiley.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. New York: Oxford University Press.

Moore, C., & Engel, S. A. (1999). Neural response to 2D and 3D objects measured with fMRI. *Investigative Ophthalmology and Visual Science*, *40*, S351.

Mountcastle, V. B., & Powell, T. P. S. (1959). Neural mechanisms subserving cutaneous sensibility, with special reference to the role of afferent inhibition in sensory perception and discrimination. *Bulletin of the Johns Hopkins Hospital 105*, 201–232.

Movshon, J. A., & Newsome, W. T. (1992). Neural foundations of visual motion perception. *Current Directions in Psychological Science*, *1*, 35–39.

Nakayama, K., & Joseph, J. S. (1998). Attention, pattern recognition, and pop-out in visual search. In R. Parasuramon (Ed.), *The attentive brain* (pp. 279–298). Cambridge, MA: MIT Press.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, *8*, 2201–2211.

Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, *341*, 52–54.

Newsome, W. T., Shadlen, M. N., Zohary, E., Britten, K. H., & Movshon, J. A. (1995). Visual motion: Linking neuronal activity to psychophysical performance. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 401–414). Cambridge, MA: MIT Press.

Pantle, A., & Sekuler, R. (1968). Size-detecting mechanisms in human vision. *Science*, *162*, 1146–1148.

Pirenne, M. H. (1967). *Vision and the eye* (2nd ed.). London: Chapman and Hall.

Plomp, R., & Mimpen, A. M. (1968). The ear as a frequency analyzer. II. *Journal of the Acoustical Society of America*, *43*, 764–767.

Ramachandran, V. S. (1990). Visual perception in people and machines. In R. Blake & T. Troscianko (Eds.), *AI and the eye* (pp. 21–77). New York: Wiley.

Ranganathan, R., Harris, W. A., & Zuker, C. S. (1991). The molecular genetics of invertebrate phototransduction. *Trends in Neurosciences*, *14*, 486–493.

Ratliff, F. (1965). *Mach bands: Quantitative studies on neural networks in the retina*. New York: Holden-Day.

Ratliff, F., & Hartline, H. K. (1959). The response of *Limulus* optic nerve fibers to patterns of illumination on the receptor mosaic. *Journal of General Physiology*, *42*, 1241–1255.

Rauschecker, J. P. (1995). Compensatory plasticity and sensory substitution in the cerebral cortex. *Trends in Neurosciences*, *18*, 36–43.

Rock, I. (1983). *The logic of perception*. Cambridge, MA: MIT Press.

Rolls, E. T., & Tovee, M. J. (1995). Sparseness of the neuronal representation of stimuli in the primate temporal visual cortex. *Journal of Neurophysiology, 73*, 713–726.

Roskies, A. L. (1999). The binding problem. *Neuron, 24*, 7–8.

Schacter, D. L. (1986). A psychological view of the neurobiology of memory. In J. E. LeDouxs & W. Hirst (Eds.), *Mind and brain* (pp. 265–269). Cambridge: Cambridge University Press.

Schafer, T. H., Gales, R. S., Shewmaker,C. A., & Thompson, P. O. (1950). The frequency selectivity of the ear as determined by masking experiments. *Journal of the Acoustical Society of America, 49*, 1218–1231.

Schiffman, S. S., & Erickson, R. P. (1993). Psychophysics: Insights into transduction mechanisms and neural coding. In S. A. Simon & S. D. Roper (Eds.), *Mechanisms of taste transduction* (pp. 395–424). Boca Raton, FL: CRC Press.

Shapiro, K. L., & Luck, S. J. (1999). The attentional blink: A front-end mechanism for fleeting memories. In V. Coltheart (Ed.), *Fleeting memories: Cognition of brief visual stimuli*. Cambridge, MA: MIT Press.

Shepard, R. N. (1984). Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review, 91*, 417–447.

Singer, W. (1999). Neuronal synchrony: A versatile code for the definition of relations? *Neuron, 24*, 49–65.

Skinner, B.F. (1953). *Science and human behavior*. New York: Macmillan.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science, 283*, 1657–1661.

Srulovicz, P., & Goldstein, J. L. (1983). A central spectrum model: A synthesis of auditory-nerve timing and place cues in monaural communication of frequency spectrum. *Journal of the Acoustical Society of America, 34*, 371–380.

Stebbins, W. C. (Ed.) (1971). *Animal psychophysics*. New York: Appleton-Century Crofts.

Stevens, S. S. (1961). To honor Fechner and repeal his law. *Science, 133*, 80–86.

Stiles, W. S. (1953). Further studies of visual mechanisms by the two-color threshold method. Coloquio sobre problemas opticos de la vision. Madrid: *Union Internationale de Physique Pure et Appliquée, 1*, 65.

Stryer, L. (1986). Cyclic GMP cascade of vision. *Annual Review of Neuroscience, 9*, 87–119.

Svaetichin, G. (1956). Spectral response curves from single cones. *Acta Physiologica Scandinavica Supplementum, 134*, 17–46.

Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science, 262*, 684–688.

Teller, D. Y. (1984). Linking propositions. *Vision Research, 24*, 1233–1246.

Teller, D. Y., & Pugh, E. N., Jr. (1983). Linking propositions in color vision. In J. D. Mollon & T. Sharpe (Eds.), *Colour vision: Physiology and psychophysics* (pp. 11–21). New York: Academic Press.

Thomas, J. P. (1970). Model of the function of receptive fields in human vision. *Psychological Review, 77*, 121–134.

Treisman, A. (1986). Features and objects in visual processing. *Scientific American, 255*, 114–125.

Treisman, A. (1999). Solutions to the binding problem: Progress through controversy and convergence. *Neuron, 24*, 105–110.

Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97–136.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–580). Cambridge: MIT Press.

Wald, G. (1968). The molecular basis of visual excitation. *Science, 162*, 230–239.

Wald, G., Brown, P., & Gibbons, I. (1963). The problem of visual excitation. *Journal of the Optical Society of America, 53*, 20–35.

Wandell, B. A. (1995). *Foundations of vision*. Sunderland, MA: Sinauer Associates.

Wheatstone, C. (1838). On some remarkable, and hitherto unobserved phenomena of binocular vision. Part I. *Transactions of the Royal Society of London*, 371–394.

Wiesel, T. N. (1982). Postnatal development of the visual cortex and the influence of the environment. *Nature*, *299*, 583–591.

Wolfe, J. M., & Cave, K. R. (1999). The psychophysical evidence for a binding problem in human vision. *Neuron*, *24*, 11–17.

Yang, Y., & Blake, R. (1994). Broad tuning for spatial frequency of neural mechanisms underlying visual perception of coherent motion. *Nature*, *371*, 793–796.

Young, T. (1802). On the theory of light and colours. *Transactions of the Royal Society of London*, *92*, 12–48.

Zwicker, E. (1974). On the psychoacoustic equivalent of turning curves. In E. Zwicker & E. Terhardt (Eds.), *Facts and models in hearing* (pp. 132–141). Berlin: Springer-Verlag.