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Neural Events and the Psychophysical Law

Power functions like those that govern subjective magnitude show themselves in neurelectric effects.

S. S. Stevens

In the year 1800 Volta assembled a large battery of his newly invented cells and connected the total array to a pair of metal rods inserted in his ears. When he closed the switch he felt a jolt in the head, followed by a noise like the boiling of thick soup. Goaded by a similar curiosity some years later, E. H. Weber persuaded his brother to submit to electrodes in the ears. Brother Weber said he heard nothing, but he saw a light that seemed to pass right across his head. Since those heroic days, many experimeters have confirmed the specificity of the sensory systems: however we excite them, they do their separate things. Sensory quality depends, it seems, on which nerve is actuated and where in the brain it leads. And there the problem rests.

But the brain can distinguish quantity as well as quality. What about the magnitude of the sensation? The noise of the approaching jet grows from a gentle rumble to a thunderous roar, all the while firing messages through the same sense organ and along the same auditory nerve. How does the system manage the processing of such vast differences in stimulus intensity? That question became a genuine scientific question only in the 1920's when the neural code was broken and it was disclosed that nerve impulses behave as all-or-none events. Prior to that discovery, it was plausible to suppose that an increase in stimulus intensity would simply cause the nerves to do more of whatever it was they were doing in the first place. But once the deciphering of the neural code had shown that each nerve fiber must carry a train of impulses—all the impulses built on a similar design—and that the train must space itself out to a limit of a few hundred impulses per second, then it became clear that the mediation of sensory intensity must count itself among the major puzzles of neurology.

The Fechner Compression

The initial impact of the all-or-none law was softened by a misconception. Beginning in 1860, the physicist Fechner had convinced much of the scientific public that sensation grows as the logarithm of the stimulus. As a consequence, little consternation seems to have been generated by the constraints imposed by an all-or-none principle coupled with a limited firing rate. If perceived magnitude was indeed subject to a range reduction as severe as the logarithmic compression that Fechner claimed, then perhaps changes in the stimulus intensity could be mediated without difficulty by changes in the frequency of the nerve impulses. As a matter of fact, some of the earliest studies of nerve impulses in Lord Adrian's laboratory had displayed a slow and approximately logarithmic growth of firing rate when the stimulus was increased.

That appeared to settle it. Vindication, it seemed, had arrived at last for Fechner, the father of psychophysics and a principal progenitor of experimental psychology. Fechner had marshaled many compelling arguments to bolster his notion that a *relative* increment in the stimulus energy produces a *constant* increment in the apparent magnitude. That idea, which entails a logarithmic relation, had come to him, he tells us, as he lay abed on 22 October 1850, a date that some psychophysicists like to celebrate as Fechner day.

In the next century, however, progress in electronics and acoustics made it possible to produce and control a sound wave and thereby to explore wide ranges of stimulus intensity. The transmission engineers had devised a logarithmic unit, called a decibel, for the specification of power levels, and that unit had been found to fit nicely the needs of acoustics. But it soon became clear that something was amiss, because the decibel scale, marking off equal ratios of intensity, did not appear to mark off equal steps in apparent loudness, as Fechner's law predicted. So it loomed as an engineering necessity to determine how loudness does in fact vary with stimulus intensity. In the 1930's several laboratories produced loudness scales. They all showed that the growth of apparent loudness departs widely from a logarithmic function, so much so that a tone of 100 decibels, instead of sounding twice as loud as 50 decibels, sounds about 40 times as loud. Fechner's law, it seems, fell wide of the mark. But scientific laws often refuse to vanish merely because they have been proved wrong. If a crippled law is to hobble off stage, a new law must take the scene.

The Power Law

An alternative law had lurked off and on in the wings ever since 1728 when the mathematician Gabriel Cra-

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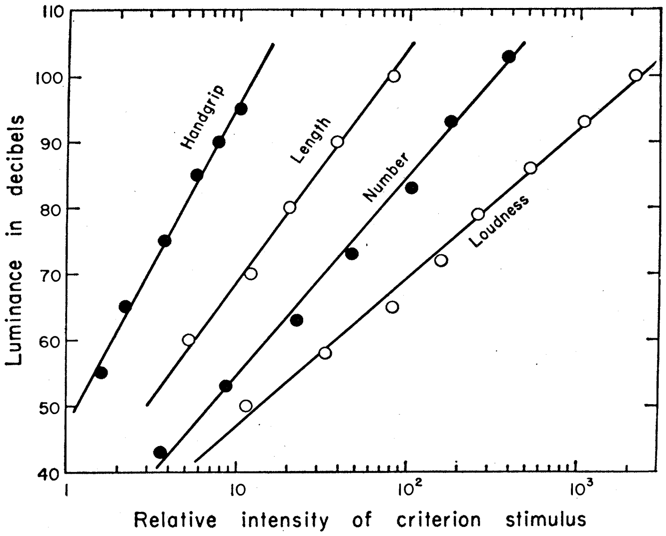

Fig. 1. Equal-sensation functions determined by cross-modality matches between brightness and four other continua. Subjects adjusted the values on each continuum in order to match the brightness of a circular luminous target viewed in a dark room. Each point is the geometric mean of matches made by ten or more subjects. Straight lines in log-log coordinates represent power functions. Subjects squeezed a precision hand dynamometer to match the apparent force to the apparent brightness. Other subjects adjusted the length of a line of light projected on a wall to match the apparent brightness of a target. Numbers were matched to apparent brightness by the method known as magnitude estimation. For the loudness-brightness matches the subjects adjusted the level of a band of noise to match the apparent brightness of a luminous target. Luminance is measured in decibels re 10^{-10} lambert, which is close to the absolute threshold.

mer conjectured that the subjective value that a person places upon money may increase as the square root of the number of dollars. Other examples of a power law were conjectured from time to time, and Fechner himself argued some of them down. Then in 1953, the pursuit of a curious but minor phenomenon that occurs in bisection experiments turned up sets of data that seemed to me to exhibit two astonishing features. First, there was a notable similarity in the responses of both the eye and the ear when sensation was measured under three different scaling methods—bisection, fractionation, and magnitude estimation. Second, the quantitative results for both light and sound appeared to support the proposition that the sensation ψ grows in proportion to the stimulus ϕ raised to a power (*1*). The relation may be written

$$\psi = k\phi^{\beta}$$

where β is the exponent of the power function and k is a constant. A convenient feature of the power function is that in log-log coordinates it describes a straight line whose slope is the exponent. Thus

$$\log \psi = \beta \log \phi + \log k$$

The results for both sense modalities, vision and hearing, appeared to call for the exponent ⅓. (Measured in terms of sound pressure the loudness exponent becomes ⅔.)

Next there began an exciting game of testing the generality of the power-law principle. Does it hold only for the distance receptors, or does it govern all sense modalities? Although in those days it seemed far from likely that a single quantitative relation would be found to apply as a first-order rule across all the senses, no firm exception has yet emerged. The exploration of more than three dozen perceptual continua has revealed an occasional second-order departure from the power function, but, in general, each sense modality has its characteristic exponent. The specific value of the exponent may depend in some modalities on such parameters as adaptation and contrast or inhibition.

Matching across Modalities

Interrelations among the exponents of the psychophysical power functions can often be established by a direct cross-modality comparison. With the proper apparatus, for example, you can adjust the loudness of a sound to match the apparent brightness of a light. If the light is set at many different levels, loudness matches made to the apparent brightness will map out an equal-sensation function. Since those two modalities happen to have the same exponent, we predict that the equal-sensation function between loudness and brightness will have the exponent 1.0, a value that experiments have confirmed (*2*). The general rule is that the exponent of the equal-sensation matching function is given by the ratio of the exponents of the two modalities being matched.

Examples of cross-modality functions representing the matching of four different continua to visual brightness are shown in Fig. 1.

Dozens of such tests have been made, and from them have emerged a pair of principles: (i) any perceptual continuum can be matched to any other perceptual continuum; (ii) the power-function exponents describe a transitive, interconnected net such that, when two continua have each been matched to a given continuum, the resulting exponents can be used to predict a third exponent.

The basic invariance that underlies the psychophysical domain can be summarized in a phrase: equal stimulus ratios produce equal sensation ratios. From that pervasive principle, all the rest may be said to follow. But now a new question presents itself: To what extent do the measured quantities of neutral activity manifest a similar invariance? The wide sweep of the ratio invariance that underlies the sensory power law ought somehow to find itself reflected in neurelectric measures if we are to comprehend the basis of the psychophysical function.

The Exponents

Across the luncheon table some years ago, K. C. Cole asked me, "Why are all those functions of yours power functions?" Not knowing the answer, I parried with my own question, "Why are nearly all the laws of physics power functions?" "Yes," said Cole, "but physical laws tend to have simple exponents, whereas the exponents of the sensory functions seem to take on all sorts of values."

Perhaps many of the laws of physics would also exhibit peculiar exponents if they had to be determined by the averaging of relatively noisy measurements. Conversely, there is a possibility that the variability in our psychophysical measurements may conceal an underlying simplicity. In any event, we are free to speculate that the exponents of the psychophysical power functions would, under ideal circumstances, prove to be simple rational numbers. In order to illustrate that hypothesis, Table 1 presents a list of some of the measured exponents together with a "best guess" concerning a possible simple exponent.

Some of the exponents do indeed appear to be simple—expressible as the ratio of small whole numbers. The exponents for loudness and brightness are perhaps the most firmly established, and they appear to be simple fractions. Many of the exponents have been determined by asking subjects to match numbers to sensory stimuli (method of magnitude estimation) because that is a very convenient procedure. Like all matching procedures, however, it suffers from the ubiquitous regression effect, and, consequently, the method of magnitude estimation underestimates the exponent (*3*). When provision can be made for the subjects to match stimuli to numbers (method of magnitude production) there is a corresponding overestimation. With the help of both methods the regression effect can sometimes be evaluated and corrected. But many stimuli do not lend themselves to easy adjustment by the subjects in the experiment.

In sense modalities like vision and hearing, which must cope with enormous ranges of energy—sometimes exceeding 10^{12}—there is an obvious need for low exponents in order to provide a compressor action. But that rule does not necessarily hold in reverse, as witness, for example, the sense of smell. There the exponent is less than 1.0 despite the fact that the effective range of stimulus concentrations is comparatively limited. Nevertheless, the low exponents in vision and hearing appear to be nature's way of providing a sufficient nonlinearity to effect a match between the wide-ranging input from the outside world and the processing capacity of the central nervous system. By means of a nonlinear interface at some point in the system, a billionfold change in light energy, or in sound energy, becomes a thousandfold change in apparent magnitude. The direct central processing of intensity ranges that exceed a billionfold would seem to lie beyond the capacity of the brain. Changes of a few thousandfold may conceivably lie within bounds.

In some of the sense modalities no compressor action seems to occur, and the corresponding exponents in Table 1 have the value 1.0. Other modalities exhibit an expander action, with exponents greater than 1.0. How would Fechner have reacted to the evidence for acceleration in sensory functions where only logarithmic deceleration was supposed to occur?

Physiological Models

Although the power law provides no automatic solution to the puzzle of sensory transduction, it may draw a helpful guideline by instructing us to look for processes that are consonant, not with logarithmic functions, but with power functions. The sentient human subject, behaving as a comparator, tells us by his reaction just where the guideline must run. When the experimenter varies the luminance of a target and the subject varies the level of a sound in order to keep the apparent loudness in step with the apparent brightness, what can the subject be doing other than comparing the operating characteristics of the visual and auditory transducers? And so also with the many other comparisons among the different sense modalities. The resulting equal-sensation functions, by providing a quantitative model of the overall first-order input-output relations of the sensory systems, may serve to prescribe directions for the development of transducer physiology.

Delbrück defined the problem in his Nobel address (*4*).

> Sensory physiology in a broad sense contains hidden as its kernel an as yet totally undeveloped but absolutely central science: transducer physiology, the study of the conversion of the outside signal to its first "interesting" output. I use the word "interesting" advisedly because I wish to exclude . . . the primary photochemical reactions of the visual systems. . . . Transducer physiology proper comes after this first step, where we are dealing with devices of the cell unparalleled in anything the physicists have produced so far with respect to sensitivity, adaptability, and miniaturization.

What Delbrück's "central science" will disclose remains to the future, of course, but one of its concerns may be to explicate the mechanisms that generate the psychophysical power functions.

The decisive insights needed here will probably not accord with the simplistic view that the sensory power function must show itself at any or every stage, all up and down the sensory system. Maybe it will and maybe it won't.

Since the sense organs themselves have been said by many experimenters to respond logarithmically, the question arises whether the power function would be precluded by a logarithmic trans-

Table 1. Measured exponents and their possible fractional values for power functions relating subjective magnitude to stimulus magnitude.

Continuum	Measured exponent	Possible fraction	Stimulus condition
Loudness	0.67	2/3	3000-hertz tone
Brightness	0.33	1/3	5° target in dark
Brightness	0.5	1/2	Very brief flash
Smell	0.6	2/3	Heptane
Taste	1.3	3/2	Sucrose
Taste	1.4	3/2	Salt
Temperature	1.0	1	Cold on arm
Temperature	1.5	3/2	Warmth on arm
Vibration	0.95	1	60 hertz on finger
Vibration	0.6	2/3	250 hertz on finger
Duration	1.1	1	White noise stimuli
Finger span	1.3	3/2	Thickness of blocks
Pressure on palm	1.1	1	Static force on skin
Heaviness	1.45	3/2	Lifted weights
Force of handgrip	1.7	5/3	Hand dynamometer
Vocal effort	1.1	1	Vocal sound pressure
Electric shock	3.5	3	Current through fingers
Tactual roughness	1.5	3/2	Rubbing emery cloths
Tactual hardness	0.8	3/4	Squeezing rubber
Visual length	1.0	1	Projected line
Visual area	0.7	2/3	Projected square
Angular acceleration	1.41	3/2	5-second stimulus

ducer. An instructive answer to that question was formulated by MacKay (*5*) who suggested that the output of the transducer may go to a comparator where it is balanced against a centrally generated signal. If the central signal is also logarithmic, then we have two log functions operating, so to speak, back to back, and the overall result would be a power function. "If the present model is valid in its simplest form," said MacKay, "it is a mistake to suppose that *any* stage or chain of stages performs a power-law transformation; but in any case it is clear that no stage or chain *need* do so in order to produce Stevens' results."

The possibility of combining logarithmic functions to produce power functions was also among the suggestions thrown out by Norbert Wiener one afternoon at my summer home in New Hampshire. I had asked him why it was that both vision and hearing seemed to follow power functions. My mistake was not providing a tape recorder, because Wiener's galloping thoughts and far-ranging conjectures covered more possibilities than can now be recalled. But the factual question remains: Do the sensory systems generate power-law transformations that can be detected as neurelectric effects?

First it may be in order to point out that the receptor action has seemed to some authors to be logarithmic when many of the recorded data suggest rather that the relation may be a power function. The compound eye of the horseshoe crab *Limulus* provides classic examples. Some four decades ago Hartline and Graham (*6*) undertook delicate dissections that enabled them to record the impulses in a single nerve fiber connected to a single ommatidium. A light stimulus produced a burst of impulses, followed a second or two later by a steady train. The frequency of the impulses in the train increased with light intensity, as shown by the stars in Fig. 2. The straight line through the stars represents a power function, and the slope of the line determines an exponent of 0.29.

Improvement of amplifiers and electrodes has permitted a sampling of the intracellular potential generated in a single ommatidium. Instead of the spikes observed in the single nerve fiber, a light stimulus produces a so-called generator potential. Fuortes and Hodgkin (*7*) stimulated various ommatidia with a brief flash of light (0.02 second) at widely varying intensities and recorded the rise and fall of the generator potential. I have undertaken to measure the approximate areas under the oscillographic response curves for three ommatidia, with the results shown by the circles, squares, and triangles in Fig. 2. The straight lines, all drawn with the same slope, represent power functions with the exponent 0.32. Except for two of the points (circles), the agreement with the straight-line power function is close.

The crosses in Fig. 2 represent another set of measures taken from recordings of the generator potential, namely, the maximum amplitude reached at the onset of a light. In this experiment, by Dodge *et al.* (*8*), the nerve spikes were blocked by tetrodotoxin. The first peak of the generator potential grows with the light intensity according to a power function with the exponent 0.21.

The five power functions in Fig. 2 are far from enough to assure us that all receptors operate by power transformations, but the five functions provide a sufficient sampling to demonstrate that power functions are not unknown in the receptor response of *Limulus*.

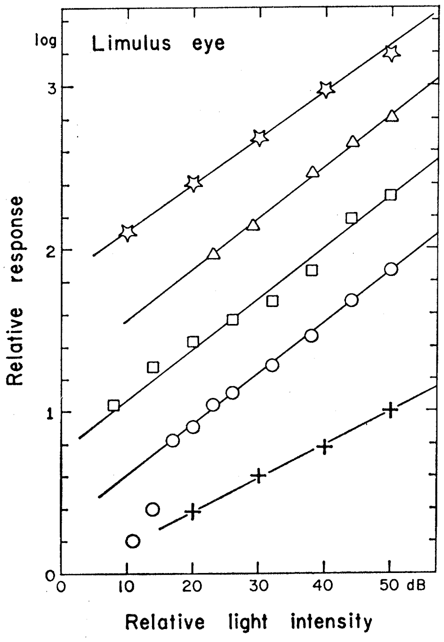

Fig. 2. Power-function responses in the eye of the horseshoe crab *Limulus*. The stars represent frequencies of nerve impulses recorded by Hartline and Graham in 1932 (*6*) from a single fiber of the optic nerve. Frequency was measured 3.5 seconds after the onset of the light. The middle three functions represent responses to 0.02-second flashes of light, recorded with intracellular electrodes in single ommatidia. The plotted points represent the areas under oscillographs published by Fuortes and Hodgkin in 1964 (*7*). The crosses show the initial amplitudes of the generator potential recorded with intracellular electrodes by Dodge, Knight, and Toyoda in 1968 (*8*). The straight lines in the log-log coordinates represent power functions. The slopes (exponents) are 0.29, 0.32, and 0.21. Both coordinates give relative values only. Eyes were dark-adapted.

Here I should remark that I have also gone back to the classic 1927 study of the eye of the eel by Adrian and Matthews (*9*) and have replotted the results of the experiments (23 and 28) for which they published the most complete data (their figures 9 and 16). The frequency of nerve impulses grows by a power function, and for both experiments the exponent is 0.32. Adrian and Matthews rather assumed, as they said, that "the frequency is evidently some exponential [logarithmic] function of the intensity. Such a relation is not surprising," they added, " . . . and the form is in general agreement with what is known of the relation between the stimulus and the brightness of the sensation in man." So there again, we find Fechner's logarithmic law misguiding the expectations of the physiologists (*9*). Remembering 20 years of my own misdirected attention, I understand how hard it is to see power functions, even your own, when you expect a different form.

Another classic from Adrian's laboratory was Matthews' study of the single stretch receptor in a toe muscle of the frog. As the pull on the muscle increased, the impulse firing rate grew as a logarithmic function, or so it seemed. "These experiments," said Matthews, "suggest that this is due in part, at least, to properties of the end organs rather than to the central interpretations of the sensory message by the brain." The end organs may indeed determine the response function, but Matthews' data for his three published experiments (his figure 6 at 0.5 second and figure 7) happen to fit a power function quite as well as, if not better than, a logarithmic function.

Auditory System

In the 1930's, before the sensory power law had asserted itself, Davis and I made a try at aligning an early version of the loudness scale to fit our measurements of the cochlear microphonic—the electrical potential so easily picked up by an electrode in the middle ear of a cat or a guinea pig. The growth of the cochlear microphonic seemed to us to parallel that early version of the loudness function, at least over a good part of the intensity range, so we were led to say "as a first approximation, the form of the loudness functions is imposed by the behavior of the cochlear mechanism" (*10*). That conclusion may still be essentially correct, but further research seems now to suggest that the cochlear microphonic, with its exponent 1.0, is probably not the direct instigator of the loudness response with its exponent ⅔.

When we inserted two concentric electrodes directly into the auditory nerve of a cat, we recorded an electrical response that also resembled the loudness function. Since the electrodes presumably recorded a partial summation of the all-or-none impulses in the nerve fibers, the congruence with the growth of loudness seemed to accord with the hypothesis that loudness depends on the total activity in the nerve. That notion still serves as a reasonable working hypothesis, but there has always remained a nagging difficulty. As the stimulus is increased, the cat's nerve response reaches a maximum at a moderate stimulus level and thereafter it declines. Even in the individual fibers the pulse rate rises to only a few hundred per second and then falls off (*11*). But loudness grows on and on, up and up. How?

Perhaps the electrode provides only a clouded window on the operation of the sensory system. Thus far, however, it is the best window we have. And there is an occasional glimpse of unusual clarity, as when, for example, Boudreau (*12*) recorded potentials in a cat that followed a power function over a range of 60 decibels. But that, he said, was a "rare cat." Rare indeed, but can we expect that the experimenter who pokes an electrode into a neural complex will record the maximum capability on every thrust? It seems safe to assume that the system can surely do better than what is recorded in the average sample.

It is nonetheless important to note that the average sample recorded in the superior olivary complex of 25 cats exhibited an interesting relation between the level of an 800-hertz tone and the amplitude of the neurelectric response. Over a considerable range of stimulus intensities the response amplitude increased in accordance with a power function with an exponent of approximately ⅔, which is the same value as the exponent of the human loudness function.

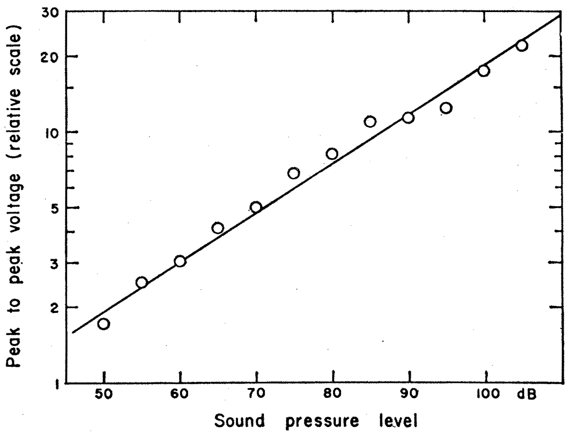

Fig. 3. Showing how the neural action potential grows in amplitude when a brief sound pulse is made stronger. The action-potential wave was picked up by electrodes driven into the cochlea of a guinea pig. One electrode was in the scala vestibuli, the other in the scala tympani. Although the points fall approximately on a power function (straight line) whose exponent (slope) is 0.42, the departures from the line may represent the involvement of different populations of nerve fibers. [Data from figure 10 of Teas *et al.* (*14*)]

If good fortune should favor us and we should find a point in the auditory system where the neural potentials keep pace with the loudness function, the happy prospect of an objective measure of the loudness exponent would appear to be opened. We could then presumably bypass the cross-modality matching procedures, with their attendant variability, in favor of a signal read directly by a meter. Unfortunately, except perhaps for such robust phenomena as the voltages provided by the cochlear microphonic, the variability seen by electrodes is seldom smaller, and sometimes greater, than the variability of cross-modality matches. Thus, for example, the exponents derived electrically from Boudreau's 25 cats ranged from about 0.3 to 1.0, with a mean of 0.68 and a standard deviation of 0.16. A study (*13*) of 11 human subjects who matched numbers to loudness gave a mean exponent of 0.73, a range of 0.4 to 1.0, and a standard deviation of 0.19. Although the two sets of results for cat and man show great similarity, the sources of the variabilities probably have little in common.

Many factors combine to create noise and variability in neurelectric responses. The sources and sinks of the electric currents depend on the vagaries of an intricate anatomy, and the resulting electrical geometry presents a tangle of complexity. Working with guinea pigs, Davis and his colleagues (*14*) have attacked the problem with a delicate procedure by which they place a pair of electrodes inside the cochlea itself, astraddle the basilar membrane on which reside the receptor hair cells. Among the several potentials picked up by the electrodes, one can identify the action potentials of the auditory nerve, which show up as a diphasic wave. In response to very brief bursts of tone the amplitude of the action potential grows roughly as a power function of the stimulus over a range that may reach 90 to 100 decibels. The irregularities in the growth of the action potentials seem to be due to the successive recruitment of at least three different populations of neurons. The irregular power functions described by the growth of the nerve response have exhibited exponents ranging from about 0.2 to 0.5. An example (*14*) is shown in Fig. 3. Seen by electrodes in the cochlea, then, the growth of the summated nerve impulses proceeds at a slower pace, with a lower exponent, than the growth of loudness in the human ear.

Cortical Potentials

If electrodes in the cochlea can be said to sample the front end in the hearing process, electrodes on the scalp presumably sample the back end. Electrodes on the human scalp normally pick up an assortment of brain waves, so-called, which tend to obscure the potentials evoked by a stimulus to a sense organ. But computer techniques have made it possible to average the cortical waves and thereby suppress or cancel their irregularities, preserving only the features that repeat in a stable fashion. With the noise thus suppressed, the potential evoked by a repeated click delivered by an earphone becomes distinct and measurable. The development of averaging led promptly to the remarkable demonstration that the evoked potential at the scalp of a normal conscious subject could be detected when the click stimulus was only a few decibels above the psychophysical threshold (*15*).

When the amplitude of the click was increased, the cortical potential became larger, sometimes conforming to a power law. But there were large individual differences among subjects, as we might well expect. For the evoked potential recorded at the scalp must represent a summation of neurelectric potentials that may have widely separated origins, so that it becomes far from obvious what aspect, if any, of the cortical potential should correlate with perceived magnitude.

In an effort to discover an aspect of the cortical potential that might grow as a power function, Keidel and Spreng (*16*) measured the amplitude of one of the slow components of the cortical wave, a part of the wave delayed by 130 to 170 milliseconds. Three kinds of stimuli—tone, electric current, and vibration—all produced power functions. All three exponents were smaller than the corresponding psychophysical values, but it is interesting to note that the relative values of the three exponents were approximately the same as those obtained in psychophysical experiments. A further study of tactual vibration produced families of power functions relating averaged potentials to stimulus amplitude (*17*). Five different frequencies of vibration were tested and the exponent was found to be smallest at 200 hertz (0.52) and largest at 50 hertz (0.62). In that respect, the relation to frequency was not unlike the relation found in psychophysical experiments (*18*), but the absolute values of the exponents for the cortical potentials were smaller than those obtained when a subject places his finger on a vibrating button.

Like other evoked potentials, the cortical response to a flash of light is a complex wave that changes form and amplitude when the light intensity is altered. When the potential was measured at an appropriate latency (190 to 300 milliseconds), the response was found to grow as a power function of light intensity, with the exponent 0.21 (*19*). The power function was shown to hold over a wide stimulus range, 48 decibels, which is a range of about 65,000 to 1. Approximately the same exponent was obtained with red, blue, green, and white light. Here again, the exponent for the visual evoked potential was smaller than the psychophysical value, but it was consistent in *relative* size with the exponents determined by cortical potentials for sound, vibration, and electric shock obtained by Keidel and his collaborators.

It appears, then, that there are at least four sense modalities in which some particular aspect of the human cortical potential has been shown to follow a power function, and in which the four exponents exhibit the same relative values as those obtained in psychophysical experiments.

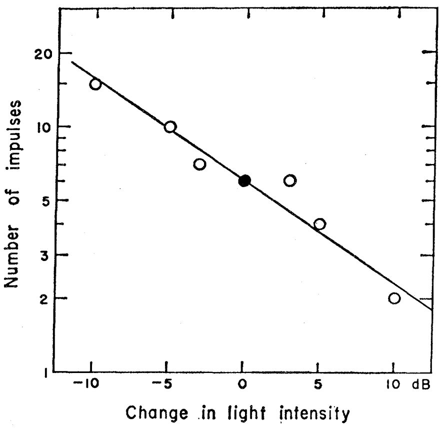

Fig. 4. A single cell in the lateral geniculate nucleus may respond by decreasing its firing rate when the intensity of a light stimulus is increased, and vice versa. The filled circle represents the steady response rate at the level to which the eye was adapted. Over a range of 20 decibels (100 to 1) the response of this cell approximated a power function with an exponent of −0.4. [Data from De Valois *et al.* (*22*)]

Numerous experiments have been carried out by Davis and his collaborators to determine the nature and properties of the vertex or V potential—an evoked potential that seems to be generated rather diffusely in the cerebral cortex and is best recorded by an active electrode on the top of the head, with a reference electrode placed near the ear. When the stimuli consist of repeated bursts of tones, the V potential grows slowly with sound pressure. Power functions fitted to the data for five subjects gave exponents that ranged from 0.10 to 0.18 (*20*). When power functions have low exponents, they can be distinguished from logarithmic functions only if the variability is small. As the exponent decreases, the power function comes more and more to resemble a logarithmic function.

The failure of the cortical V potentials to exhibit growth functions having the same exponents that govern perceived sensory magnitude does not, of course, rule out other interesting comparisons. We may ask, for example, whether stimuli that appear subjectively equal produce similar V potentials. Despite a considerable variability, it appears that when sounds of different spectra were equated for loudness they gave rise to approximately equal voltages at the cortex.

The same question can be extended to cross-modality comparisons. If stimuli in different modalities have been equated for apparent magnitude, do they produce similar cortical potentials? A preliminary answer was given by Davis, Bowers, and Hirsh (*20*), who said, "In a set of cross-modality comparisons of V potentials evoked by sounds, flashes of light, vibration, or electric shock . . . we found that stimuli that were adjusted to equal subjective magnitude evoked similar V potentials."

Neural Responses to Light

Electrical recording directly from nerves and cells can be most easily accomplished with animals, but the implantation of electrodes for the stimulation and recording of neural activity in the human brain is a developing art. An example of the possibilities for sensory investigations with implanted electrodes was given by Pinneo and Heath (*21*), who recorded from stainless steel electrodes located near the left optic tract. The patient made judgments of the apparent brightness of a flickering field. The judgments reflected the well-known brightness enhancement that oc-

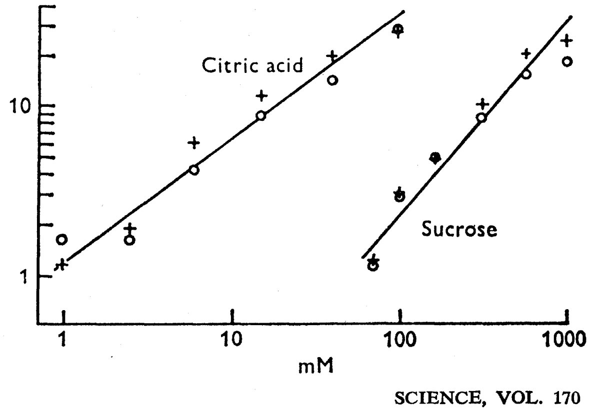

Fig. 5. Mean values of neural response (open circles) and of subjective response (crosses) from two patients, plotted against molarity of citric acid and sucrose solution, in log-log coordinates. [From Borg *et al.* (*30*)]

curs when the frequency of the flicker lies in the vicinity of 10 per second.

Corresponding to the brightness enhancement there was a change in the average amount of electrical activity measured by means of a recording voltmeter. As the frequency of the flicker changed from 1.5 to 50 flashes per second, the recorded voltage passed through a maximum corresponding approximately to a frequency of 10 flashes per second. Above about 35 flashes per second, the voltage was comparable to that produced by a steady light of the same average intensity—a direct neural verification of the basic principle known as the Talbot-Plateau law.

When we look for power functions among the neural potentials in the visual system, we encounter numerous curiosities. The single cell of the lateral geniculate of the monkey may respond to steady light with a steady rate of discharge. But, depending on the type of cell involved, an increment in the light intensity may cause either an increase or a decrease in the firing rate. A typical cell of the kind that slows its firing when the light increases was found to produce neural impulses in the manner shown in Fig. 4. There we see a kind of upside-down effect. A decrease in the light level produces more impulses per unit time; an increase produces fewer. The rate of discharge can be described quite well by a power function with an exponent of about −0.4 (*22*).

Neurelectric functions measured over relatively short ranges are afflicted with much variability and consequent uncertainty. Whether a logarithmic or a power function provides the best description is often moot. In a study by Creutzfeldt *et al.* (*23*), both types of function were fitted to data relating light intensity to neuronal discharge in the optic tract and in the lateral geniculate body. The combined effects of a low exponent and a large variability meant that the power function was not notably superior to the logarithmic function. Nevertheless, the question still remains: How does the visual system manage to mediate a sensation of brightness that grows as the cube root of the stimulus intensity?

A novel approach to the problem of the operating characteristic of the visual system was devised by Easter (*24*) who recorded the neurelectric spikes produced by single ganglion cells in the goldfish retina in response to brief flashes of red light carefully localized on either one or two retinal areas. The problem was to compare the responses to single-spot and double-spot stimuli. Question: What intensity, falling on a single spot, is needed to produce a response as large as that produced by a given intensity falling on two spots? The two small spots, it should be said, were equally sensitive points within the same receptor field, in fact, within the same "critical area" as would be defined by Ricco's law. If it is assumed that the stimulation of two equally excited spots in the same receptor field produces twice the value of excitation E, then it becomes possible to determine how E varies with light intensity. Easter showed that the excitation function, thus defined, is a power function of intensity with an exponent of about 0.5. It is interesting to note that when the value of the exponent for a point source, or a brief flash, is determined in psychophysical experiments, the exponents are also about 0.5 (*25*).

The temptation is great to conclude from the coincidence of exponents that a powerful method for the analysis of the operating characteristic of the visual transducer has at last been formulated by Easter's splendid experiments, and that the site of the psychophysical power law has been pushed into the retina. Caution must prevail, however, for the variety and richness of current physiological findings speak with many voices and they do no more, at the present stage of knowledge, than signal directions for future excursions.

Visual Reaction Time

How long it takes for the visual system to process an optical input has fascinated investigators for almost a century. As the light intensity increases, so does the speed of the visual reaction. A classic study by Liang and Piéron (*26*) made use of the Pulfrich effect to measure how light intensity affects the delay in the visual response, and more recently Mansfield (*27*) explored the same problem by means of a conventional reaction-time procedure—how quickly can the subject move his finger when the light comes on? The speed of the visual reaction can also be measured by electrical recording from various points in the visual system, including, of course, the back of the head (*28*). There appears to be a remarkably close agreement between the electrical and the behavioral measures. Except for a small and irreducible latent period, the speed of the visual reaction increases as a power function of intensity with an exponent equal to about ⅓. Since that value coincides with the exponent that governs the growth of subjective brightness with intensity, it appears that the velocity of the visual reaction, measured either behaviorally or neurelectrically, is directly proportional to subjective brightness.

Where does the variable time delay take place? In the retina, it seems. Electrical recordings from the more peripheral parts of the visual systems of various animals have exhibited approximately the same exponents. The cube-root law is the approximate rule at the periphery, at the cortical level, and in the behavioral response (*29*).

The Taste Nerve

The sense of taste has provided a unique testing ground for the hypothesis that subjective magnitude is mediated by the total activity in a nerve. By a quirk of anatomy, the gustatory nerve from the anterior part of the tongue passes through the cavity of the middle ear. During certain types of middle-ear surgery, this taste nerve, the chorda tympani, may be exposed in a way that permits a direct electrical recording of the neural responses to substances applied to the tongue. The summated neural responses may then be compared with the quantitative estimates of taste intensity made by the same patients for the same substances. A series of such experiments was performed with the taste substances sucrose, sodium chloride, and citric acid. Both the subjective estimates and the neural responses could be described by power functions. Borg *et al.* summed up their work by saying, "Quite aside from the question whether the function describing the relation between the strength of a sapid solution and the summated electrical response satisfies a Stevens power function or a Fechnerian log function, it is apparent that there is a fundamental congruity between neural activity and perceptual intensity" (*30*). Averaged data from two patients for citric acid and sucrose are shown in Fig. 5. A demonstration as direct and dramatic as that shown in Fig. 5 may or may not prove reproducible. In other sense modalities, anatomy has not favored us with sensory nerves that are so easily accessible to electrodes.

Nevertheless, several additional sensory systems have been shown to respond with power-law outputs (*31*). In the somatic and cutaneous systems especially, it has been shown by Mountcastle and his co-workers (*32*) that stimulus and response can be usefully related by power functions. Of course, the occurrence of such power functions may or may not relate to psychophysical functions. That question stands wide open. What the neurelectric power functions demonstrate is a capability: sensory systems are capable of power-function transformations. The precise role of the recorded transformations remains to be determined.

Central Processing

At the Ciba Symposium in 1966 (*33*) there was a general discussion on the topic, "Linearity of transmission along the perceptual pathway." In that discussion, and elsewhere at the symposium, Sir John Eccles turned forceful attention to the question of whether the sense organ could account adequately for the nonlinearity in the coupling between stimulus and sensation, leaving the central nervous system with the task of performing only linear transformations. He observed that "there is no great impediment to the idea that . . . the transfer functions across the synaptic mechanism are approximately linear." To which Professor Mountcastle added, "The interesting point for me here is the great importance that we must now place upon the transducer process itself, at the periphery."

Therein lies a pivotal concern. Is it at the interface between man and world, at the peripheral sense organ, that the operating characteristic of the system imposes its transformation? In particular, can it be the receptor process that bends the sensory function by a ratio-preserving compression, and thereby permits the eye and the ear to couple the organism to dynamic ranges of stimuli that may exceed billions to one? Is it then to transducer physiology, Delbrück's "totally undeveloped but absolutely central science," that we must look for an understanding of the ratio invariance that underlies the psychophysical power law? The presence of power functions in neural events would seem to affirm that possibility.

Epilogue

Whenever a natural law achieves acceptance, the spread of our expectations regarding the outcome of experiments becomes channeled within new constraints. Over the span of the past dozen years the constraining force of natural law has so asserted itself that a topic of inquiry has been turned through an angle of 180 degrees. Until psychophysics could lay down a principle to guide our expectations, any empirical function describing the growth of sensation intensity could have appeared acceptable, and the burden of establishing the power function rested on the experimenter. The burden of proof appears now to have shifted, so that henceforth it becomes the exception to the power law that calls for solid demonstration. A proven exception to the principle that equal stimulus ratios produce equal sensation ratios would have startled no one a few years back. But now an exception to ratio invariance would qualify as an anomaly, a breach of a rule, and as such it would become a prime target for inquiry. The leverage inherent in a natural law may help to pry new insights from evident exceptions.

The same compelling constraints of ratio invariance cannot yet be said to pilot our expectations through the turbulence of electrophysiology. To be sure, the power function has been found to govern the growth of neurelectric effects in numerous experiments, but few investigators would feel astonished if their electrodes recorded a different function. The guiding constraints of a natural law may provide a firm rock to stand on as we reach for new discoveries, but the physiological footing will likely remain mushy until the neurelectric power function can either prove itself the rule or give way to some sturdier principle. For what stands to be won here is a grasp of the mechanisms that generate the input-output characteristics by which the sensory systems preserve the ratio invariance that is manifest in psychophysical functions.

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