

## *Psychophysical Measurement of Thresholds: Absolute Sensitivity*

The measurement of the absolute threshold, though perhaps not as important for the development of psychology as Fechner's insights into difference thresholds, has led to many significant advances in understanding sensory systems. Before considering in detail the various psychophysical methods for measuring DL's and RL's, let us consider examples of how measuring absolute thresholds has facilitated our understanding of vision, audition, touch, and olfaction.

### **The Absolute Sensitivity of the Eye**

The eye is an extremely light-sensitive instrument capable of responding to almost unbelievably small amounts of light energy. However, a simple answer cannot be given to the question: How sensitive is the eye to light? The absolute sensitivity of the eye cannot be gauged by a single threshold value, since the minimum amount of light necessary for vision has been found to depend on the conditions of stimulation. Therefore, the absolute sensitivity of the visual system is best understood by examining the functional relationships between the absolute threshold and the conditions that determine its value.

The value of the absolute threshold depends upon previous stimulation. Exposing the eye to intense light greatly decreases the absolute sensitivity of the eye. Sensitivity is recovered gradually if the eye is subsequently kept in darkness. Nearly complete recovery of sensitivity occurs after about one hour in the dark. The dark adaptation curve is traced out by measuring an observer's absolute threshold periodically

during the recovery period and plotting its value as a function of time in the dark. The threshold at the beginning of dark adaptation may be as much as 100,000 times as high (5 log units) as the threshold after complete dark adaptation.

In an experiment by Hecht, Haig, and Chase (1937), the test stimulus was presented to a region of the retina containing both rods and cones, and the dark adaptation curve was found to be biphasic (Figure 2.1). The first phase shows a relatively rapid reduction in the absolute threshold as a function of time in the dark and shows the threshold stabilizing after 5–8 min. The second phase, starting after about 10 min in the dark, was a relatively gradual decrease in the threshold which was complete after about 40 min. The point on the curve where the second phase begins is called the rod–cone break. The biphasic curve is caused by the intersecting of the cone and rod recovery curves, which start at different intensity levels, change at different rates, and approach different asymptotes. Before the rod–cone break, the absolute threshold of the rods is so high that the adaptation curve is determined completely by the changing sensitivity of the cones. The rod–cone break represents the point where rod sensitivity finally begins to exceed cone sensitivity, and thereafter the remainder of the dark adaptation curve is determined by the continuing recovery of the rods.

Under most conditions, the electromagnetic radiation is visible when its wavelength is between 400 and 750 nanometers (nm). However, the

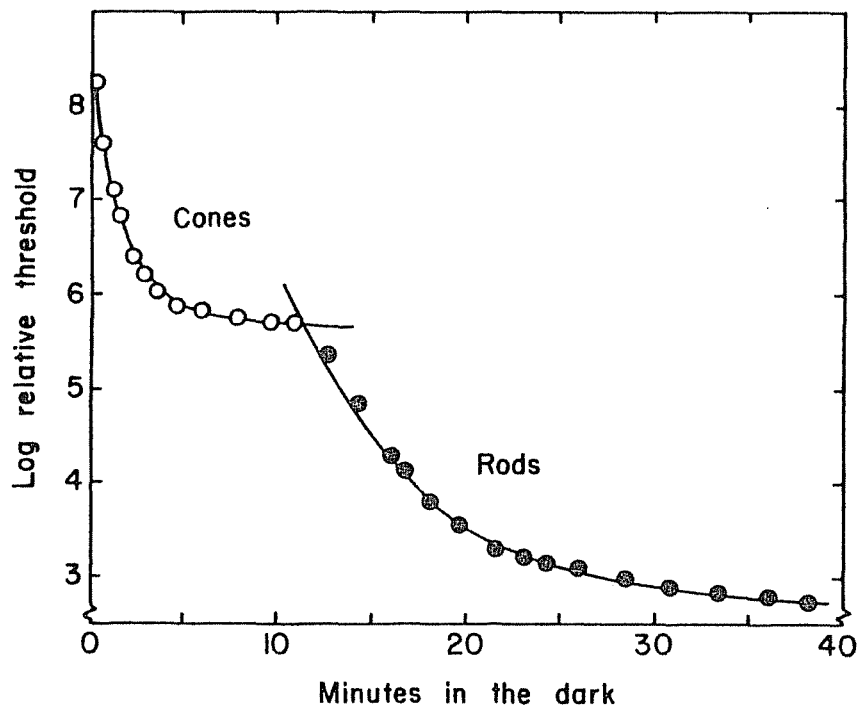


FIG. 2.1. Biphasic curve for dark adaptation. The logarithm of the threshold intensity is plotted against time in the dark. (From Hecht, Haig, & Chase, 1937.)

eye is not equally sensitive to light of all wavelengths. Spectral sensitivity curves showing the absolute threshold as a function of stimulus wavelength have been obtained for cone (photopic) and rod (scotopic) vision. In one such experiment, Wald (1945) measured the absolute thresholds of 22 observers for detecting a  $1.0^\circ$ , 40-msec test stimulus of variable wavelength presented either within the fovea or  $8^\circ$  above the fovea. Figure 2.2 illustrates that light in the extreme blue or red regions on the visual spectrum is relatively ineffective in producing visual responses. The periphery of the retina is most sensitive to light with a wavelength of approximately 500 nm, and the fovea is most sensitive when the stimulus wavelength is about 560 nm. For all wavelengths, the stimulus flash at threshold appeared to be colored for foveal stimulation, indicating the operation of cones, but all threshold stimuli appeared achromatic for peripheral stimulation, indicating the operation of rods. That rods are considerably more sensitive than cones at all but the longest wavelengths is illustrated by the fact that much less energy is required at threshold for peripheral stimulation than for foveal stimulation. The difference between rod and cone thresholds is clearly illustrated by gradually increasing the intensity of a colored light presented to an extrafoveal region of the retina containing both rods and cones. When the rod threshold is reached, the light appears colorless; however, with continued increases in intensity, a point is reached where the light is above the cone threshold, and color is finally perceived. The difference between the rod and cone thresholds measured in this way is called the photochromatic interval. It is an interval on the stimulus intensity scale in which a colored light is perceived, but as colorless. As Figure 2.2 shows us, the size of the photochromatic interval varies with wavelength, being smallest for the long wavelengths and becoming larger for shorter wavelengths.

In physics, it has been shown that light can be described as both a wave and a particle, or quantum. Prior to this development it was thought that energy varied on a continuum. We now know that—due to its quantal nature—energy, including light, changes in discrete steps. The light quantum, also known as a photon, is the smallest possible unit of light energy. It has been determined that vision occurs when the number of quanta absorbed by retinal receptors exceeds some small critical number.

The receptors are able to summate energy over space, as indicated by the fact that, within certain spatial limits, the total number of quanta is constant at threshold, whether they are distributed sparsely over a large area (up to about 10 min of arc in the fovea and  $1^\circ$  in the periphery of the eye) or are concentrated in a small area. This process is called *spatial summation*. Likewise, the visual receptors are able to summate energy over time up to about .1 sec, since it has been found that the total number of quanta at threshold is the same when exposing the eye to a weak

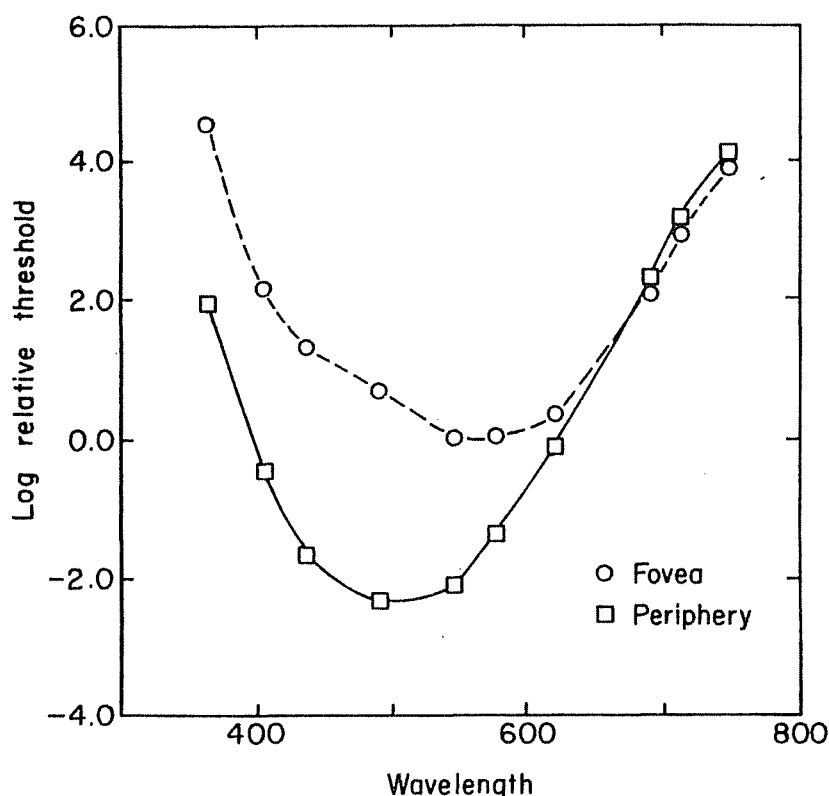


FIG. 2.2. Relative thresholds for detection of light as a function of wavelength and location of the stimulus on the retina. (From Wald, 1945. Copyright 1945 by the American Association for the Advancement of Science.)

stimulus for a long time as when exposing it to a strong stimulus for a short time. This process is called *temporal summation*. Because the eye is unable to summate energy completely over time intervals exceeding .1 sec or areas exceeding about 10 min in diameter, beyond these limits a greater number of quanta are required at absolute threshold.

In what has become a classic experiment in visual science, Hecht, Schlaer, and Pirenne (1942) determined the amount of light at the retina necessary for vision under conditions yielding optimal sensitivity. The following steps were taken to provide optimal conditions for visual sensitivity: (a) the retina was dark-adapted for at least 30 min prior to the making of threshold measurements; (b) stimuli were presented on the temporal retina 20° from the fovea, since this area contains a maximum concentration of rods; (c) a very small test field (10 min in diameter) was employed to ensure that within the visual system there would be complete spatial summation of the stimulus<sup>1</sup>; (d) similarly, the exposure time was

<sup>1</sup>For stimuli smaller than 1° presented to the periphery of the dark-adapted eye there exists a perfect reciprocal relation between stimulus size and stimulus intensity at the threshold of detectability (Graham, Brown, & Mote, 1939); that is, the total effective energy for the eye is determined by the product of stimulus intensity and stimulus area for areas up to 1° diameter.

very short (.001 sec) so temporal summation would operate; (e) a light of 510 nm was used because of the optimal scotopic sensitivity to light of this wavelength; and (f) so that he would be maximally set for each stimulus, the observer operated the shutter through which the stimulus was presented.

Stimulus intensity was measured by a thermopile which was substituted for the observer's pupil. A thermopile is a thin strip of metal which exhibits an increase in temperature when struck by light. The increment in temperature was then converted into units of light intensity. Thresholds were defined as the stimulus energy resulting in a sensation 60% of the time. They were measured over a period of months for seven observers and ranged between  $2.1 \times 10^{-10}$  and  $5.7 \times 10^{-10}$  ergs at the cornea. These minute amounts of energy represent between 54 and 148 quanta of light.

To specify the number of quanta absorbed at threshold by the photochemical pigment of the visual receptors (rhodopsin), the threshold values measured at the cornea were corrected for losses of light within the eye. Approximately 4% of the light reaching the cornea is reflected back instead of entering the eye. Ludvigh and McCarthy (1938) found that 50% of the light of 510 nm entering the eye is absorbed by the ocular media before reaching the retina. Finally, it has been estimated that at most only 20% of the light reaching the retina is absorbed by the rhodopsin of the receptors, the remainder being absorbed by other tissues such as blood vessels. The threshold value of 54 to 148 quanta measured at the cornea, when corrected for the above factors, is only 5 to 14 quanta absorbed by rhodopsin. In the 10-min retinal area stimulated, there are approximately 500 rods, thus making it highly unlikely that more than one quantum will strike a single rod at threshold levels of intensity. On this basis, Hecht et al. (1942) concluded that, in order to see, it is necessary for only one quantum of light to be absorbed by a single molecule of photochemical pigment in each of 5 to 14 rods. The maximum sensitivity of the eye approaches a limit imposed by the nature of light.

It is of considerable interest that in order to exceed the observer's absolute threshold, 5 to 14 rods must each be activated by the absorption of a single quantum of light. Given the exquisite sensitivity of these visual receptors, why is a single quantum absorption by a single rod not sufficient for seeing? The answer is that, as discussed earlier in this chapter with regard to the measurement of differential sensitivity, sensory thresholds are limited by the presence of internal noise in the nervous system. In the case of vision, at any moment, rods, in the absence of light, spontaneously send neural signals to the brain. Thus, because the visual system, with its ever present spontaneous neural activity, is inherently noisy, it is not possible for the observer to discriminate the neural activity generated by an external light stimulus from that generated internally as

spontaneous background noise unless the light produces neural activity in at least 5 to 14 rods. When encountering the Theory of Signal Detection in Chapter 5, the reader becomes increasingly aware of the fundamental importance of the concept of internal noise to our understanding how we detect environmental stimuli. At this point, it suffices to say that, because of internal noise, absolute and differential sensitivity are very similar. In both cases, the observer must discriminate between two things. In the measurement of differential sensitivity it is the difference between two stimuli that must be discriminated, whereas in absolute sensitivity it is the difference between a stimulus and internal noise that must be discriminated.

### The Absolute Sensitivity of the Ear

The remarkable sensitivity of the eye under optimal conditions of stimulation has been found to be nearly matched by that of the ear. Under normal conditions, a young person can hear sound when its frequency of vibration is between 20 and 20,000 Hz. However, the auditory system is most sensitive to vibrations between 2000 and 4000 Hz and is least sensitive to vibrations at the extremes of the audible range of frequencies. In Figure 2.3, the absolute threshold in decibels (dB) sound pressure level<sup>2</sup> is plotted for the frequencies that are employed in standard hearing tests. This graph, prepared by the International Organization for Standardization, is based on the combining of results from a number of studies in which an attempt was made to determine normal hearing for young people (Davis & Krantz, 1964). The extremely low thresholds for the middle frequencies can be better appreciated when the physical effects of such low sound pressure on the eardrum are determined. Wilska (1935) attached one end of a light wooden rod to the eardrum and the other end to a loudspeaker coil. The rod was vibrated, and voltage across the speaker coil was adjusted, so that a tone could hardly be heard. The vibration amplitude of the rod, and thus the amplitude of the in-out movement of the eardrum, was then measured under stroboscopic illumination with a microscope. Direct measurements of the movement of the rods could be made only for the low frequencies of vibration. At high frequencies, the movement was so slight at threshold that it had to be calculated from larger movements of the rod at low frequencies.

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<sup>2</sup>Sound pressure is often expressed on a logarithmic scale as the number of decibels above a reference sound pressure. The most frequently used reference is .0002 dyne per square centimeter. The number of decibels can be computed by the formula

$$N_{dB} = 20 \log p_1/p_0,$$

where  $p_0$  is a sound pressure of .0002 dyne/cm<sup>2</sup> and  $p_1$  is the measured sound pressure.



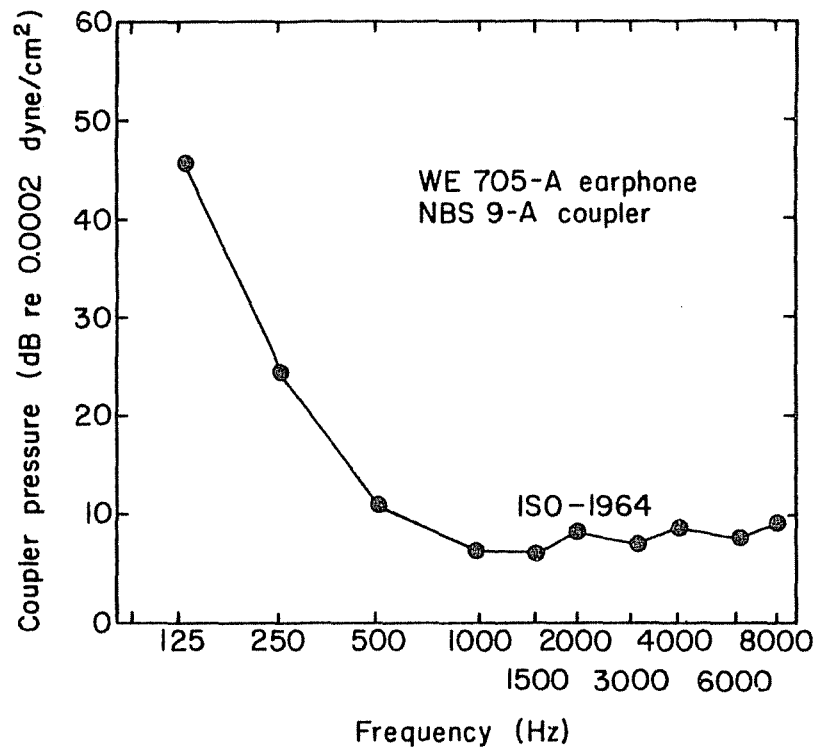


FIG. 2.3. Absolute threshold in decibels sound pressure level for the detection of pure tones as a function of stimulus frequency. (From Davis & Krantz, 1964.)

The results of the study indicate that, for frequencies of between 2000 and 4000 Hz, the eardrum has to move only  $10^{-9}$  cm in order for a sound to be heard. This amount of movement is less than the diameter of a hydrogen molecule. By using a highly precise laser interferometer to measure vibration amplitude of the cat's eardrum at threshold, Tonndorf and Khanna (1968) were able to confirm Wilska's findings. Peak displacement amplitude at threshold was  $10^{-10}$  cm at 1000 Hz and close to  $10^{-11}$  cm at 5000 Hz.

It has also been estimated that the hair cells serving as sensory receptors in the inner ear, when vibrated at 2000–4000 Hz by presenting a tone to the ear, must also be moved by less than the diameter of a hydrogen molecule for hearing to occur. These remarkably low psychophysical thresholds for detection of sound suggest that, as in vision, the sensitivity of the auditory system may be approaching a limit imposed by the nature of the stimulus.

Is the sensitivity of the ear limited by its construction and physiological efficiency, or is it limited by the nature of air as a transmitting medium for sound? Sivian and White (1933) calculated the sound pressure generated by the constant random movement of individual air molecules within the frequency range of 1000–6000 Hz. These calculations indicate that a constant sound pressure exists which is only 10 dB lower than the average auditory threshold of approximately .0002 dyne/cm<sup>2</sup> for sounds within

this frequency range. Furthermore, people with excellent hearing have thresholds which are approximately the same as the constant sound pressure from the random movement of air molecules. Therefore, for people with excellent hearing, having more sensitive ears would be useless because of the thermal noise continuously present in the air.

### The Absolute Sensitivity for Touch

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One way of measuring tactile sensitivity is to determine the smallest amplitude of vibration of the skin that can be detected by an observer. Vibrotactile thresholds depend on stimulus factors such as the locus of stimulation, the size of the stimulated skin area, the duration of the stimulus, and the frequency of vibration. An experiment by Verrillo (1963) will serve to illustrate the relationship which is found for the absolute threshold for vibration and the frequency of the vibratory stimulus. In Verrillo's experiment, a stimulator attached to a vibrator was placed in contact with the skin of the prominence on the palm at the base of the thumb. The stimulator protruded up into a hole in a rigid surface upon which the observer's hand rested. There was a 1-mm gap between the circularly shaped stimulator and the rigid surrounding surface. The small gap between the stimulator and the rigid surface upon which the hand rested served to control the area of stimulation by confining the vibration to the area of the stimulator. The data presented in Figure 2.4 were obtained when the size of the stimulator was varied over a range of .005 cm<sup>2</sup> to 5.1 cm<sup>2</sup>.

It can be seen in Figure 2.4 that when the stimulator was larger than .02 cm<sup>2</sup>, vibrotactile sensitivity was a U-shaped function of frequency and that sensitivity was greatest in the frequency region around 250 Hz where the amplitude of vibration needed to exceed threshold was approximately .1 micron (μm) for the largest contactor. Thus, under the best conditions in which large areas of skin on a relatively sensitive part of the body are stimulated, vibration amplitude had to be 10<sup>-5</sup> cm for the mechanical disturbance to be detected. This vibration threshold, although impressive, does not compare favorably with a vibration threshold of 10<sup>-11</sup> cm for movement of the eardrum necessary for hearing a 5000-Hz tone. The superiority of auditory sensitivity may be due to the greater efficiency of the auditory system in conducting mechanical disturbances to the receptors and/or the greater sensitivity of the auditory receptors.

Variation of the size of the stimulator had an interesting effect in Verrillo's study. Increasing the size of stimulators larger than .02 cm<sup>2</sup> resulted in a proportional decrease in the threshold. This finding indicated that the tactile system is capable of summing stimulation over a relatively large area. For stimuli that were .02 cm<sup>2</sup> or smaller, no spatial



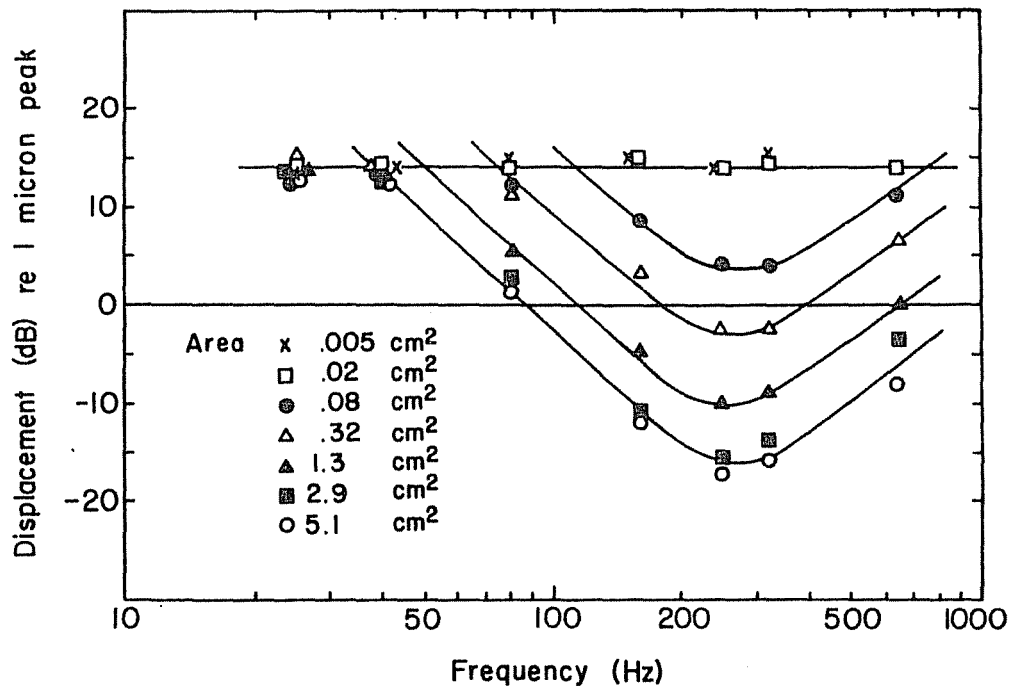


FIG. 2.4. Vibrotactile thresholds for seven contactor sizes as a function of vibration frequency. (From Verrillo, 1963.)

summation was observed. Furthermore, it can be seen that the frequency curve for these small stimulators is not U shaped, but rather that the threshold is uniformly high at all frequencies. Verrillo concluded from these findings that the skin contains at least two receptor systems which are involved in the detection of mechanical disturbances. One system summates energy over space and accounts for the U-shaped frequency function obtained when all but the smallest stimulators are used. The other system, which is not capable of spatial summation, accounts for the flat frequency function when thresholds are measured for very small contactors. By comparing psychophysical data with data on the electrophysiological response of individual tactile receptors, Verrillo (1966) was able to identify the Pacinian corpuscle as the receptor responsible for spatial summation and the U-shaped frequency response curve. There is remarkable correspondence between the U-shaped psychophysical function and the neural response of a Pacinian corpuscle (Figure 2.5). More recently, the flat portion of the psychophysical curve has been associated with other mechanoreceptors, such as Meissner corpuscles and Merkel discs.

Vibrotactile thresholds for stimuli presented within a much wider frequency range than employed in the earlier study by Verrillo are seen in Figure 2.6. These results obtained by Bolanowski, Gescheider, Verrillo, and Checkosky (1988) provided the basis for a four channel model of mechanoreception. The data points are average thresholds for five ob-

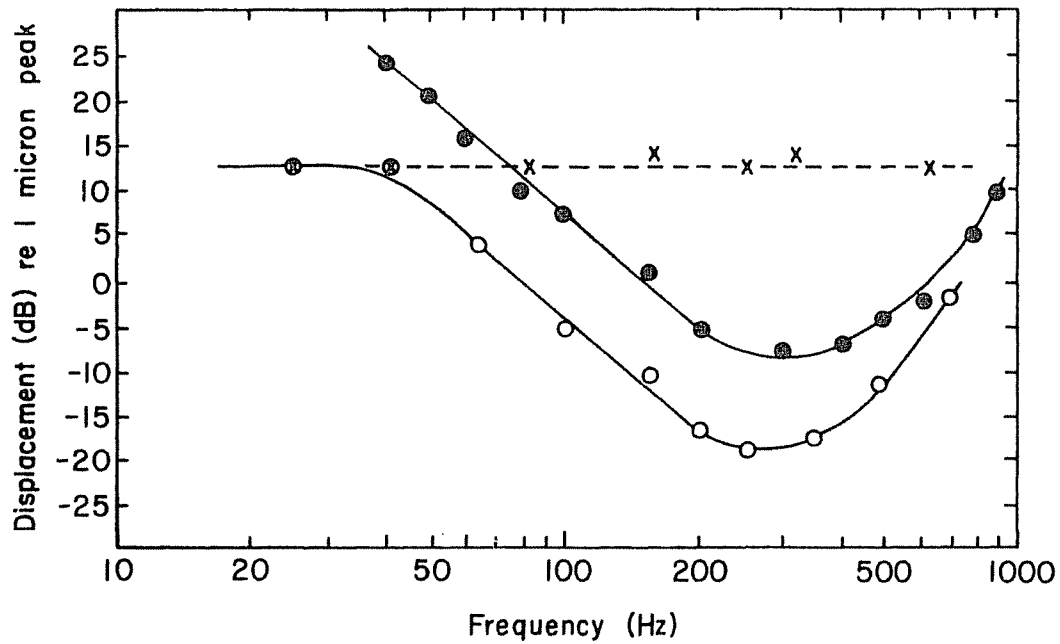


FIG. 2.5. Human psychophysical thresholds for the detection of vibrotactile stimuli (unfilled points) compared with the electrophysiological response of the Pacinian corpuscle in the cat (filled points). The flat curve is obtained when skin containing no Pacinian corpuscles is stimulated or when very small contactors are used. (From Verrillo, 1975. From *Experimental Sensory Psychology* by Bertram Scharf. Copyright © by Scott, Foresman, and Company. Reprinted by permission of the publisher.)

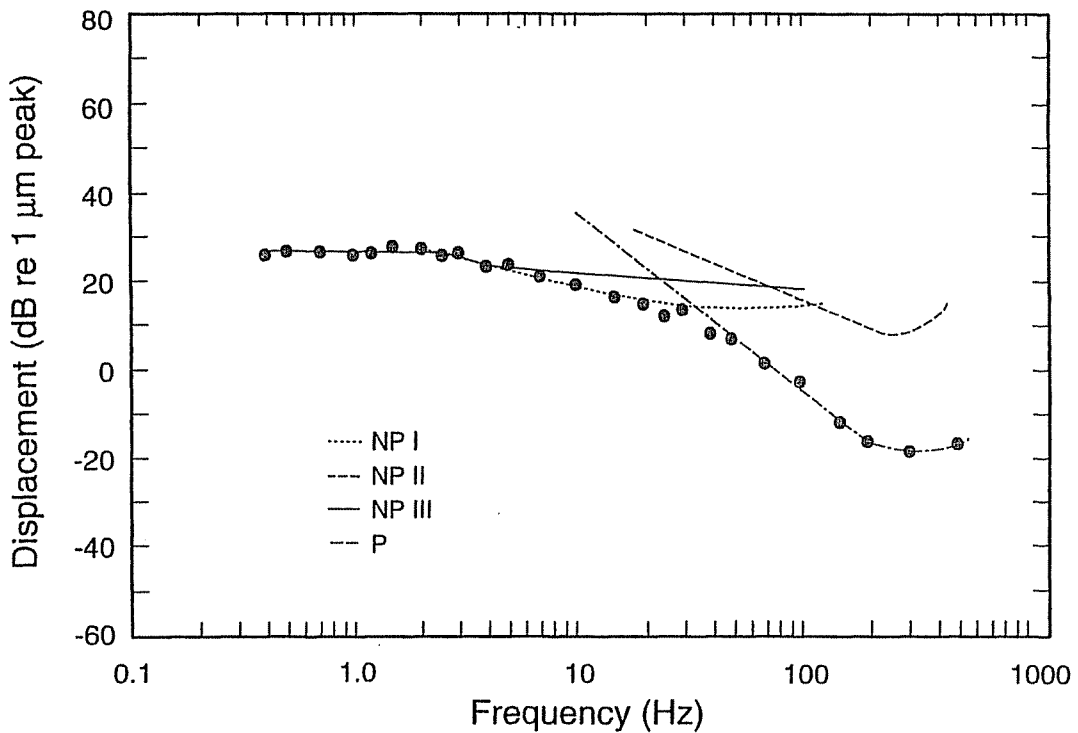


FIG 2.6. Vibrotactile thresholds as a function of frequency (filled data points). The curves are the frequency characteristics of each of four tactile information processing channels. (From Bolanowski, Gescheider, Verrillo, & Checkosky, 1988.)

servers and each of the four curves describes how the threshold of a neural channel is thought to change as vibration frequency changes. According to the model, the psychophysical threshold of the observer, measured at a particular vibration frequency, is determined by the neural channel with the lowest threshold at that frequency. Thus, thresholds, at high frequencies, are determined by the P channel with Pacinian corpuscles as receptors. Thresholds within the midrange of frequencies, between 2 and 40 Hz, are determined by the NPI channel with Meissner corpuscles as receptors, and thresholds at low frequencies (between .4 and 2 Hz) are determined by the NPIII channel with its Merkel receptors. Only when Pacinian corpuscles are absent, defective, or are inadequately stimulated with a very small contactor would the psychophysical threshold for high frequency vibration be determined by the NPII channel with Ruffini end organs as receptors.

Each of the receptor types for touch just described consists of a single sensory nerve fiber surrounded by a specialized end organ that contributes to the overall sensitivity level and frequency tuning of the neural channel. The Pacinian corpuscle, for example, consisting of many layers of tissue, each separated by fluid, is known to greatly attenuate the vibrating stimulus such that the amplitude of vibration at the outer surface of the corpuscle is always much greater than that at the nerve fiber surrounded by the corpuscle. So great is this attenuation of the stimulus that it appears that movement of the nerve fiber required to detect the stimulus may be approximately as low as that observed in hearing (Petrus & Bolanowski, 1996). Thus, mechanoreceptive nerve fibers, whether for hearing or for touch, appear to have extremely low thresholds. The function of the corpuscle surrounding a Pacinian nerve fiber may be to keep the highly sensitive fiber from being overstimulated by intense stimulation in the natural environment.

The four channel model was developed to account for the detection of mechanical stimuli applied to the glabrous, hairless, skin of the palm of the hand. When the hairy skin of the forearm, an area containing a different set of receptors than those found in glabrous skin, was studied, only three channels were discovered (Bolanowski, Gescheider, & Verrillo, 1994) and thresholds were generally higher than those observed for glabrous skin.

In conclusion, the absolute sensitivity of touch depends on a number of factors. From our discussion it is clear that the threshold is greatly influenced by the size of the contactor used to stimulate the skin, the frequency of vibration and the type of skin stimulated. Four separate types of mechanoreceptors in glabrous skin and three types in hairy skin seem to underlie the detection of mechanical stimulation of the skin. The

most sensitive of these receptors, optimally responsive to high frequency vibration of approximately 250 Hz, is the Pacinian corpuscle.

### **The Absolute Sensitivity for Smell**

An experiment reminiscent of the work of Hecht et al. (1942) on vision was performed by Stuiver (1958), a Dutch investigator. After determining the smallest number of molecules of a substance that must enter the nose to be detected, Stuiver calculated the number of molecules that had to be absorbed by the olfactory receptors within the nose. Calculations were based on experiments with a physical model of the nasal cavity, which revealed that only 2% of the molecules entering the nose make contact with the olfactory receptors, while the remaining 98% are absorbed in mucus, are carried in air streams that never make contact with the receptor area, or are carried in air streams over the receptor area without affecting it. From his psychophysical data, Stuiver estimated that each of 40 receptor cells had to absorb only a single molecule for a substance to be detected. The sensitivity of the nose, like that of the eye and the ear, approaches a limit imposed by the nature of the stimulus. In other words, under the very best conditions these systems are as sensitive as any sensing device could possibly be for detecting certain specific forms of energy.

## **TWO FUNCTIONS OF PSYCHOPHYSICS**

From the discussions of threshold measurement, it should be apparent that psychophysics serves two basic functions. One function is descriptive and involves the specification of sensory capacities; the other is analytical and involves the testing of hypotheses about the underlying biological mechanisms that determine sensory capacity.

### **Descriptive Psychophysics**

The descriptive function of psychophysics is illustrated by the experiment of Wald (1945), the results of which were seen in Figure 2.2. Through this experiment, we know how the visual threshold changes as the wavelength of light changes for stimuli presented to the fovea or to the periphery of the retina. It is evident from the results of this experiment that vision occurs only within a narrow band of wavelengths within the electromagnetic spectrum which ranges from approximately 350 to 750 nm. It can also be seen that, within this narrow range of visible energy, sensitivity of the visual system changes greatly as the wavelength of light changes; that we are more sensitive to lights presented peripherally than to those

presented centrally; and that the most effective wavelength for vision is about 560 nm (yellow) for the fovea and 500 nm (green) for the periphery. In the discussion of visual sensitivity, we also saw that other properties of the visual system, such as adaptation, spatial summation, and temporal summation, could be studied by measuring the threshold as a function of time in the dark after light exposure, size of the stimulus, and duration of the stimulus, respectively. In addition to increasing our understanding of human sensory capacity, knowing this kind of information has had significant practical benefits. For example, an architect must have knowledge of visual sensitivity in order to design a lighting system that will properly illuminate the rooms in a building as inexpensively as possible. In fact, the design of any environment or instrument in which vision is used must take into account the psychophysical capacities of the visual system. In the production of television sets, microscopes, and even in the publication of this book, the characteristics of the human visual system have been a central consideration.

Psychophysics has also been successful in providing quantitative descriptions of the capacities of the other sensory modalities, and such information has been helpful in designing environments and equipment for people's use. For example, the function relating the auditory threshold to the frequency of sound seen in Figure 2.3 has been indispensable in designing rooms for listeners, such as concert halls and classrooms. This function is also essential in designing any system that converts sound into some other form of energy and then back to sound again, such as a radio, phonograph, or telephone. The function tells us that the ear, in acting as a filter, can process information only within a limited range of frequencies. Thus, it is the frequencies of sound within this range that must be faithfully transmitted to the ear in a good sound system. Anything short of fulfilling this requirement will mean that some information in the form of audible sound in the original message will be missing in the transmitted message received by the listener. The consequences of this loss of information will depend on how much information is lost, where in the frequency spectrum the loss occurs, and the objectives of the listener. For example, if the listener is trying to comprehend a verbal message coming over a telephone, the essential information can be transmitted through a telephone, which fails to transmit very low and very high audible frequencies in the voice. On the other hand, if the objective is to listen to recorded music that sounds much like it did in the concert hall in which it was recorded, records, discs, or tapes should be played through a hi-fidelity system capable of transmitting all audible frequencies in the original sound.

Threshold functions for the detection of vibration on the skin, such as the one seen in Figure 2.6, have been useful in designing vibrotactile

communication systems for deaf and blind people. For example, much of the early research on vibrotactile communication systems focused on the problem of developing devices capable of transducing speech and music into mechanical vibrations capable of being felt by the skin. In such a system, speech sounds might be converted through a microphone to electrical signals which, after amplification, are converted back to mechanical energy through a vibrator placed in contact with the skin. The design was based on the evolutionary fact that the eardrum, which does so well at responding to the wide range of frequencies present in speech, is a descendant of the skin. Thus, it was thought that we should be able to train the skin to do what the eardrum does (Gault, 1926). The results were disappointing. Although observers could learn to recognize certain speech sounds through their skin, performance was generally poor and unreliable.

A comparison of the psychophysical thresholds for detecting movement of the skin and movement of the eardrum reveals one reason for the skin's relatively poor ability in speech perception (Figure 2.7). The amplitudes of vibration of the skin needed to feel the stimulus are much higher than the amplitudes of vibrations of the eardrum needed to hear. This difference in sensitivity, however, could be compensated for through amplification. A more serious deficiency of the skin is seen in the inability of observers to detect vibrotactile stimuli of frequencies above about 1000

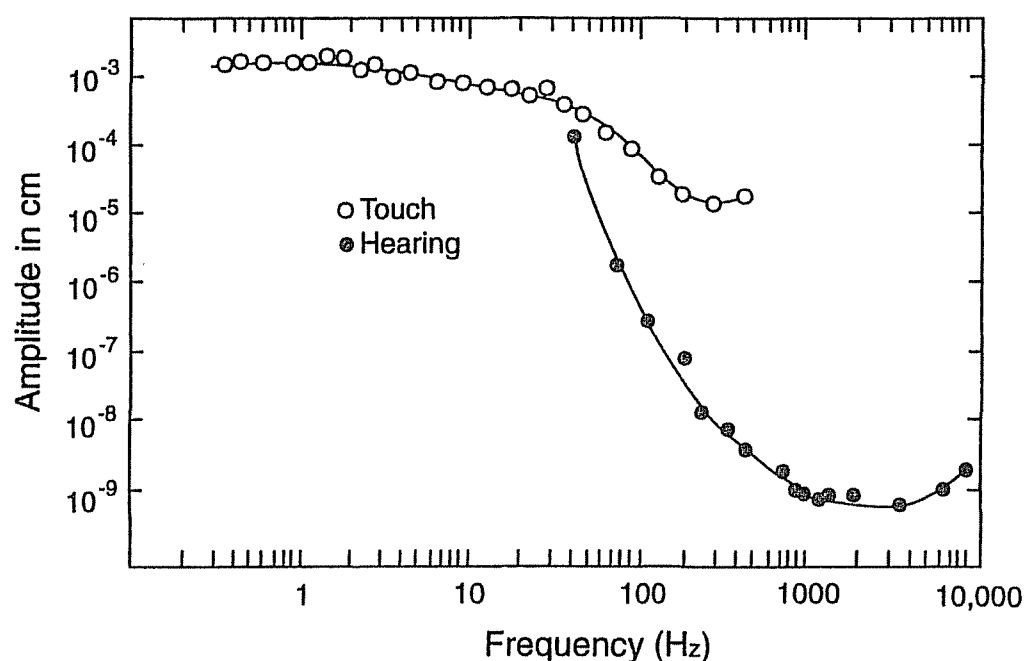


FIG. 2.7. Amplitude of vibration of the skin of the hand needed to feel the stimulus (Bolanowski, Gescheider, Verrillo, & Checkosky, 1988) and amplitude of vibration of the eardrum needed to hear (Wilska, 1935.)



Hz. Since frequencies of vibration contained in speech extend well above 1000 Hz, an accurate representation of speech cannot possibly be transmitted through the skin to the brain. On the other hand, as shown in Figure 2.7, the auditory system can detect very small movements of the eardrum for frequencies up to 10,000 Hz or higher. In addition to having a restricted frequency range, the skin is very poor in discriminating changes in frequency (Goff, 1967). The difference threshold for detecting changes in vibration frequency ( $\Delta F$ ) is plotted as a function of frequency for the skin and for the ear (Figure 2.8). Compared to the ear, the skin, although reasonably good at detecting changes in low frequencies, is poor in discriminating high frequencies. In the range of frequencies important for speech perception, the performance of the skin is very poor compared to that of the ear. For example, when the frequency of vibration is 200 Hz, an increase in frequency of only 2 or 3 Hz is detectable by the ear, while the required increase in frequency for the skin is over 100 Hz. Because of the relatively narrow frequency range and poor frequency discrimination of the skin, it will probably never be possible to "hear" speech through the skin by directly converting the sound to tactile vibration. Attempts are currently being made, however, to design tactile communication systems that operate within the frequency range and frequency discriminative capacities of the tactile sense. If successful, these systems will be a great help to deaf people.

Our brief treatment of descriptive psychophysics illustrates, through a few examples, the use of psychophysical measurements to define the sensitivity of a sensory system. It should be evident that this information can often be used for practical purposes.

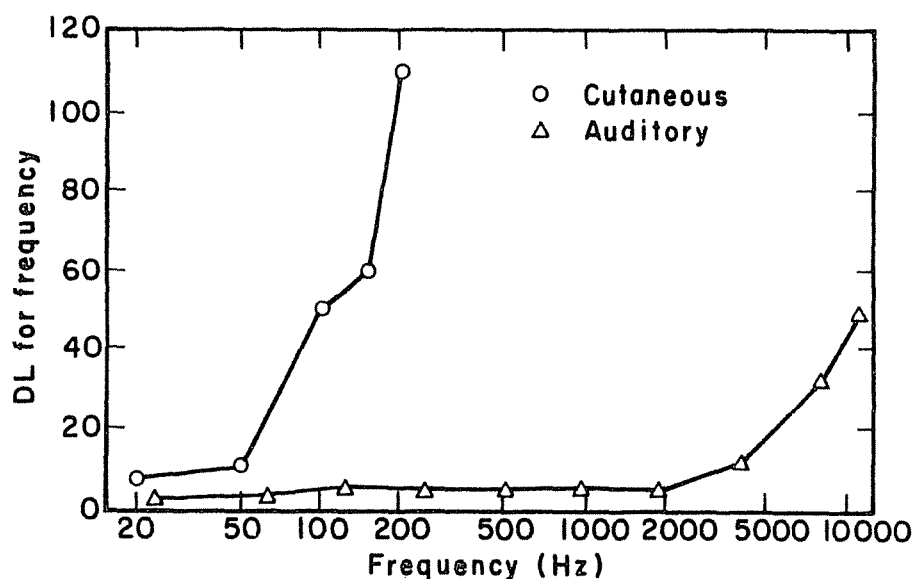


FIG. 2.8. Auditory and tactile difference thresholds for discriminating changes in frequency of vibration. (From Goff, 1967.)

## Analytical Psychophysics

The second function of psychophysics has been the testing of hypotheses about the nature of biological mechanisms underlying sensory experience. The work of those investigators who use psychophysics in this way is based on the assumption that there is a basic correspondence between neural activity and perception. The *Principle of Nomination*, as Marks (1978a) has called it, declares that identical neural events give rise to identical psychological events. Thus, according to the principle, when stimulus A and stimulus B produce the same neural response, they will yield the same sensory experience. The reflexive form of the Principle of Nomination states that, when stimulus A and stimulus B produce the same sensory experience, they produce the same neural response. This principle, used in conjunction with those psychophysical procedures in which different stimuli are adjusted to yield identical sensations, constitutes a powerful tool for discovering the neural events that determine sensory experience.

The results of Wald (1945) plotted in Figure 2.2 provide an example of the use of the reflexive Principle of Nomination. In Wald's experiment, identical sensations of colorless light were experienced when the observer detected lights of different wavelengths presented to the peripheral retina. In other words, the rod (scotopic) spectral sensitivity curve gives the physical intensities of stimuli of different wavelengths needed to produce identical sensations. According to the reflexive Principle of Nomination, these combinations of wavelengths and intensity of light will produce identical responses in the nervous system. Indeed, it has been discovered that the number of photons that must be absorbed by the photochemical pigment in rods, rhodopsin, is identical at any wavelength—about 10 photons—for the observers to detect light. Specifically, as illustrated in Figure 2.9(a), the number of photons incident on the cornea of the eye at the detection threshold varies as a function of the wavelength of the stimulus. Since the lens and other ocular media of the eye absorb light, the number of photons at the retina needed for detection must be less than that measured at the cornea. The number of photons at the retina can be calculated at all wavelengths from the absorption spectrum of the ocular media (b). The values in (a) multiplied by the corresponding values in (b) gives the number of photons absorbed by the ocular media. Subtracting these values from (a) gives the number of photons at the retina needed for vision. The results of this calculation are plotted in (c). Of the photons reaching the retina, the number absorbed by the photochemical pigment rhodopsin (e) is determined for each wavelength of light by multiplying the number of photons at the retina needed to exceed threshold (c) by the absorption spectrum of rhodopsin (d). It can be seen in Figure 2.9(e) that

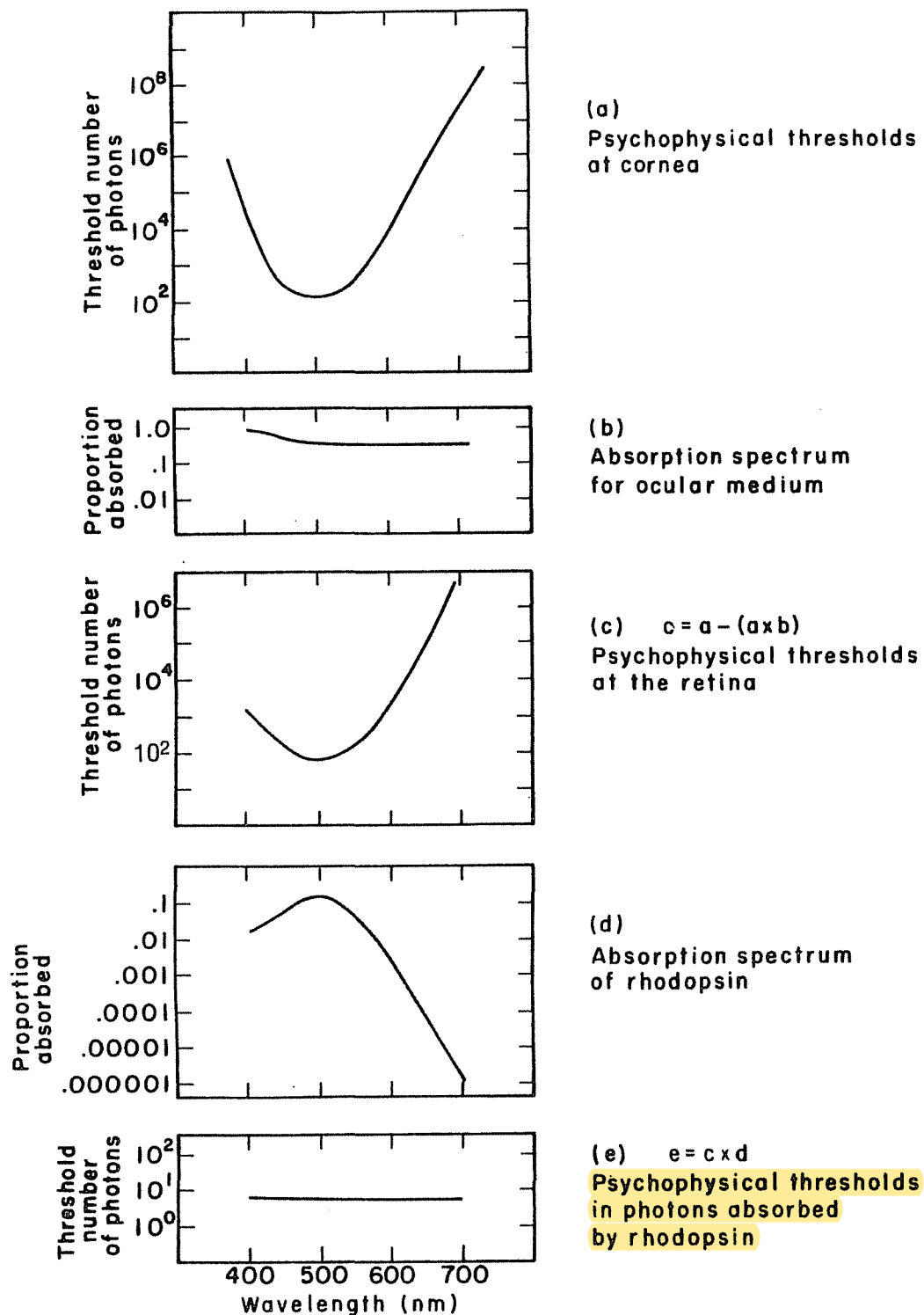


FIG. 2.9. Absolute threshold measured at the cornea of the eye as a function of the wavelength of light (a). Absorption spectrum of the ocular medium of the eye (b). Absolute threshold at the retina of the eye as a function of wavelength of light (c). Absorption spectrum of rhodopsin (d). Absolute threshold expressed as photons absorbed by the photochemical pigment rhodopsin contained in rod receptors in the retina (e).

the number of photons that must be absorbed by rhodopsin in order to exceed the threshold for vision is exactly the same at all wavelengths of light. Thus, combinations of stimulus intensity and wavelengths that produce identical sensations also produce identical photochemical reactions. A fundamental fact of visual science was discovered through integration of data from two fields as different as psychophysics and photochemistry.

More generally, it is by assuming the reflexive Principle of Nomination that it is possible to bridge the gap between psychophysical and biological facts. Because identical sensations are based on identical physiological reactions, a physiological hypothesis can be tested by a psychophysical procedure. Without this principle, the task of correlating sensory experience with physiology would probably be impossible. A biochemist studying visual pigment and a visual psychophysicist studying absolute thresholds would have no common language through which to inter-relate their findings. Because of differences in language, the two scientists would be restricted to working on problems within their own mutually exclusive subdisciplines of visual science. The research described above on the photochemical basis of the spectral sensitivity curve illustrates how the language barrier can be crossed. The hypothesis that changes in an observer's visual sensitivity with changing wavelengths of light are caused by corresponding changes in the degree to which the ocular media and photochemical pigments of the visual receptors absorb light was tested through the *method of response invariance*. In this method, termed by Rodieck (1973), the investigator seeks to discover, not how the response changes as the stimulus is varied, but rather the combinations of stimulus variables that generate identical responses. Threshold responses are considered identical because, within an experiment, the same criterion of performance (e.g., detecting the stimulus 50% of the time) is always used. The intensities of light needed to produce threshold responses were determined for a wide range of wavelengths of light. These combinations of light intensities and wavelengths were also found to result in identical physiological responses (10 photons absorbed by the photochemical pigment of the receptors).

Another name for the method of response invariance is the *criterion response technique*. When it is used to determine the spectral sensitivity of the visual system, the resulting graphed function is called an *action spectrum*. The action spectrum of rods, determined by measuring psychophysical thresholds for detecting lights of various wavelengths, can be compared to the one determined by measuring the number of photons required at each wavelength for a criterion number of photons absorption by rhodopsin. In addition, these two action spectra can be compared with one obtained through electrophysiology, in which the number of photons at each wavelength needed to cause a criterion neural response from rods

is measured. A hypothetical set of results is seen in Figure 2.10, in which the action spectra have the same forms when measured psychophysically, photochemically, and electrophysiologically. An implication that has been drawn from the finding that the action spectra are essentially identical when measured in these three ways is that the spectral sensitivity of the observer, as revealed through threshold measurements made at various wavelengths of light, is determined by the spectral sensitivity of the neural responses of rods that, in turn, is determined by the spectral sensitivity of the visual pigment, rhodopsin, found in rods.

Although this approach has been known for many years, it was Brindley (1960) who first explicitly stressed its importance for psychophysics. Brindley distinguished between two general types of psychophysical observations, termed Class A and Class B observations (Figure 2.11). Class A observations are those in which the two stimuli are adjusted so that they elicit the same response from the observer. Threshold experiments and matching experiments in which two stimuli are adjusted to produce identical sensations consist of Class A observations. In both cases, the experimenter determines stimulus conditions needed to produce identical responses and, according to the reflexive Principle of Nomination, identical neural responses. Any observation that cannot be expressed as the identity or nonidentity of two sensations is a Class B observation.

The difference between Class A and Class B observations can be illustrated by examples from research in visual perception. Using Class A

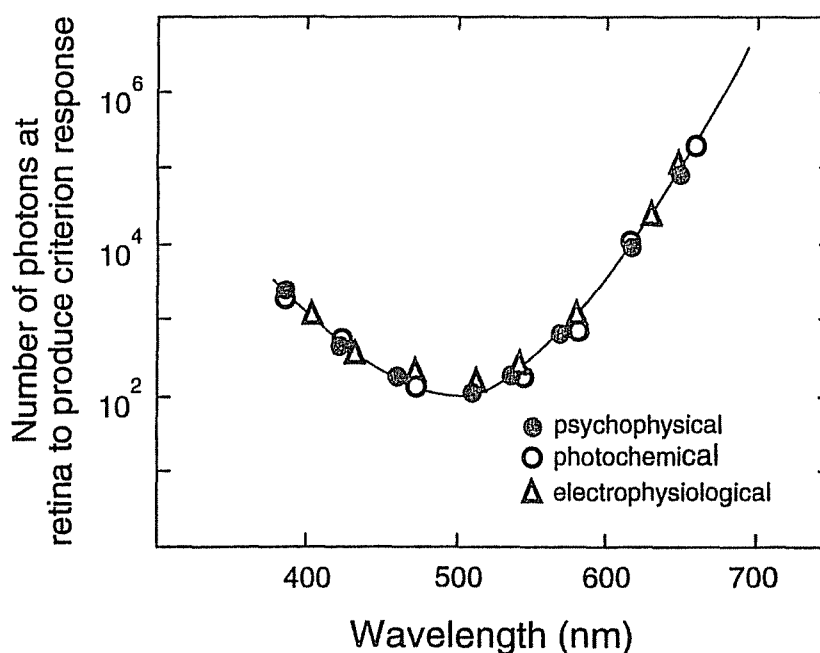


FIG. 2.10. Psychophysical, photochemical, and electrophysiological action spectra. Results are hypothetical but typical of those obtained from actual experiments.

### Class A Observation

Stimulus A → Neural Response X → Sensation Y

Stimulus B → Neural Response X → Sensation Y

### Class B Observation

Stimulus A → Neural Response X → Sensation Y

Stimulus P → Neural Response Q → Sensation R

FIG. 2.11. Distinction between Class A and Class B observations as described by Brindley (1960).

observations, it is possible for an observer to adjust the intensity and wavelength of a yellow light so that when it is projected on a surface, it produces, in the observer, a yellow sensation identical in brightness and hue to that of a mixture of red and green light projected adjacent to it. For example, with proper adjustment of light intensity, the yellow hue and brightness of a 565-nm light will appear identical to the mixture of a 590-nm red light and a 510-nm green light.

In contrast to Class A observations, Class B observations are when the observer's adjustments of two stimuli, although achieving a match over some dimension of perception, do not make the two sensations indiscriminable. For example, if you match two different hues, say, red and green, so that they appear equal in brightness, then you are making a Class B observation. The two sensations are still different by virtue of their differences in hue, although they are matched on the brightness dimension. Because the two sensations are not identical you cannot apply the reflexive principle of nomination. Thus, although valuable information may be obtained through Class B observations, they have limited implications for determining underlying physiological events.

In many Class B observations, the experimenter determines how the sensory response of the observer changes as the stimulus changes. Included as Class B observations are all those in which an observer reports that his sensation changes from blue to green when the wavelength of light is changed, or that a light has become twice as bright when its intensity is increased. That observers can reliably make these kinds of judgments forms the basis of many of the psychophysical scaling procedures discussed in chapters 9 through 14. Although Class B observations



can be made reliably, they lack what Brindley calls a *psychophysical linking hypothesis*, which would provide a rigorous means by which psychophysical observations could be used to test hypotheses about underlying physiological mechanisms. Class A observations, on the other hand, coupled with the assumption that identical sensations are based on identical physiological events, provide a means for testing a physiological hypothesis with a psychophysical procedure. By using the method of response invariance for both the domains of sensation and physiology, it is possible to look for physiological responses that are absolutely identical when different stimuli produce sensations that are absolutely identical. Many psychophysicists have argued that it is only from such invariances that the physiological bases of sensation will be discovered. At the very least, the method of response invariance has made explicit certain methodological implications of the philosophy of materialism and has provided a powerful tool for the scientific study of sensory processes.

A second example of the use of the method of response invariance is seen in the work of Verrillo on the neurophysiological basis of the detection of vibration of the skin. In examining the absolute sensitivity for touch, we saw that the threshold for detecting vibration is independent of stimulus frequency at low frequencies and is a U-shaped function of frequency for higher frequencies (Figure 2.4). To account for this observation, Verrillo (1963) proposed a duplex theory of mechanoreception, in which he hypothesized that one type of receptor was responsible for detecting low frequencies and another for detecting high frequencies.

A sharp break in a psychophysical threshold function often represents a transition from the operation of one type of sensory receptor to another. In using psychophysical threshold functions to identify receptor systems, the assumption is made that the psychophysical threshold is always determined by the receptors that have the lowest threshold. Recall that the initial segment of the dark adaptation curve of Figure 2.1 was determined by cones because immediately after exposure to the adapting light their thresholds are lower than rod thresholds. However, after several minutes in the dark, the reverse was true and rods determined the threshold for the remainder of the experiment.

Verrillo (1966) subsequently identified the Pacinian corpuscle as the receptor responsible for detecting high frequency vibration. Verrillo's comparison of psychophysical threshold functions for human observers with neural threshold functions of Pacinian corpuscles is an example of the method of response invariance. Both functions seen in Figure 2.5 represent combinations of stimulus intensity and frequency needed to produce threshold responses. Because of the close correspondence between the U-shaped segment of the psychophysical function and the neural threshold function, Verrillo concluded that high frequency vibra-

tion is detected exclusively through stimulation of Pacinian corpuscles. Recent evidence strengthening this argument comes from Bolanowski and Verrillo (1982), who compared psychophysical thresholds for humans with neural thresholds for Pacinian corpuscles of cats. As in the Verrillo (1966) study, the relationship between threshold and stimulus frequency was examined. In addition, the skin temperature of the observer's hand and the temperature of the bathing solution of the cat's Pacinian corpuscles were experimentally varied. The results seen in Figure 2.12 show that variation in temperature has a strikingly similar effect on psychophysical and neural thresholds. In both cases, the frequency of maximum sensitivity (i.e., the frequency with the lowest threshold) shifted to higher frequencies as temperature increased. Thus, a correspondence between psychophysical and neural threshold functions was observed over a wide range of temperatures, even though the shape of the functions changed with temperature. This result is expected if a single receptor-type mediates the detection of high frequency vibration. When the frequency response of the Pacinian corpuscle is changed by manipulation of a variable such as temperature, there should follow a corresponding change in psychophysical thresholds. Bolanowski and Verrillo's findings strongly support this hypothesis.

When it is not possible to compare psychophysical and neural threshold functions, the full power of the method of response invariance cannot be exploited. Nevertheless, in the absence of neural response data it may be possible to identify underlying neural mechanisms from psychophysical data. For example, the *method of selective adaptation* has been used to study the properties of sensory receptors. When using this method, the assumption is made that, by exposing the observer to a carefully selected adapting stimulus, the thresholds of all types of receptors but one are sufficiently elevated so that the one type of receptor that remains sensitive will determine the psychophysical threshold. This method has been successfully used to study how the sensitivity of visual receptors changes as the wavelength of light changes (Stiles, 1959; Wald, 1964). Spectral sensitivity curves, as determined psychophysically under conditions of adaptation, were found to be in substantial agreement with those determined physiologically for individual receptors. Figure 2.13 illustrates a typical threshold function where small stimuli are presented exclusively to the fovea, an area of the retina containing only cone receptors. The three segments of the curve reveal the wavelengths at which each of the three types of cone, blue sensitive, green sensitive, and red sensitive, have their lowest thresholds. Because the threshold curves for each type of cone overlap substantially, it is not possible, in this experiment, to determine the entire curve for each of the individual cone types. One can, however, examine the threshold curve of one cone type if the threshold of the other two are elevated by selectively

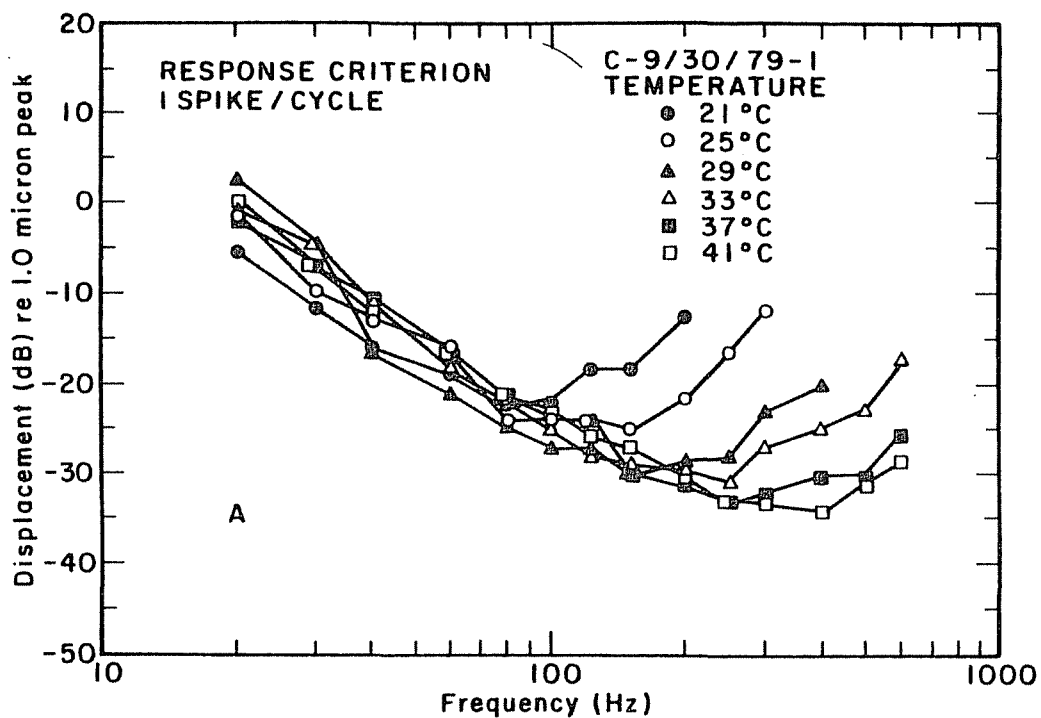
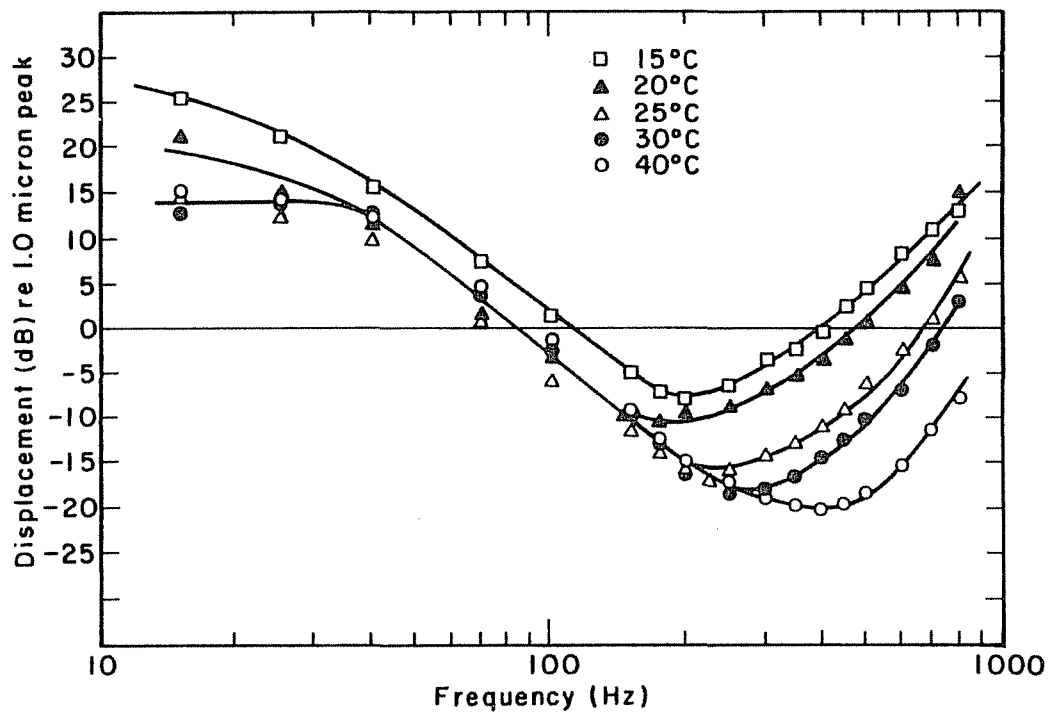


FIG. 2.12. Psychophysical threshold for detection of vibration on the hand as a function of frequency and skin temperature (top). Neural threshold of Pacinian corpuscle as a function of frequency and temperature of bathing solution (bottom). (From Bolanowski & Verrillo, 1982.)

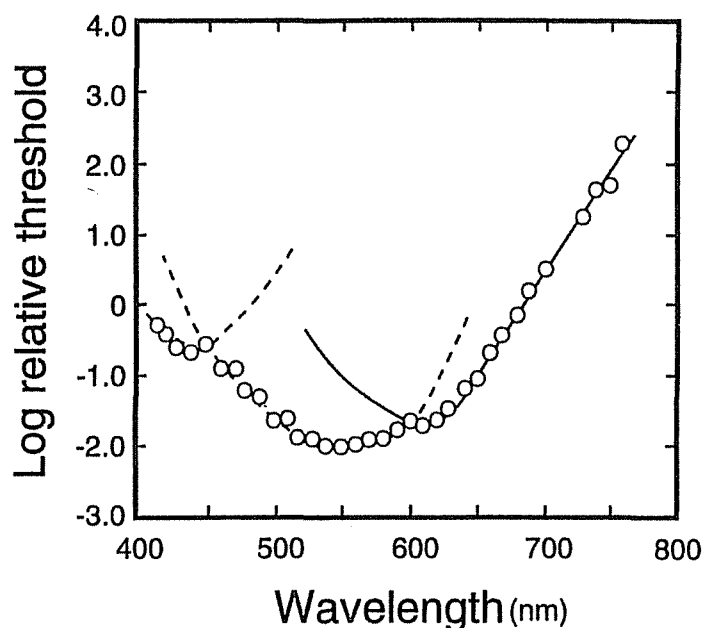


FIG. 2.13. Logarithm of relative threshold as a function of the wavelength of a stimulus presented to cones in the fovea. (Data from Hsia & Graham, 1952.)

adapting them. Figure 2.14 illustrates typical results obtained with this procedure when the fovea is exposed to short wavelength light that elevates the threshold of the blue- and green-sensitive cones but has no effect on the thresholds of the red-sensitive cone. The thresholds obtained in this experiment reveal how the threshold of the red-sensitive cone varies over a wide range of wavelengths. The procedure of selective adaptation is based on the principle that the psychophysical threshold is always determined by the receptor with the lowest neural threshold. In the present example, the blue-sensitive and green-sensitive cones are adapted so that, over a wide range of wavelengths, the threshold of the red-sensitive cone is lowest, and therefore determines the psychophysical thresholds. Thus, it is possible, by measuring for a wide range of wavelengths, the psychophysical threshold for detecting light, to determine the spectral sensitivity curve for the red-sensitive receptor. We turn now to a specific experiment in which

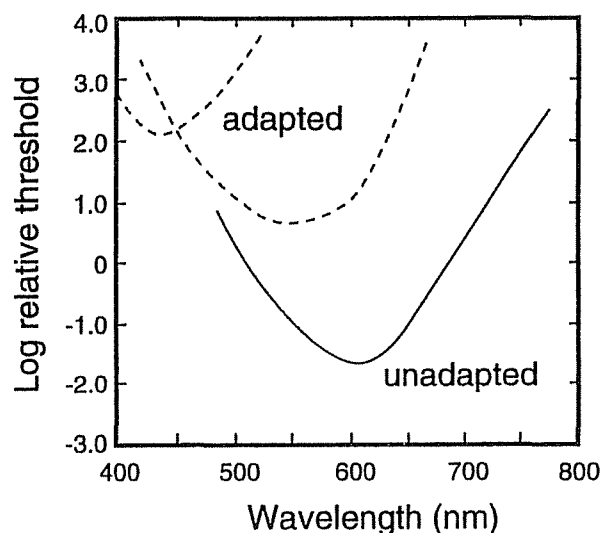


FIG. 2.14. Logarithm of relative threshold after adaptation of the eye to short wavelength light. Thresholds mediated by red-sensitive cones along the unadapted segment of the curve were unaffected by the adapting stimulus. Thresholds mediated by blue-sensitive and green-sensitive cones were elevated through exposure to the adapting stimulus.

George Wald measured the spectral sensitivity curves for each of the three cone types.

In Wald's (1964) experiment, the observer was required to detect a small circle ( $1.0^\circ$ ) of variable wavelength presented against a larger ( $3.5^\circ$ ) illuminated background of fixed wavelength. By having the observer visually fixate a small point where the test stimulus was presented, no rods, and only the cones of the fovea, were stimulated. The objective of the experiment was to measure, through psychophysical procedures, the spectral sensitivity of each of the three types of cones in the fovea.

Spectral sensitivity curves, where sensitivity is plotted as a function of the wavelength of the test stimulus, had to be determined for each type of cone. The wavelength and intensity of the background were carefully chosen so that the background, through sensory adaptation, would cause substantial elevations in the thresholds of two types of cones, but have little effect on the third. Thus, measurements of psychophysical thresholds for detecting test stimuli of varied wavelength should reveal the spectral sensitivity of a single type of cone. The psychophysical thresholds for detecting light would always be determined by the cone with the lowest neural threshold.

To obtain the spectral sensitivity curve for the blue-sensitive cone, Wald's observers detected stimuli of variable wavelength presented against a bright yellow background containing all visible wavelengths longer than 550 nm. A yellow background stimulus such as this should elevate the neural thresholds of red-sensitive and green-sensitive cones, while having little effect on the thresholds of blue-sensitive cones. Psychophysical thresholds for detecting stimuli of varied wavelength presented against the yellow background should reveal the spectral sensitivity of the blue-sensitive cone. On the other hand, having the observer detect the test-lights against a blue background should elevate the thresholds of the blue-sensitive and green-sensitive cones, while having little effect on the sensitivity of the red-sensitive cone. The spectral sensitivity of the red-sensitive cone should be revealed by measuring psychophysical thresholds for detecting lights of varied wavelength presented against the blue background. Finally, to isolate the spectral sensitivity of the green-sensitive cone, Wald had observers detect lights of varied wavelength presented against a purple background containing wavelengths in both the blue and red regions of the visual spectrum. In this condition, the green-sensitive cone should be much more sensitive than the adapted blue-sensitive or red-sensitive cones, and consequently, the psychophysical thresholds should reveal the spectral sensitivity of the green-sensitive cones.

The results obtained for one of Wald's observers are presented in Figure 2.15. Sensitivity was expressed as the reciprocal of the measured threshold ( $1/\text{threshold}$ ). The logarithm of sensitivity is plotted as a function of the wavelength of the test stimulus. The absolute height of each curve was not

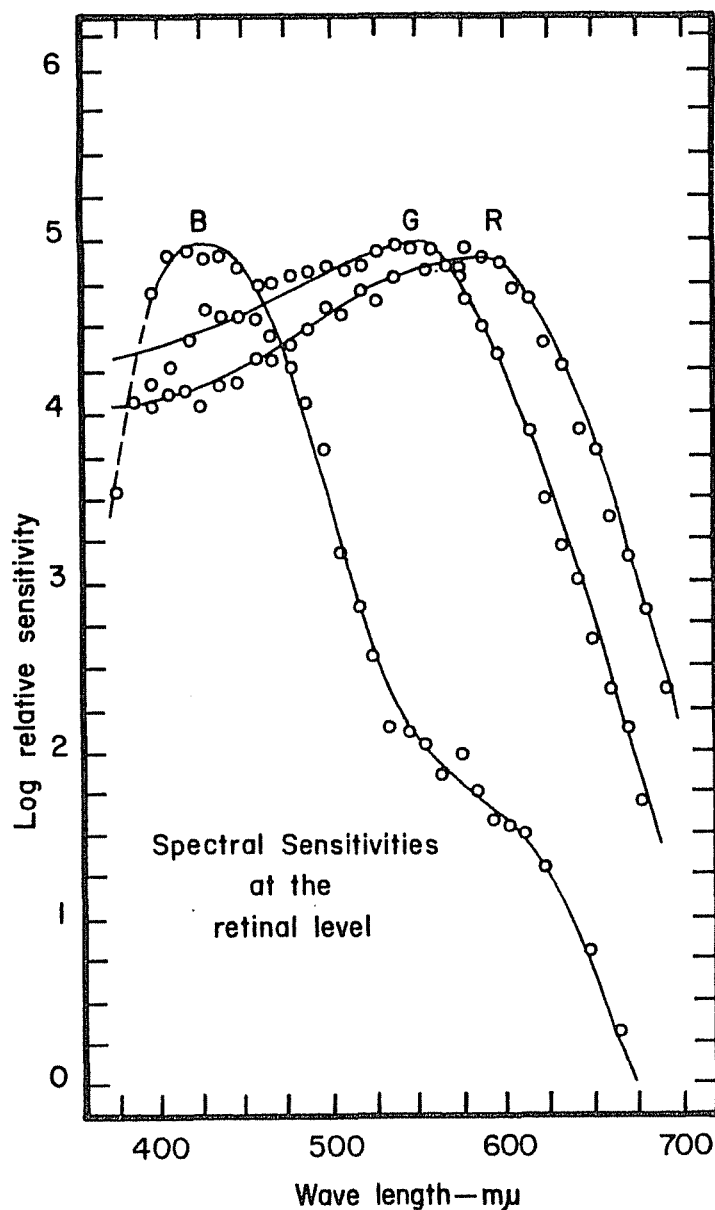


FIG. 2.15. Visual sensitivity ( $1/\text{threshold}$ ) for stimuli presented to the fovea after adaptation. The blue curve (B) represents the psychophysical thresholds measured after adaptation to a yellow light. The green curve (G) represents the psychophysical thresholds measured after adaptation to a purple light. The red curve (R) represents the psychophysical thresholds measured after adaptation to blue light. (From Wald, 1964.)

determined, and thus a measure of relative sensitivity (i.e., sensitivity changes of a cone with changes in wavelength) was plotted. It can be seen that foveal spectral sensitivity curves obtained with different adapting backgrounds peaked at different wavelengths of the spectrum. After adaptation by yellow light, the curve peaked in the blue region of the spectrum. Presumably, this curve was determined entirely by the blue-sensitive cone. When the eye was adapted to purple light, the curve peaked



in the green region of the spectrum, presumably reflecting the sensitivity of the green-sensitive cone. Adaptation to blue light resulted in a spectral sensitivity curve which peaked in the red region of the spectrum. Presumably, this curve was determined by the red-sensitive cone.

It must be pointed out that the measurements of light corresponding to the absolute threshold were made at the cornea of the eye and not inside the eye at the receptors. Consequently, the spectral sensitivity curves in Figure 2.15 might not be entirely accurate indicators of the spectral sensitivity of the cones. Wald thought that each of the three spectral sensitivity curves obtained in the presence of adapting background stimuli reflected the sensitivity curve of the cone plus the filtering action of non-neural structures in the eye. In other words, the psychophysical threshold measured at the cornea, in addition to being influenced by the sensitivity of the receptor, was also influenced by how much light reached the receptor after passing through the eye. Wald used absorption curves for non-neural structures in the eye (e.g., cornea, lens, ocular media, and non-visual pigments of the fovea) to correct psychophysical thresholds measured at the cornea, so that they became psychophysical thresholds at the receptors. Under conditions of selective adaptation, having specified the amount of light of various wavelengths that must reach the receptor in order for the observer to see, Wald was able to estimate the spectral sensitivity curve of the cone. Psychophysically measured spectral sensitivity curves for the three types of cones are seen in Figure 2.16.

The method of selective adaptation has also been used to study the characteristics of mechanoreceptors in the skin (Gescheider, Frisina, & Verrillo, 1979; Hollins, Goble, Whitsel, & Tommerdahl, 1990; Verrillo & Gescheider, 1977). In the study by Verrillo and Gescheider (1977), psychophysical thresholds for detecting vibration on the hand were measured before and after adaptation. Adaptation consisted of applying an intense 10-Hz stimulus to the skin for a period of 10 min. It can be seen in Figure 2.17 that adaptation by the 10-Hz stimulus had the selective effect of elevating thresholds at low, but not high, frequencies. Presumably, the low frequency adapting stimulus elevated the thresholds of all receptors except Pacinian corpuscles. Under these conditions, the frequency response of a single receptor type—the Pacinian corpuscle—could be examined over a wide range of frequencies through the measurement of psychophysical thresholds. As a consequence of elevating the thresholds of the non-Pacinian receptors, the flat portion of the psychophysical curve was eliminated, and what remains is the entire U-shaped threshold curve of the Pacinian corpuscle.

From this brief exposure to analytical psychophysics, it should be clear how the reflexive Principle of Nomination that identical sensations produced by stimuli are mediated by identical neural responses has provided the philosophical foundation for a very ambitious approach to psycho-

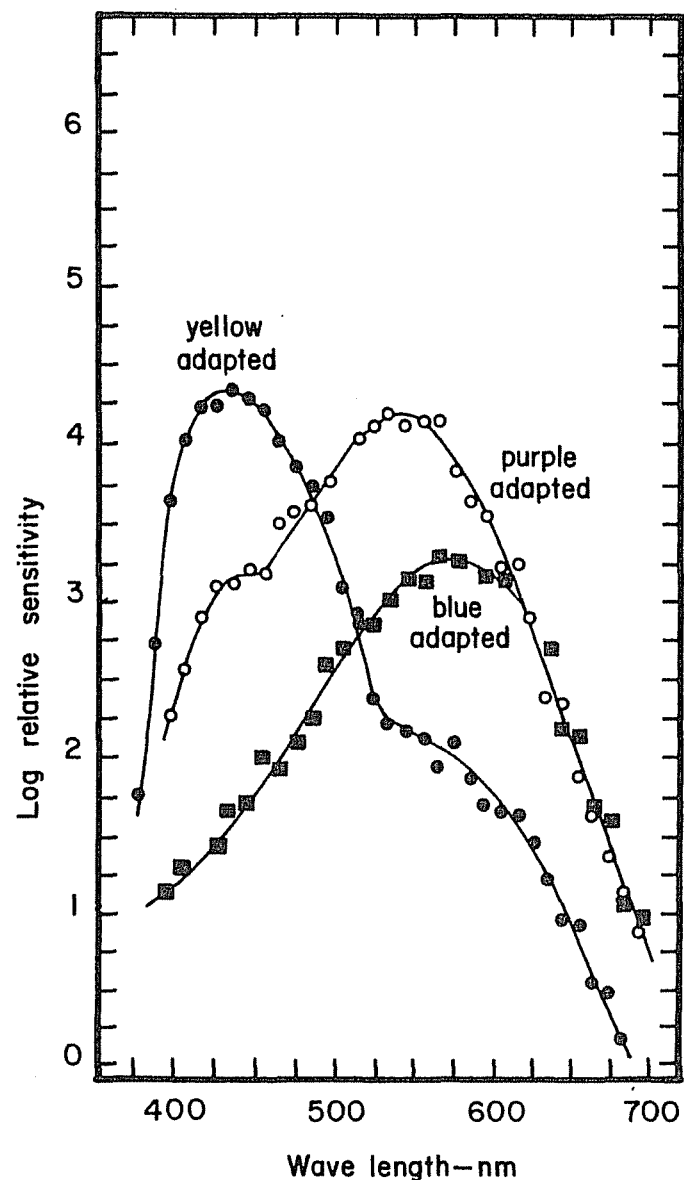


FIG. 2.16. Visual sensitivity corrected for absorption of light by elements of the eye before the retina. The three curves represent sensitivity functions for blue-, green-, and red-sensitive cones in the fovea of the human eye. (From Wald, 1964.)

physics, the goal of which is no less than to determine the neural basis of sensation. According to the analytic psychophysicist, the method of response invariance must be used to determine combinations of stimulus variables that result in identical sensations. Identical sensations are specified through invariant sensory responses, such as the absolute threshold or a psychophysical match of sensations above absolute threshold. Thus, the experimental data always consist of measurements of properties of the stimulus (e.g., intensity and wavelength) that correspond to a constant sensory response. Only after the stimulus conditions that produce identical sensation have been determined is it possible to discover the underlying neural response. After the psychophysical measurements are made, the investigator may then proceed to search for neural responses that remain constant under the same stimulus conditions that resulted in constant sensation. The discovery of such invariances in neural response

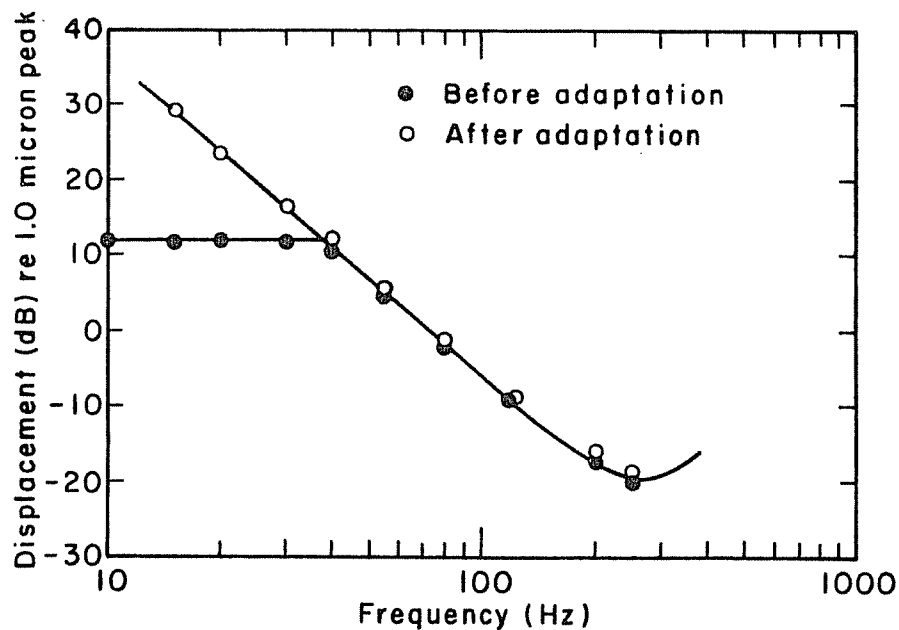


FIG. 2.17. Vibrotactile thresholds on the hand as a function of frequency measured before and after adaptation. (From Verrillo & Gescheider, 1977.)

has greatly enhanced our understanding of the neural basis of sensation and has provided strong support for the basic assumption and procedures of analytic psychophysics.

We have considered the methodological assumptions for investigating the biological bases of psychophysical responses. It is appropriate to turn now to the various techniques for measuring sensory thresholds.

## PROBLEMS

- 2.1. Below are the neural thresholds for hypothetical neural systems A and B at various wavelengths of light. Plot these values and draw a smooth curve indicating the predicted psychophysical thresholds.

	Wavelength in nm											
	400	420	440	460	480	500	520	540	560	580	600	620
System A	80	52	40	38	37	37	36	36	38	40	43	48
System B	140	108	80	56	38	20	10	7	8	12	15	30

- 2.2. Draw the curve describing absolute thresholds for detecting vibration on the hand as a function of vibration frequency. Assuming that the four-channel model is correct, draw the threshold function for each of channels (see Figure 2.6). Now draw the threshold curve predicted after adaptation of the P channel with a 250 Hz adapting stimulus.