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A Neural Quantum in Sensory Discrimination

An all-or-none step function shows itself in visual and auditory experiments.

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Soon after the physiologists had demonstrated that conduction in the sensory nerves takes place by all-or-none firings —a kind of impulse code—the question arose whether, under the proper circumstances, we can perceive an all-or-none increase or decrease in sensation. In other words, does a smooth increase in a stimulus produce finite jumps in perception? No such step functions had yet been reported in 1926 when Boring hypothesized what he called Sensory Quanta and speculated about their relation to the sensory continuum. "It should be perfectly feasible experimentally," he wrote, "to determine the presence or absence of critical points . . ." (*1*).

It was indeed feasible, as it turned out, but a critical point meant that there must be a difference threshold, a step function of some kind. Most experimenters thought they knew better, though, for as early as 1884 Peirce and Jastrow had formulated the case against critical-point steplike thresholds by showing that, when they tried to detect small changes in pressure on the skin, their judgments agreed with the predictions of the normal probability model. At no point did a discontinuity intrude itself. Concerning the steplike threshold, the authors concluded that "the retention of this false notion can only confuse thought" (*2*). Thereafter it became customary to emphasize that the difference limen, so-called, reduces to a statistical concept, usually defined as the size of the difference that can be correctly detected half the time.

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Most experiments devoted to the perception of small differences produce a scatter of judgments, a variegated or poikilitic ensemble, which can be plotted as percentage correct against the size of the stimulus difference. The result may be called a poikilitic function (often inappropriately termed a psychometric function). The form of the poikilitic function has often been invoked to answer the question, is there a sensory threshold? Under most procedures used to measure difference limens the answer appears to be no. Under the classical method of constant stimuli, for example, the number of correct responses grows greater as the stimulus increment grows larger. When the percentage correct is plotted as a poikilitic function, it typically swoops upward along an S-shaped curve that may resemble the ogive produced by a normal probability integral, the so-called phi function of gamma. The normal ogive, of course, shows no evidence of critical points or threshold steps.

In a currently popular procedure the increment to be detected is a brief signal added to an on-going random noise, and in that circumstance, as we might expect, the probability model proves superior to a threshold model. A frequent strategy in such studies is to apply to the human observer the statistical theory of signal detection—a mathematical theory that generates useful models for detection problems in radar and sonar (*3*). The human detector, it appears, does not achieve the performance predicted by the mathematical conception known as the "ideal observer." Nevertheless, other features of human reactions can be modeled by appropriate features of the mathematical apparatus of detection theory (*4*). The formal theory of signal detection usually does not assume the existence of a stepwise threshold. In any case, the experimenter who deliberately immerses the signal in a noise insures against the discovery of a step function, even where there is one.

It is not surprising, therefore, that the denial of sensory thresholds voiced in the 19th century finds itself echoed anew in the 20th century, this time by those who ask observers to dig signals out of a random noise. Yet in other kinds of experiments the feasibility that Boring envisaged in 1926 has proved sufficiently real to cause critical threshold points to emerge, sometimes in experiments that were designed with other purposes in view.

Békésy's Neural Model of Fechner's Law

The conception that motivates a given experiment sometimes commands less interest than the experimental outcome. Thus, it matters little to us now, that Békésy, who later won a Nobel Prize, was attempting in 1930 to demonstrate the basis of Fechner's logarithmic law of sensory intensity (*5*). Fechner made two assumptions: (i) the difference that is just noticeable is a constant proportion of the stimulus, and (ii) each just noticeable increase produces a constant increment in sensation.

Békésy translated those two ideas into neural terms and proposed that the strength of a sensation such as loudness depends on the number of cells excited. "Each time an additional cell is stimulated," he wrote, "there is an increase in loudness, and thereby the difference threshold stands explained. Since the cells are very much alike," he continued, "it seems anatomically plausible that the excitation of each new cell entails the same sensation increase, regardless of how many cells are already active. In this neural conception, then, both of the Fechnerian laws [the two assumptions] are contained" (*5*, p. 331).

Fechner's logarithmic law proved ill founded, as it turned out. Experiments that I began in 1953 have shown that sensory intensity in each of the sense modalities grows not by a logarithmic law but by a power law (*6*). Nevertheless, until a sufficient array of experimental evidence for the power law could displace the earlier notion, the logarithmic law prevailed for almost a century. The fact that the entire Fechnerian conception now needs revision is of less moment, however, than the experiment it led to.

Békésy reasoned approximately as follows. A given stimulus excites a particular number of cells, 50, say, but there is often a small stimulus excess left over. Not enough excess, however, to excite the 51st cell. If at that point we add a stimulus increment, it will combine with the excess and may possibly excite the 51st cell. How large must the increment be in order to excite an additional cell? That depends, of course, on how much surplus stimulus is left over. So the question becomes simply, how does the excess residue distribute itself from moment to moment? If, as seems probable, one amount of excess residue is as likely as any other, then as we sample the process over and over, the required increment will vary linearly between zero and the size of the difference threshold.

Békésy tried to test the foregoing conception by the method of constant stimuli: A standard tone (300 hertz at 40 decibels above threshold) was presented first and was followed 2 seconds later by a comparison tone that was made stronger or weaker than the standard. Békésy plotted the percentage judged different against the size of the difference and obtained an S-shaped function, not the linear function he expected. Perhaps, Békésy reasoned, the time interval between the standard and the comparison tone opened the gates to other sources of variability. He therefore arranged for the comparison tone to follow immediately after the standard, with no intervening time interval. A tuned filter removed the switching transients.

After much practice, some observers achieved the predicted straight-line poikilitic function. In most instances, however, the straight line did not pass through the origin but resembled the examples shown in Fig. 1F. How Békésy's results speak for a threshold step function I shall try to explain later.

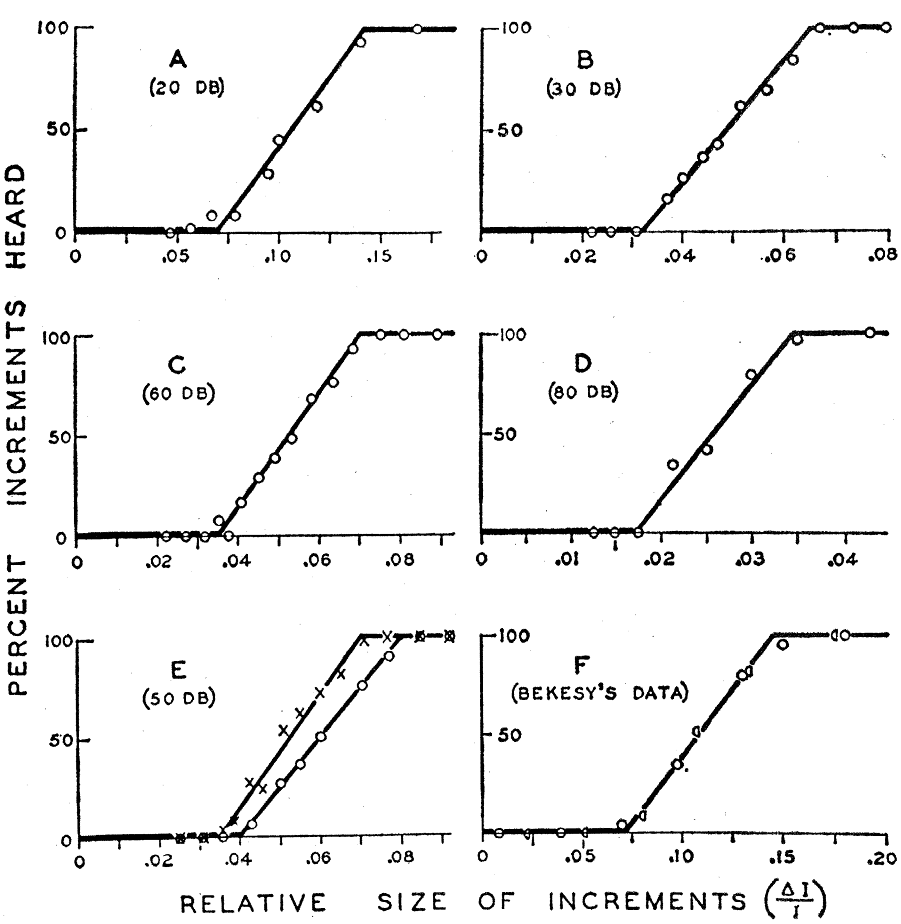


Fig. 1. Poikilitic functions showing the percentage of increments heard as a function of the intensity of the increment added to a steady 1000-hertz tone. The size of the NQ is measured by the point on the abscissa where the function first departs from zero. The function reaches 100 percent at the value corresponding to two NQ. The level of the steady tone is indicated on each plot. Békésy obtained the data in plot F by a different procedure. The circles are for positive and the half circles for negative increments. [From Stevens and Volkmann (*7*)]

Pulsed Increments Added to a Steady Tone

My own concern with what is called the neural quantum, the NQ, began by accident—a bit of serendipity. During a summer project in 1940, John Volkmann and I decided to try to duplicate a newly published Russian experiment in which Lifshitz had claimed to track the ups and downs of a person's absolute threshold. The observer was given a brief series of tone pulses close to his threshold and he was supposed to say how many pulses he heard. Our sound room, it turned out, was too noisy, and in desperation we introduced a steady 1000-hertz tone in order to mask the irregular background noises. We then added brief incremental pulses to the steady tone, one pulse every 3 seconds, and the observer pressed a key each time he heard a pulse as a momentary increase in loudness. Volkmann listened first, and I adjusted the size of the pulses until he was hearing some but not all of the increments.

After several hundred judgments, involving blocks of increments of various sizes, I plotted the number of increments heard against the size of the increment. The plot was a remarkably straight line—a line that only a step function could produce. It struck us that with our new procedure we were in fact measuring the NQ.

Some of the first poikilitic functions we obtained are shown in Fig. 1. Those functions show three features of special importance. (i) Increments below a critical size produce no response. (ii) Above that critical size, the number of increments heard increases linearly with the size of the increment. (iii) All the increments are heard when the increment reaches a second critical size, which is twice the size of the largest increment that is never heard.

Granted that functions exhibiting those three features have been obtained, and by two rather different procedures (Békésy's method of constant stimuli and our new method of pulsed increments added to a steady background stimulus), what kind of model do the three features suggest? One possibility assumes that somewhere in the neural centers of the sensory system there are functional gates or neural units, and that each unit operates in all-or-none, quantal fashion once its threshold is crossed. (The functional gating mechanism of the neural quantum is probably more centrally located than the afferent nerve cell that Békésy seemed to identify with Fechner's just noticeable difference.)

The NQ Model

How the NQ model may work is as follows.

A stimulus of a given magnitude excites, at a particular instant, a certain number of NQ units, and it does so with a little to spare, as illustrated by the schema in Fig. 2A. The small stimulus surplus p is insufficient to cross the threshold of the unit next in line, but is available to be combined with the stimulus increment $\Delta\phi$. When the increment $\Delta\phi$ comes along, it and the surplus p add together, and if their sum is large enough they excite one or more additional NQ. Now there enters a new factor: the overall fluctuation in the sensitivity of the organism, a fluctuation that is large relative to the size of the NQ and slow relative to the time taken for a stimulus increment to be added and removed. The overall fluctuation in sensitivity causes one value for the surplus p to be as likely as any other. Hence if we measure the size of the NQ in terms of the stimulus increment Q that will just succeed in always exciting it, the value of $\Delta\phi$ that is just sufficient to complement p and thereby excite one additional NQ is given by

$$\Delta\phi = Q - p \qquad (1)$$

A given $\Delta\phi$ will excite an additional NQ whenever $\Delta\phi \geqq Q - p$. Since p is distributed nearly uniformly over the interval $0 \leqq p \leqq Q$, the additional NQ is excited a proportion of the time r_1 given by

$$r_1 = \Delta\phi/Q \qquad (2)$$

Under the procedure of pulsed increments that led to the results in Fig. 1, the observer is not able to report when only a single additional NQ is excited. The reason is presumably because the overall fluctuation in his own sensitivity causes an apparent fluctuation in the "steady" tone. Such a process would produce randomly occurring increments and decrements, each equal in size to a single NQ. Against that fluctuating, steplike background, the observer adopts

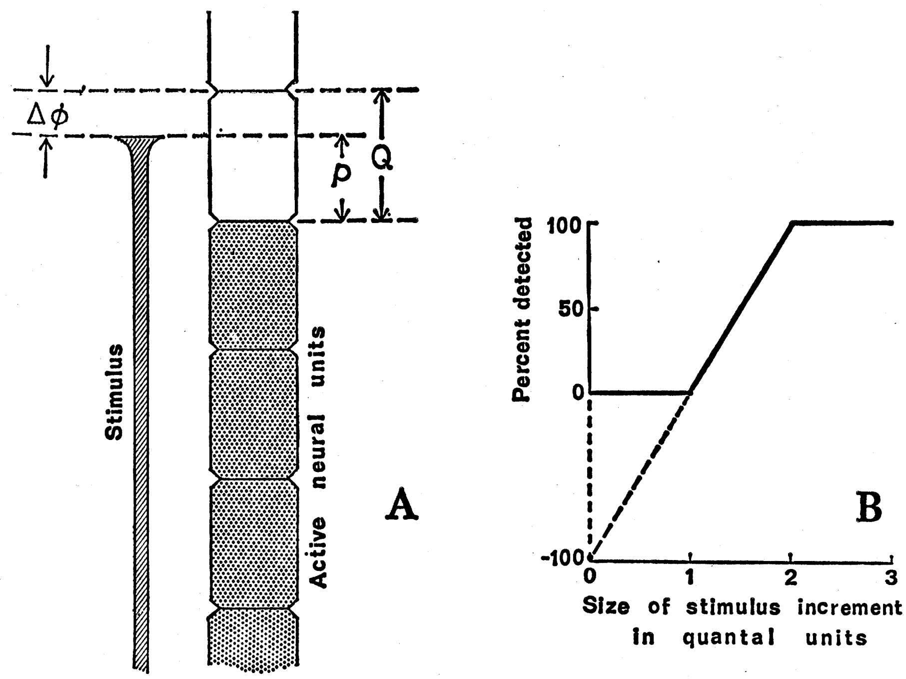


Fig. 2. (A) The neural quantum schema. The stimulus on the left is strong enough to activate several neural units, but it leaves a leftover surplus p, which remains insufficient to activate the next unit until an increment $\Delta\phi$ is added. Q represents the size of the neural quantum measured in terms of the stimulus. When the addition of two neural quanta is needed to produce a response, the requisite stimulus increment becomes $\Delta\phi + Q$. [After Békésy (5)] (B) Form of the poikilitic function predicted when the observer adopts a 2-quantum criterion. Stimulus increments produce no response (zero detections) unless the size of the increment exceeds one neural quantum. With further increase in the size of the increment the percentage detected grows linearly and reaches 100 percent at the point where the increment equals 2 quanta. The downward projection of the line passes through a point that corresponds to the ordinate value −100 percent.

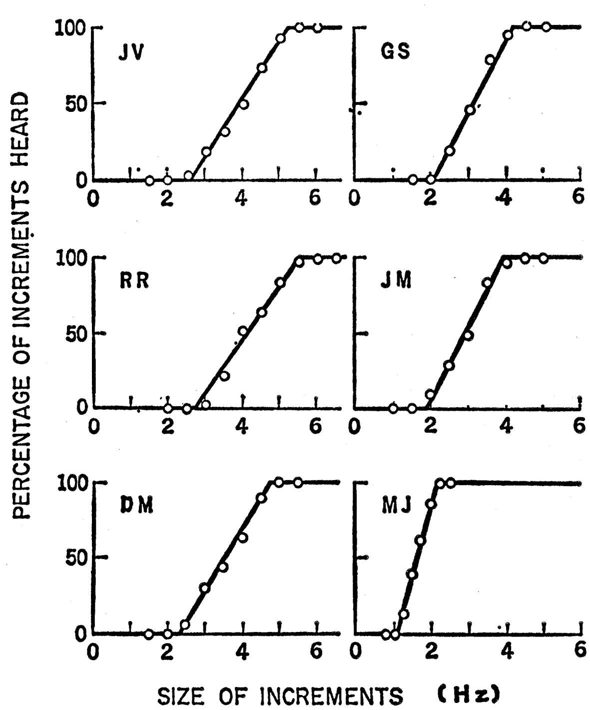


Fig. 3. Poikilitic functions relating percentage of pitch increments heard to the size of the increment in frequency for six different observers. To a steady, continuous reference stimulus (1000 hertz) an increment lasting 0.3 second was added every 3 seconds. Each point is the average of 100 judgments. The lines were drawn to fit the points and at the same time to satisfy the slope requirement that the intercepts at 100 and 0 percent should stand in the ratio of 2 to 1. The size of the NQ, measured in stimulus terms, differs almost threefold between observers RR and MJ. [From Stevens, Morgan, and Volkmann (8)]

for his report the criterion of a double quantal jump. Since the single quantal jump is indistinguishable from the background, the observer ignores it.

If two added NQ are required to produce a response, Eq. 2 becomes

$$r_2 = \left(\frac{\Delta\phi - Q}{Q}\right) = \frac{\Delta\phi}{Q} - 1 \qquad (3)$$

Or, in terms of the percentage R of increments that an observer should be able to detect, we have

$$R = 100\left(\frac{\Delta\phi}{Q} - 1\right) \qquad (4)$$

Equation 4 gives a good account of the data in Fig. 1. A graphical representation of Eq. 4 is also shown in Fig. 2B. The predicted line projects to a point at −100 percent, as shown by the dashed lines in Fig. 2B. That projection point provides a useful aid when NQ functions are fitted to data by eye.

The many NQ functions presented in this article were all fitted by eye.

Why so many examples? Two reasons. (i) The nature of the problem entails a sampling procedure. The objective is to sample extensively enough to reveal the form of an underlying distribution. Specifically, is the distribution rectangular? Sampling is a noisy process, however, and no given set of samples that we use to determine a poikilitic function corresponds precisely to any other set of samples. (ii) The many doubts and dissents that have been expressed over the past decades call for a generous sampling of the accumulated evidence. More examples of NQ functions could have been presented, but the present sample of about 140 functions is varied enough, I hope, to answer many of the questions that have heretofore been raised.

Neural Quantum for Pitch

If increments in intensity can be gated by a neural quantum, what about increments in frequency? Can we demonstrate a quantal step for pitch? With the apparatus rearranged to produce frequency increments we soon obtained functions that were almost indistinguishable in form from those obtained with intensity increments. Results for six different observers are shown in Fig. 3.

Volkmann, in the meantime, had returned to his teaching at Columbia, and C. T. Morgan dropped in one day. As I recall it, the functions I showed him elicited total skepticism.

"Let me listen to those tones," he said. He settled himself in the observer's chair, and after he had judged about a thousand increments, I told him he could come out of the sound room.

"I'll bet those judgments don't lie on a straight line," he said.

But the line looked quite straight, and Morgan said, "You go in there and let me run the apparatus."

So I showed him how to operate the response counters and how to set the controls to produce any desired frequency increment. An hour or so later, I emerged from the sound room feeling the same doubts that Morgan had expressed. But Morgan had transferred the numbers from the counters to points on a graph and he was scratching his head. The points fell approximately where they were supposed to.

Sets of NQ functions for Morgan and me are shown in Fig. 4. The parameter is the level of the 1000-hertz tone above threshold, and it can be seen that the size of the NQ for pitch increases when the sound pressure decreases. At a given level, Morgan's NQ is smaller than mine, and the difference between us remains remarkably constant over a wide range of sound levels. Those results suggest that the measure we have called the NQ can pinpoint in a stable fashion a basic feature of the sensory system.

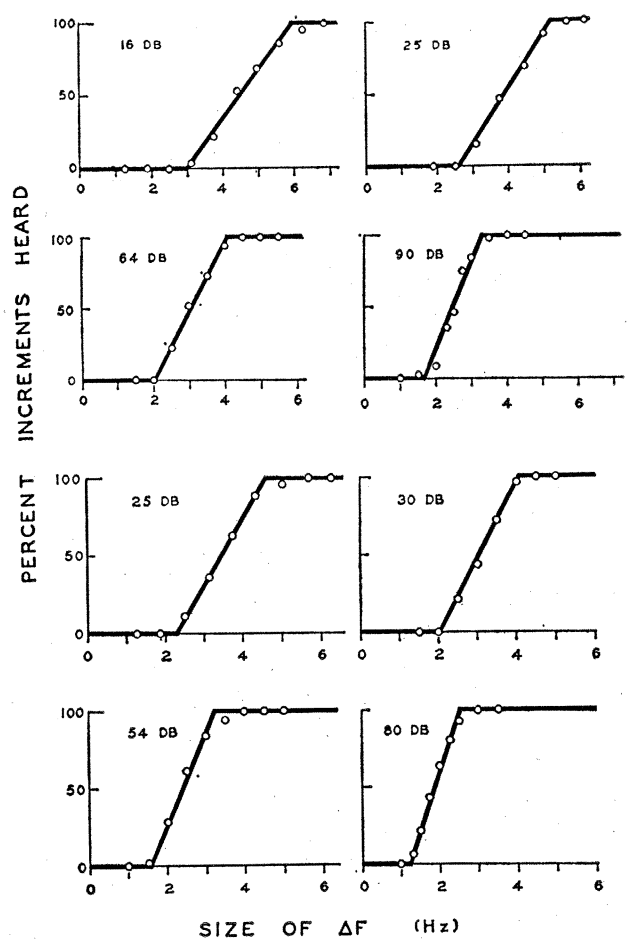


Fig. 4. The effect of stimulus level on the measured size of the NQ for pitch. The upper four curves are for observer SSS, the lower four curves for observer CTM. [After Stevens *et al.* (8)]

Statistical Test

We next tried to analyze the problem in a way that I now believe was inappropriate. Morgan undertook a series of calculations that seemed to show that the straight line provides a better fit to the data than does the normal ogive, the so-called phi function of gamma. Why was that curve-fitting comparison not appropriate? Mainly, I think, because the two alternatives differ in their degrees of freedom. The classical phi-gamma theory assumes that the observer's judgment is conditional on an assortment of random errors, but the theory does not say how the standard deviation (S.D.) of the error distribution is related to the mean. The mean and the S.D. may therefore vary independently. Translated into the language of the normal ogive, the classical theory specifies no explicit relation between the slope of the ogive and the location of the midpoint.

The two degrees of freedom enjoyed

by the normal ogive reduce to one degree of freedom under the NQ theory. When the observer uses a 2-quantum criterion, the slope of the poikilitic function is a definite function of the midpoint. The two parameters are not free to vary independently. It seems inappropriate, therefore, to try to decide, by means of curve fitting, the relative merits of two conceptions, the one loosely specified and the other tightly specified. By specifying the relation between S.D. and mean, the NQ theory predicts more and thereby acquires greater power than the phi-gamma theory.

Figure 5 presents an interesting comparison on two experiments. For the circles a brief increment in frequency was added to a steady standard tone. For the triangles a short interval (0.5 second) elapsed between the standard tone and the comparison tone. Otherwise the procedures were as similar as possible, and the same observer served in both experiments. The time interval between the standard tone and comparison tone seems to have obliterated all trace of the NQ step function. Instead, the resulting data (triangles) are fairly well described by a normal ogive with a rather flat slope.

Because there is no restriction on its slope, the normal ogive (dotted curve) can also be made to describe the unfilled circles in Fig. 5, at least to a fair approximation. The NQ function, as shown by the straight line in Fig. 5, gives a poor fit to one point near the upper end, but an excellent fit elsewhere.

The restriction of the NQ function to one degree of freedom is illustrated graphically in Fig. 2B, where the dashed lines converge to a point whose ordinate value is at −100 percent. In fitting the NQ function to the data, the slope must be such that it projects to the point at −100 percent. Consequently, the only degree of freedom enjoyed by the NQ function lies in the angle between the dashed lines in Fig. 2B.

A statistical test that pits the one-parameter straight line against the two-parameter normal ogive is unfair in another sense. The straight line is a kind of asymptotic or limiting case, and those factors that operate to degrade the performance of an observer tend generally to move the data points in the direction of the normal ogive. The experimental errors are subject to asymmetrical constraints, because the observer cannot perceive more than 100 percent or less than 0 percent. Therefore, false responses and lapses of attention serve to round the corners of the poikilitic function in such a way that the fit of the normal ogive becomes better. As a general rule, the goodness of fit of the normal ogive may provide a rough index to the amount of noise or variability that encumbers the experiment.

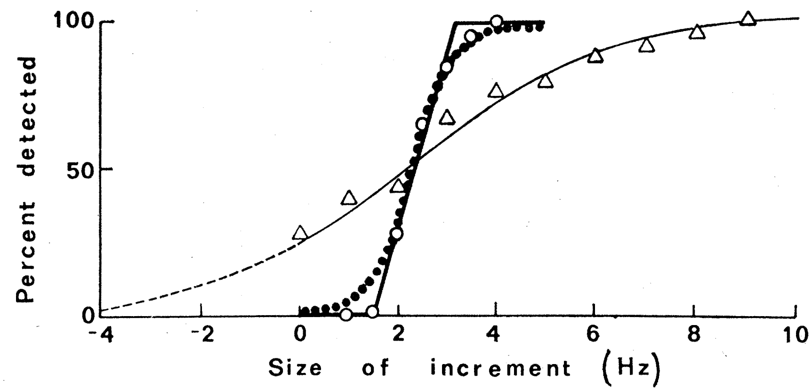


Fig. 5. The effect of a time interval between the standard stimulus and the comparison stimulus. For the circles the transition from the standard frequency to the higher frequency was nearly instantaneous. For the triangles the standard tone was followed 0.5 second later by a comparison tone at a higher frequency, and the observer responded each time the second tone sounded higher in pitch.

Sources of Noise

It is inherent in the concept of error that we cannot fully anticipate its size or location. If we could we would cease to call it error. Nevertheless, experimental studies can often reveal some of the principal sources of noise or variability —the *scatter* to which the term poikilitic refers. Studies designed to measure the NQ have identified several major avenues through which the rectilinear quantal function can be distorted and made to resemble the normal ogive.

1) *Stimulus jitter.* Successful NQ experiments have usually employed definite, well-controlled stimuli. What happens when the standard and comparison stimuli are themselves subject to random fluctuation? That question was answered in an experiment by Miller (*9*). The stimulus was a white noise, a signal that exhibits ceaseless agitation from the point of view of a person listening to its loudness. With a jittering stimulus we should expect to find a smearing of the stepwise quantal function. The linearity of the poikilitic function should give way to a form more nearly like the normal ogive.

Figure 6 shows the pooled results for

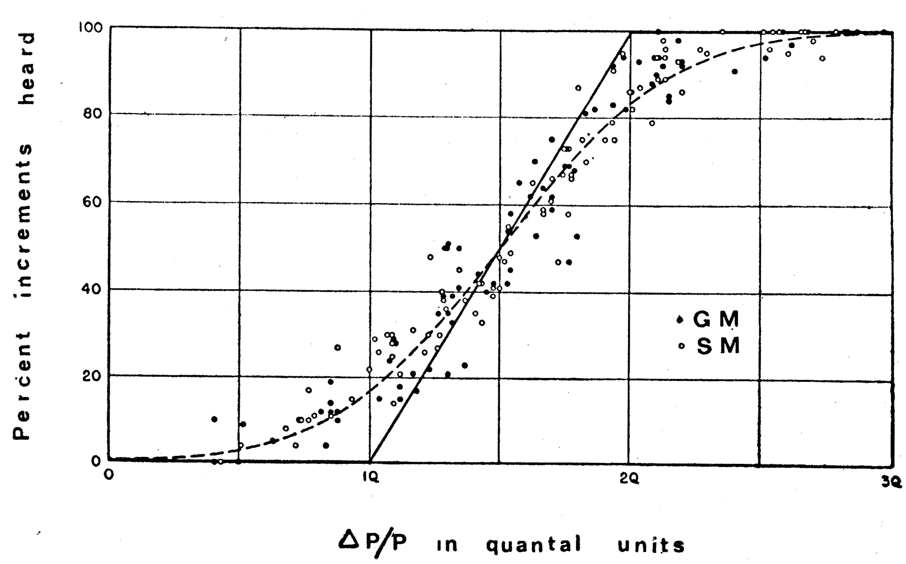


Fig. 6. The results of 32 experiments with white noise as the stimulus. The straight line through the 50 percent point shows the NQ function normally obtained with tonal stimuli. With white noise the results show a random scatter that is well represented by the dashed line—the ogive of the normal probability distribution. [From Miller (*9*)]

two observers who produced 32 poikilitic functions covering a range of stimulus levels from 3 to 100 decibels above threshold. Except for the use of a white noise, the procedure followed that used by Stevens and Volkmann, the method of pulsed increments (*7*). All 32 functions were made to pass through a common 50 percent point. It can be seen that the general trend of the data is better depicted by the dashed ogive than by the rectilinear quantal function.

Yet, despite the variability of the data, an important feature shows itself in the relation between the 50 percent point and the slope of the ogive. The S.D.'s of the probability distributions whose integrals best describe the data are approximately constant at a value equal to one-third the value of the mean. Thus the S.D.'s are about half the size of the NQ's indicated by the straight line in Fig. 6. Now, an invariant relation between the S.D. and the mean is a feature called for by the NQ theory, but not by the phi-gamma hypothesis, which limits itself to a prediction of the normal ogive. Consequently, despite any verdict that curve fitting may render, the results shown in Fig. 6 seem to speak in favor of the NQ hypothesis.

Stimulus noise can also be introduced into experiments in other configurations. For example, the background or standard stimulus may be a white noise, and bursts of tone may provide the increments to be judged. That was one of the procedures explored by Markowitz in experiments designed to study the time course of quantal effects (*10*). When the noise background was present, the observer's responses tended to be independent from moment to moment. With a tonal background, however, the responses tended to be correlated from moment to moment. Markowitz noted that such findings are "compatible with the assumptions governing neural quantal theory." The NQ theory postulates large but relatively slow fluctuations in the observer's overall sensitivity. A noise background introduces a rapid jitter which is sufficient to upset the normal tendency for the observer's responses to exhibit a fair degree of perseveration from trial to trial. The perseverative runs of positive or negative responses were also studied by Neisser who found them to be influenced by several factors (*11*).

2) *Observer's criterion.* Although in many experiments the observers have seemed to adopt a 2-quantum criterion, it may be possible, as Békésy showed with tones of brief duration and the method of constant stimuli, for the observer to respond to the activation of a single additional NQ. An observer may also, of course, shift his criterion from one number of quanta to another. If the criterion changes in the course of an experiment, the effect on the poikilitic function will tend to lower the overall slope and to introduce an S-shaped curvature.

There is no obvious way to tell whether the observer's criterion has shifted or whether some other perturbation has occurred. In an experiment with loudness increments presented in random order, Miller and Garner (*12*), serving as observers, seemed to shift their criterion in a way that gave rise to flat, S-shaped poikilitic functions which could be fitted fairly well by three straight-line segments, each segment spanning a neural quantum. The size of the NQ for each observer was also determined independently in an experiment in which blocks of 25 increments were presented before a change was made to a different size. Those results are shown in Fig. 7, A and B.

The fact that Miller and Garner obtained S-shaped functions when they used randomized increments led to the serious misconception that blocks of constant-size increments constitute a procedural necessity. Not so. Although randomized increments may have affected the responses of Miller and Garner in the way they suggested, increments in random sizes have been used in other experiments to determine recti-

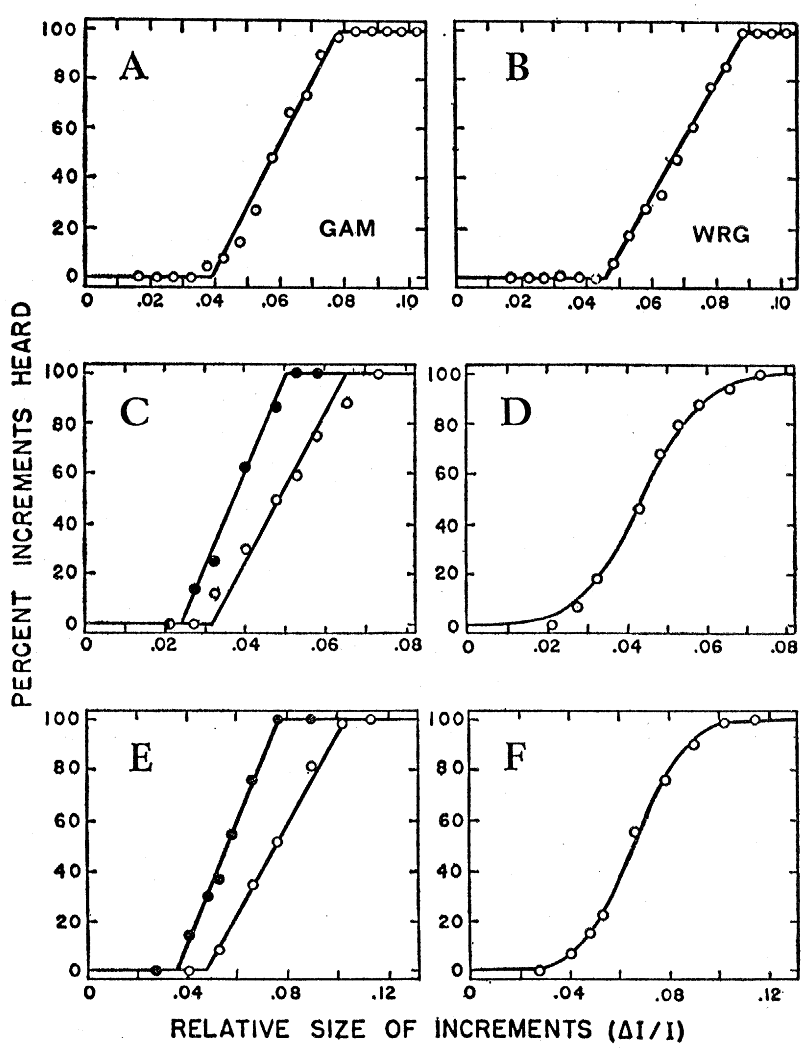


Fig. 7. Plots A and B show the NQ functions for Miller and Garner, determined with a 1000-hertz tone. Plot C shows two functions obtained from one observer, under identical conditions, but in two different experimental sessions. Plot D shows the result of combining the data from the two sessions. The two NQ functions in E represent two different increment durations, 200 milliseconds (filled circles) and 100 milliseconds (unfilled circles). The results of combining the data of the two experiments are shown in F. [Adapted from Miller and Garner (*12*)]

linear NQ functions. Békésy's experiment with loudness provides one example, and in three other laboratories randomized increments of brightness have produced quantal functions, as described below. The presentation of blocks of pulsed increments may facilitate the observer's judgmental task, but block presentation does not seem to be a necessity.

3) *Changes in the NQ.* For a given observer responding to increments under a given procedure, the measured size of the NQ may vary from one time to another. As noted by Stevens and Volkmann (*7*), it was startling to find a new poikilitic function, defining a smaller NQ, when the observer returned to the experiment after a coffee break (see Fig. 1E). If the data taken before and after the coffee break are pooled, the rectilinearity disappears and the result resembles the normal ogive. The NQ for a given observer usually shows remarkable stability, but it seems clear that internal factors may occasionally produce a dramatic change.

Another example of changes in the poikilitic function obtained under identical conditions, but in different experimental sessions, was published by Miller and Garner (*12*) and is shown by the filled and unfilled symbols in Fig. 7C. By combining the two sets of data in Fig. 7C, the authors obtained the S-shaped ogive shown in Fig. 7D.

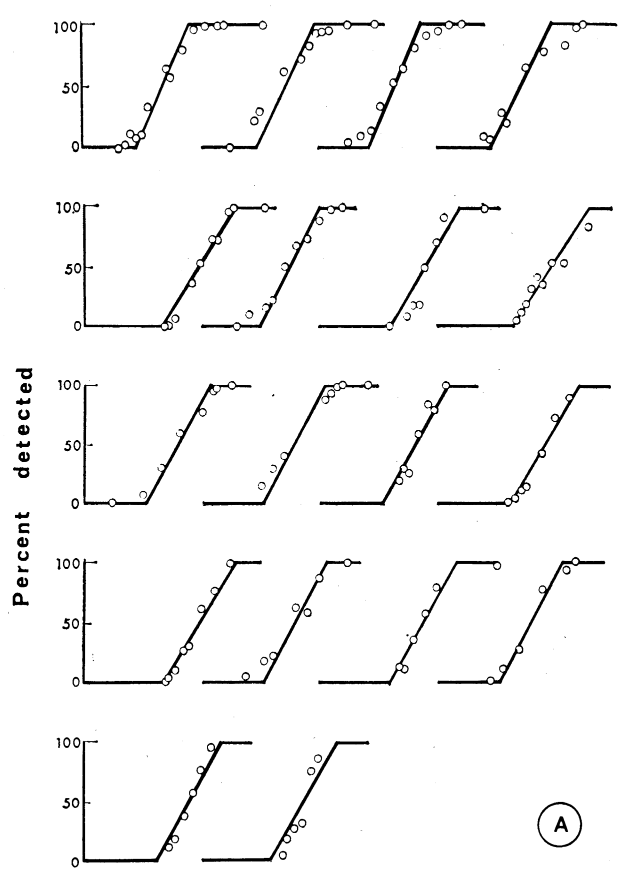
Other experimental parameters may also alter the measured size of the NQ. Among them are the stimulus level, the nature of the transition from the standard stimulus to the increment, and the duration of the increment. An example of the effect of increment duration is shown in the bottom row of Fig. 7. In Fig. 7E the longer increment (200 milliseconds) produced a smaller NQ than the shorter increment (100 milliseconds). Here again, the combining of the two sets of data produced the S-shaped curve of Fig. 7F.

4) *The observer.* Some observers can adopt a fixed 2-quantum criterion and hold to it throughout the tedious task of responding to a thousand or more increments. It is a demanding exercise in concentration, a performance that many observers find exhausting. Sustained, unwavering concentration does not lie within the repertoire of all observers.

Although a certain amount of practice is often required, some observers have produced fairly good quantal functions on the first try. In fact, several of our observers did so, a circumstance that misled me into thinking that, given the proper experimental arrangement, anyone could verify the NQ. The production of a good NQ function is not always easy. The four students employed as observers in Neisser's experiment (*11*) gave rather noisy results despite our best efforts with the apparatus. The results remained noisy even after the observers had had considerable training. Nevertheless, the intercept ratio of the best-fitting straight lines for those four observers hovered around the 2-to-1 value predicted by the NQ theory.

Since a high degree of involvement is needed to motivate the steady concentration required in the NQ experiment, it is perhaps not surprising that many of the nearest approaches to the ideal quantal function have been achieved in experiments where the authors themselves also served as observers. On the other hand, in our experiments on pitch we had no better observer than MJ, then a Radcliffe undergraduate and now a physician teaching in a medical school.

5) *Separated stimuli.* Most accounts



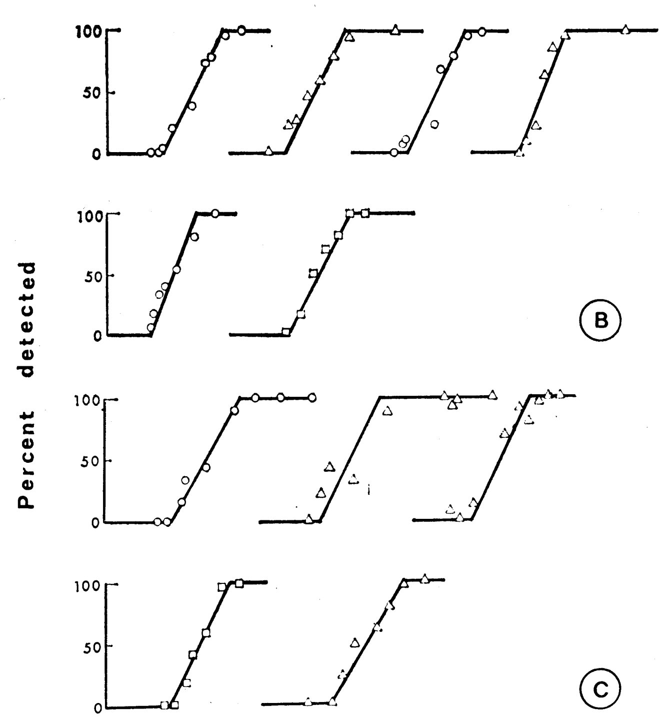


Fig. 8 (left). Eighteen poikilitic functions for subject A responding to brief changes in frequency of a 1000-hertz tone at 44 decibels above threshold. The number of observations for each point varied from 35 to 200. The lines through the points show the NQ prediction. In order to save space, in this and most of the following figures the functions are spaced arbitrarily along the abscissa. The main purpose is to show how well the data fit the NQ hypothesis. [Data from Flynn (*15*)] Fig. 9 (right). Six NQ functions for subject B and five for subject C. [Data from Flynn (*15*)] of the NQ theory make quite explicit the requirement that the transition from the standard to the comparison stimulus must be brief. The increment must be added (or subtracted) in such a way that the observer's overall sensitivity has little time in which to change to a new state. The ability of a time interval to obliterate the NQ was demonstrated by Békésy (*5*), and another example is shown in Fig. 5. Nevertheless, some investigators have based their opposition to the NQ theory on experiments employing a time interval between the standard and comparison stimuli.

In an experiment by Duncan and Sheppard (*13*) the observer lifted a standard weight (100 grams) and then a variable weight (ranging from 97 to 103 grams). He repeated the lifting until he was satisfied, and then said whether the variable was heavier or lighter than the standard. Like the many experiments on lifted weights performed during the past century, that experiment produced data that showed no evidence of a stepwise, quantal jump. Instead, the results were consistent with a continuous normal ogive.

If an experiment could be so contrived that the subject picked up a weight and then judged whether a momentary increment was added by some means or other—perhaps by a magnetic impulse—it might then prove possible to measure a quantal effect for lifted weight. But with a time interval between the standard and the variable stimulus, it remains unlikely that the NQ function will show itself.

"It is concluded," said Duncan and Sheppard, "that there is, at present, no evidence for the existence of a genuine sensory quantum." Concerning the array of rectilinear NQ functions obtained by other workers, they wrote that the result "stems entirely from the fact that he [Stevens] presents his test stimuli sequentially [in blocks] and not in random order." They apparently ignored the fact that Békésy presented stimuli in random order and yet obtained rectilinear poikilitic functions. As I shall show later, random stimulus order has also given good results in visual experiments.

6) *Absolute threshold.* Some investigators have tried to obtain evidence of the NQ at the absolute threshold and have expressed disappointment at the outcome. At or near the absolute threshold the NQ ought not to prove detectable unless a means can be invented to stabilize the overall fluctuation of the observer's sensitivity. Of course, if a complete stabilization of sensitivity should prove possible, then we should obtain a poikilitic function that ascends vertically with no values between 0 and 100 percent—a true all-or-nothing step function. In the absence of such stabilization, what we find is a relatively slow but irregular fluctuation in the observer's overall sensitivity, and the absolute threshold wanders irregularly up and down.

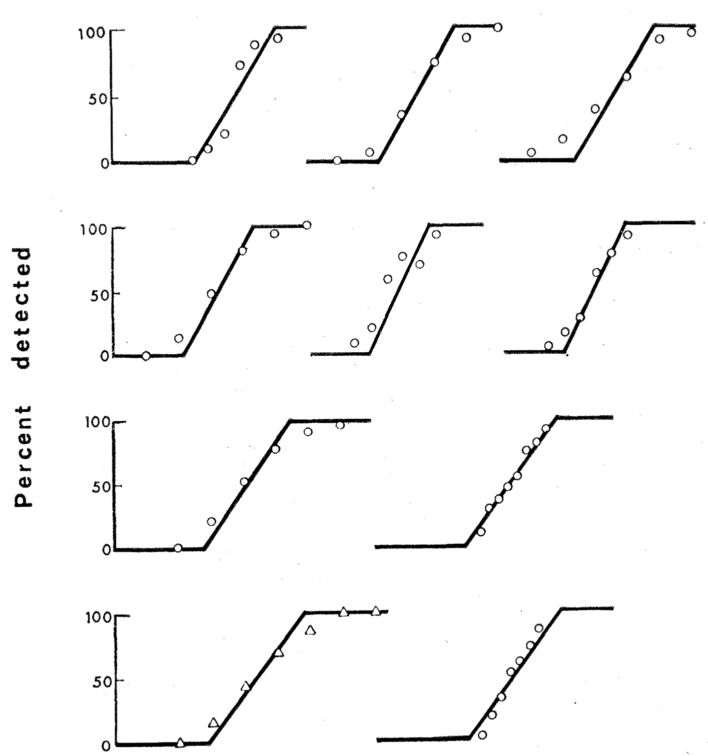


Fig. 10. The upper six functions are for six different observers who judged frequency increments to a 1000-hertz tone. The lower four are for different observers who judged frequency increments in tones of 3000 hertz (circles) and 300 hertz (triangles). [Data from Corso (*16*)]

Other Auditory Studies

In a series of 58 experiments, Garner and Miller (*14*) measured the size of the NQ for loudness as the duration of the stimulus increment was varied from 20 to 750 milliseconds. They used two frequencies, 500 and 1000 hertz, and two levels above threshold, 40 and 70 decibels. The measured size of the NQ was as much as three times as large for an increment duration of 20 as for 750 milliseconds. Yet both observers (the authors) found that the increments at the shortest durations were the easiest to judge. The briefer increments seemed more definite and their onset more abrupt.

The NQ for pitch was studied by Flynn (*15*) who used the procedure employed earlier by Stevens *et al.* (*8*). From three observers Flynn obtained 29 poikilitic functions, shown in Figs. 8 and 9. The rectilinear functions are all drawn with the 2-to-1 intercept ratio in order to show to what extent the data agree or disagree with the NQ theory. It is clear that Flynn's three observers sometimes produced noisy data, but the judgments seem generally to accord with the predicted form of the poikilitic function. Except for an occasional lapse, subject A did remarkably well in producing 18 NQ functions of approximately the predicted form.

The results for pitch discrimination obtained by Corso have an added interest, because the author has been a critic of the NQ hypothesis, partly on the grounds that his 20 undergraduate observers did not produce the predicted functions. Actually, the data he published show that the observers did fairly well, as can be seen in Fig. 10.

"The theory of the neural quantum," said Corso, "predicts that under quantal experimental conditions (i) the form of the psychophysical [poikilitic] function in pitch and in loudness discrimination will be linear, and (ii) the size of the smallest increment always heard will be twice that of the largest increment never heard" (*16*, p. 365).

Actually, Corso's statement is almost but not quite correct. The words "will be" should be replaced by "may be." The NQ theory does not guarantee the success of an experimenter's effort. Rather it says that if all goes well and if the observer fulfills the task of concentration, steadily adhering to a 2-quantum criterion, then the results may in the limit approach the ideal rectilinear function with the 2-to-1 intercept ratio. Consequently, the failure of some of Corso's observers, if we can call it such, does not provide evidence one way or the other.

Corso also undertook to measure the NQ for loudness, but something appears to have gone awry. Corso expressed the values of the increment in decibels, which would provide a suitable measure if properly computed. (See the example below, where all the increments in luminance are expressed in decibels.)

When the increment is measured in decibels, the NQ theory predicts that all the poikilitic functions will have the same slope, going from 0 to 100 percent over a range of 3 decibels. The value 3 decibels represents the 2-to-1 intercept relation. For the six examples published by Corso, the slopes cover ranges as small as 0.4 decibel and as large as 1.7 decibels. None of them are close to 3 decibels.

Such steep poikilitic functions are without precedent. A function that rises from 0 to 100 percent in 0.4 decibel seems too steep to be credible. Neisser (*11*) fitted straight lines to the 52 poikilitic functions obtained from his student observers. The intercept ratio averaged 2.15, which corresponds to a value close to but slightly greater than 3 decibels. That indeed is the typical finding for the 200 or more experimental determinations that I have had occasion to examine, except for the six examples reported by Corso.

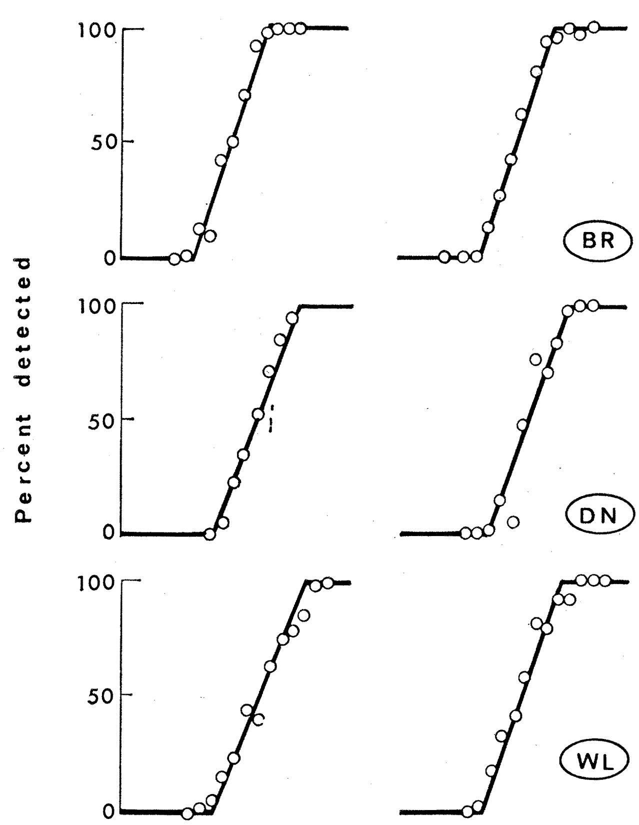
In more than 60 experiments on loudness, Larkin and Norman showed that well-motivated subjects can produce good approximations to the ideal NQ function (*17*). Figure 11 gives typical examples for three observers who listened to pulsed increments presented in blocks, the procedure used by Stevens and Volkmann (*7*). In order to guide his attention to the occurrence of the increments, the listener watched a rotating star-shaped wheel. The continuously indicating, clocklike device was found to be superior to a flashing light, which some of the observers had found helpful in the experiments of Stevens *et al.* (*8*).

Larkin and Norman also explored negative increments (decrements). Sample functions are shown in Fig. 12. The observers found that negative increments sounded different and could be distinguished from positive increments.

The next step was to present both positive and negative increments in the same session. The observer then has three options: he can respond louder, softer, or nothing. The results of such an experiment are shown in Fig. 13. Even those increments and decrements that were rarely detected were correctly identified when heard. Some stimulus changes were detected in fewer than 3 percent of the trials, and yet the observer was correct in his calls of louder or softer.

Békésy also obtained quantal functions for decrements as well as increments, but he used a very different method. A brief standard stimulus (0.3 second) was followed immediately by a brief comparison tone whose intensity was selected at random. Békésy seems not to have asked the subject to identify which was which, for he says, "Whether there is an increase or a decrease in loudness is not considered, because this involves a further cognitive process that is unnecessarily trying and prevents the direction of full attention on whether a change has occurred" (*5*, p. 242).

The controversy over the degree of linearity required in the NQ function has impressed Larkin and Norman as "really not a crucial aspect of the theory." Their observation seems eminently reasonable, for the theory predicts precise linearity only if the residual excitation impinging on the neural quantum next in line distributes itself, as a function of time, uniformly over the quantum. Certain additional assumptions concerning sampling and units of measurement must also be made. Nevertheless, a good approxima-



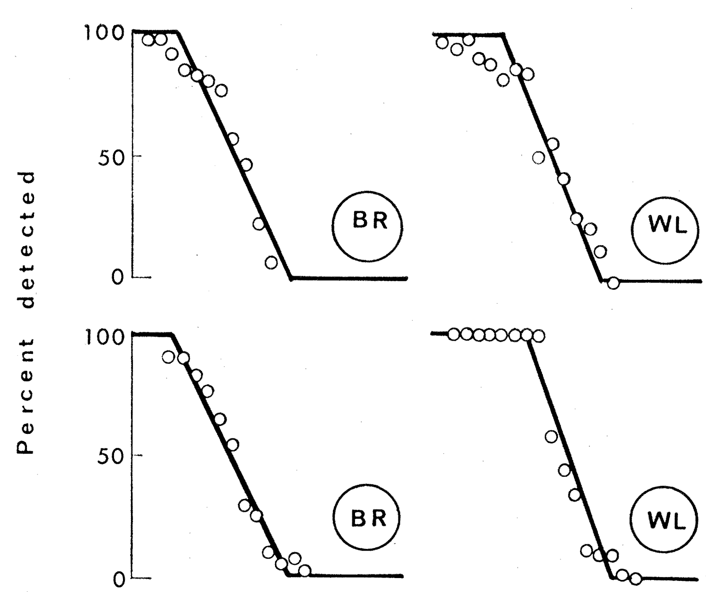


Fig. 11 (left). Two NQ functions for each of three observers who judged increments in the intensity of a tone of 1000 hertz. Increments, each lasting 150 milliseconds, were added to a tone 60 decibels above threshold and were presented in blocks. Each point is based on 100 judgments. [Adapted from Larkin and Norman (*17*)]

Fig. 12 (right). Four NQ functions for negative increments (decrements). Upper functions represent the first attempt by one observer and the second attempt by the other. The lower functions represent data from later sessions. Frequency 1000 hertz. [Adapted from Larkin and Norman (*17*)]

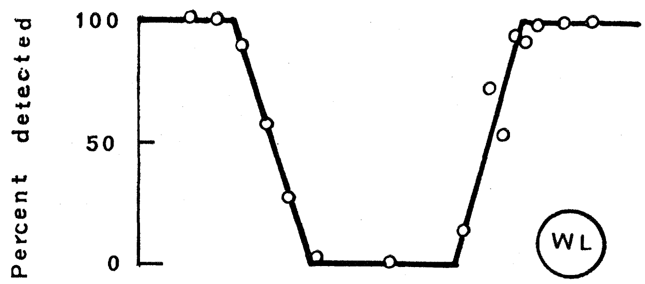


Fig. 13 (left). The observer judged both increments and decrements in the same session. He was able to distinguish increments from decrements. The NQ for decrements is larger than that for increments. Each point represents 100 judgments. [From Larkin and Norman (*17*)]

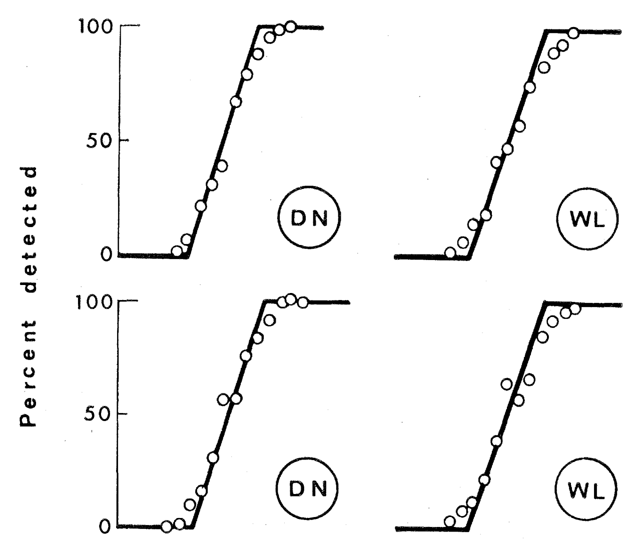


Fig. 14 (right). The four NQ functions are like those of Fig. 11 except that catch trials were used—a certain percentage of the increments were ommitted entirely. The catch trials may have caused an increased scatter of the points, but catch trials have been used with apparent success in at least three other studies. [Adapted from (*17*)]

tion to the linear form shows itself over and over. What is more important, the slopes bear out the prediction of the NQ theory.

In one part of their experiment Larkin and Norman modified the procedure in order to introduce "catch trials" by simply omitting the increment on a certain percentage of the trials. The catch trials seemed to distort the poikilitic function, although not by very much, and it led the authors to apply to their data a poikilitic function based on a two-stage process, as proposed by Luce (*18*). The two-stage model distinguishes between detecting the signal and responding to it. It is assumed that different biases may attach to each stage. The added flexibility inherent in the two-stage conception made it possible to fit modified quantal functions to the data. In Fig. 14 those same data are presented, but with a 2-to-1 quantal function fitted by eye. The fits are not bad, although the modified two-stage functions appeared to fit better. Although the use of catch trials may have degraded the observer's performance in those experiments, it is not clear that catch trials need be detrimental. Catch trials have not seemed to upset performance in several visual experiments.

Once we assume that a quantal gating process underlies the observer's responses, new opportunities for exploration beckon both the experimenter and the model maker. The terrain teems with hazards, however, because the experimental test usually requires a sampling process—the drawing of a finite set of responses from an observer. The responses are mediated by internal processes that vary as a function of time. The sampling of responses becomes, therefore, a process that carries a large burden of noise, to which may be added one or more of the noise-creating factors discussed above. Nevertheless, a promising beginning has been made in the exploration of some of the parameters that affect the poikilitic function. Led by Luce, we have seen the creation and analytic dissection of NQ models designed to reflect the response biases that result from payoffs, stimulus probabilities, and learning processes. The analysis of such problems has also been furthered by Norman (*19*).

Visual Studies

Both the eye and the ear are so sensitive to their respective stimuli that under optimal circumstances the nature of the physical stimulus is thought to set limits on the sense organ's performance. In visual studies especially, there has long been concern whether the quantal nature of light may manifest itself in visual thresholds. Troland noted that the absolute threshold in the periphery of the eye may require only about 10 quanta of energy (photons) to produce a visual sensation. Since the 1920's, other investigators have claimed even a smaller number (*20*). As a result there has grown up a large literature concerned with quantum (photon) theory applied to thresholds, both absolute and differential.

When the number of photons becomes sufficiently small, they make up a stream that patters irregularly, like rain on the roof, and it becomes conceivable that the statistical properties of the photon bombardment may determine the distribution of the observer's visual responses. On the other hand, if we are asked to assume that all the variability resides in the photon stream, and that the noise of the observer approaches absolute zero, then I for one find my credulity exceeded. For I rather suppose that the warm, pulsating human observer provides most of the variability, the controlling share of the noise. In that case we might expect discrimination experiments to give evidence, not for bombardment by discrete photons, but for the operation of a quantal gate within the observer—the same effect that reveals itself in the NQ for pitch and loudness.

As it turns out, most of the evidence for a neural step function in vision has been gathered by investigators who apparently had no interest in the NQ. Nevertheless, their measurements produced poikilitic functions having the predicted form and slope, but only as a by-product of their main concern. In some ways a result carries even more conviction when it verifies a theory that the experimenter does not believe in.

An extensive study of the differential threshold covering a stimulus range of almost a millionfold (59 decibels) was carried out by Mueller in order to test the relevance of the photon theory to brightness discrimination (*21*). The 27 poikilitic functions determined for one observer are shown in Fig. 15. Mueller concluded that those functions do not appear to be determined by the statistical properties of the photon beam. On the other hand, construed as a confirmation of the NQ hypothesis, the data look good.

Although not intended, the procedure of the experiment was nicely designed to reveal the NQ. The observer looked at a steady field subtending 12 degrees. Every 10 seconds a brief 20-millisecond increment, subtending 40 minutes of arc, was added to the center of the field. The observer reported each time he perceived the increment. It is important to note that the size of the increments was randomized, so there was no block presentation of the kind that some writers have thought to be necessary.

Since Mueller varied the luminance of the steady background field over the wide range of almost a millionfold, he found it convenient to express the increment in logarithmic measure. In logarithmic or decibel measure the slope predicted by the NQ theory remains constant at all stimulus levels. The predicted poikilitic line passes from 0 to 100 percent in 3 decibels, because 3 decibels represents a doubling of the increment. Even though each point in Fig. 15 is based on only 20 judgments, the consensus of the data shows congruence with the NQ prediction.

In keeping with Weber's law, the absolute size of the stimulus increments varied roughly as a linear function of the background luminance. For the highest background level, the increment needed to operate the NQ gate was many times larger than the increment needed for the lowest background level. Consequently, if the poikilitic functions in Fig. 15 were plotted against a linear instead of a logarithmic abscissa, the slope for the lowest background would need to be many times steeper than that for the highest background.

While exploring various methods for measuring visual thresholds, Blackwell obtained data that bear upon the NQ—in his opinion negatively, in my opinion positively (*22*). The four observers viewed a screen at a luminance of 76 decibels above 10^{-10} lambert and subtending 20 degrees, on which an increment lasting 60 milliseconds appeared at intervals of 12.25 seconds. The increment was a spot subtending 18.5 minutes of arc and was placed 7 degrees to the right of the central fixation point. In some series the increments were presented at 14 contrast levels and in blocks of 20 increments of the same size. In other series the increments were randomized. With both the block and the random presentations, catch trials involving the omission of the increment were also used.

Poikilitic functions having 2-to-1 intercepts have been fitted by eye to all the data presented by Blackwell. As shown in Figs. 16–18, the evidence for a quantal effect looks fairly impressive. Certain features of the data command particular interest.

All the data in Fig. 16 are for one observer. The top three poikilitic functions were obtained with randomized increments. For the first function (top left), the incremental stimuli produced a contrast so faint that most of them were seen less than half the time. For the next function the increments were spread out over a rather wide range. For the third function, only two increments, plus catch trials, were used. It is noteworthy that the straight line through the two points turns out to have the slope predicted by the NQ theory.

The two lower functions in Fig. 16 were obtained with blocks of pulsed increments—20 similar increments in a row before a different size was presented. The catch trials were also in blocks. All in all, Fig. 16 shows that the observer was able to produce acceptable quantal results under a rather wide variety of stimulus spacings and presentation procedures.

The four functions in Fig. 17 for observer 2 were all obtained with block trials. Data for subjects 3 and 4, with block trials, are shown in Fig. 18. Observer 3 produced one fairly good set of data and two that were not so good. Observer 4 showed "extreme scatter," both in the data shown (lower right) and in nine other sets of data. Blackwell notes that she had left school and had been diagnosed "pre-schizophrenic." The responses of observer 4 make it clear that people may differ dramatically in their ability to carry out the demands of the NQ experiment.

Blackwell concluded, "It should be entirely apparent that the neural quantal theory is totally inadequate to rationalize the present data" (*22*, p. 113).

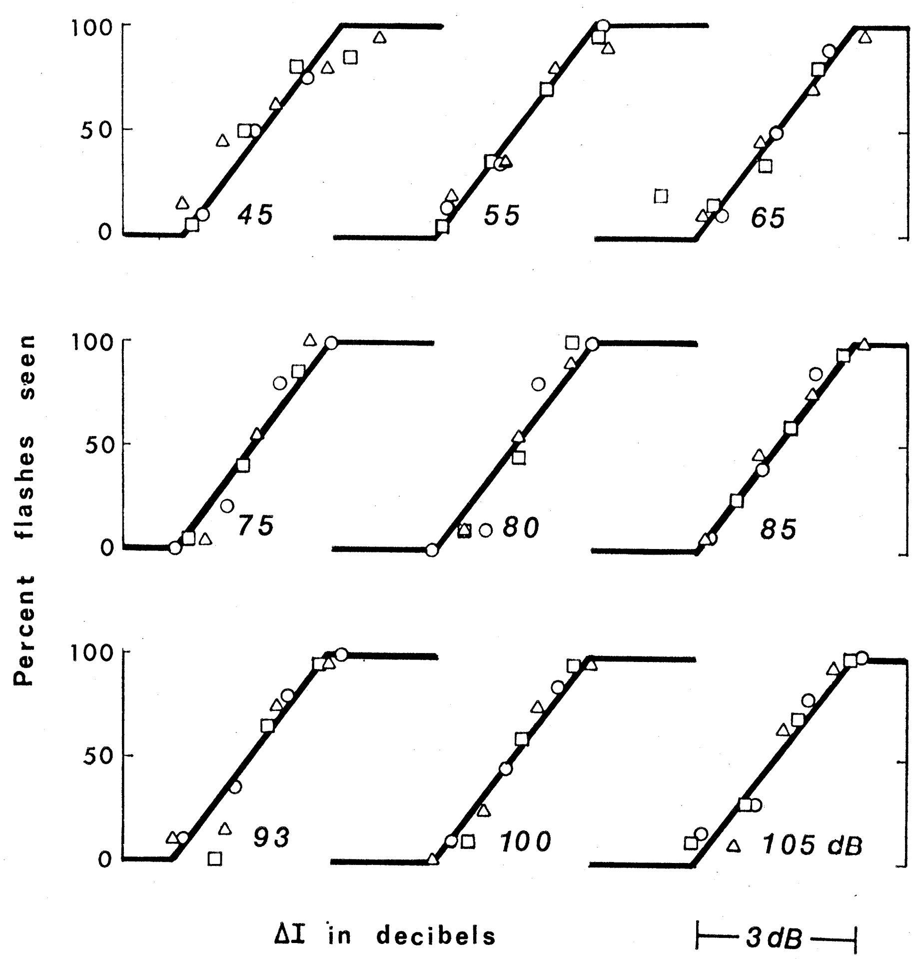
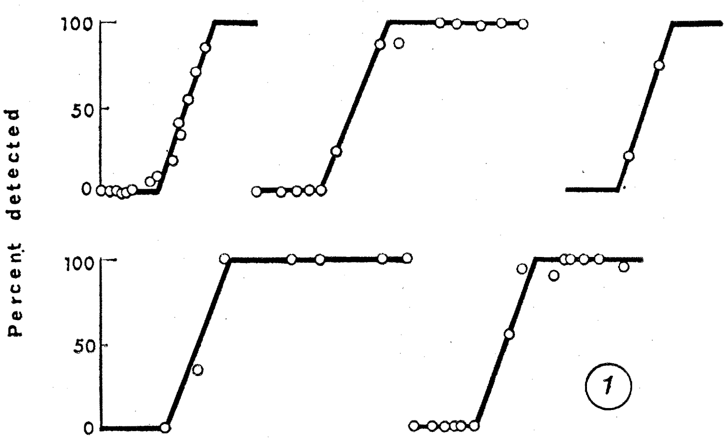


Fig. 15. Brightness increments presented in random order were judged by an observer who produced 27 poikilitic functions, 3 at each of 9 stimulus levels. The background luminance ranged from 45 to 105 decibels above 10^{-10} lambert. The increments were brief flashes of a small target seen in the fovea. Each type of symbol represents a different experiment, 20 judgments per point. Since the abscissa is logarithmic (decibels) the slopes of the NQ functions are all the same, spanning a range of 3 decibels. [Data from Mueller (*21*)]

It seems to me, however, that Blackwell wrought better than he surmised, even though some of his procedures may have imposed rather severe burdens on the subject. The subject was sometimes presented with a large number of increments calling for zero response, or for 100 percent response, or both. The presentation of stimuli much above and below that range provides little or no information regarding the size of the NQ. On the other hand, it is helpful to have it demonstrated once again that increments of many different sizes can elicit zero response. When the observer gives zero response to a wide range of finite increments, it creates an embarrassment for certain alternative theories,



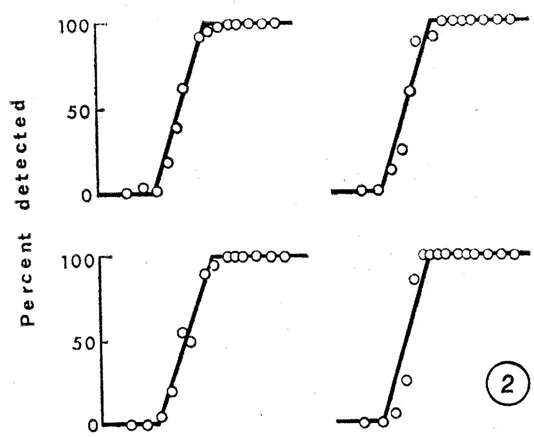


Fig. 16 (left). Brightness increments were presented as brief flashes of a small target seen 7 degrees to the right of center. The background luminance was 76 decibels re 10^{-10} lambert. All the NQ functions are for subject 1. For the top three functions the increments were randomized. For the two lower functions the increments were presented in blocks of 20. Catch trials were used in all the experiments. [Data from Blackwell (*22*)]

Fig. 17 (top right). Four NQ functions for subject 2 obtained with brightness increments presented in block trials. [Data from Blackwell (*22*)]

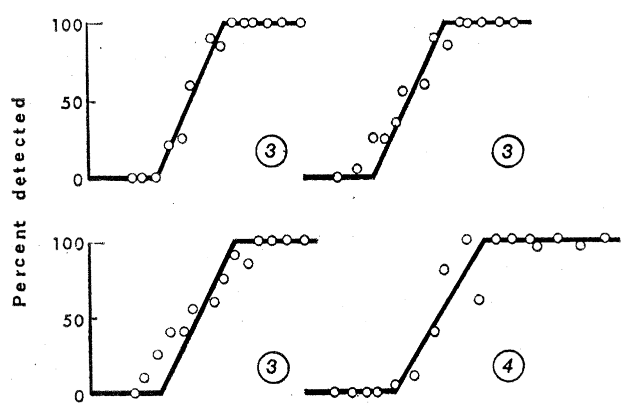


Fig. 18 (bottom right). Three NQ functions for subject 3 and one function for subject 4, who was described as "pre-schizophrenic." [Data from Blackwell (*22*)]

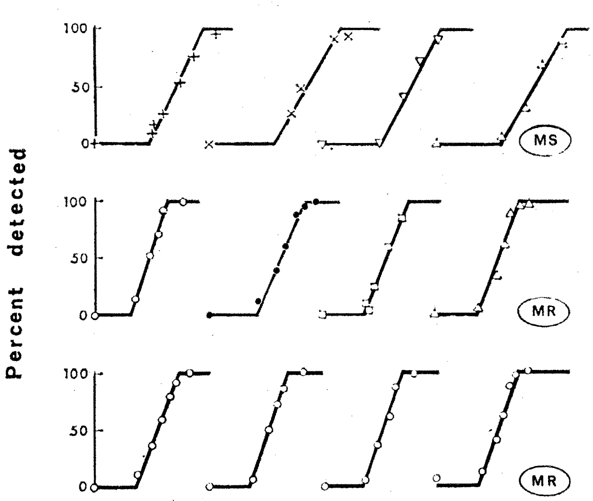


Fig. 19. The increment was a striped pattern that appeared for 0.76 second on the face of a cathode-ray tube whose normal luminance was 83 decibels (20 millilamberts). The pattern of vertical stripes contained 14 stripes per degree. Data for two observers are shown. Each poikilitic function was determined on a different day. Increment size (contrast) was varied randomly from trial to trial and catch trials were included. [Data from Sachs *et al.* (*23*)]

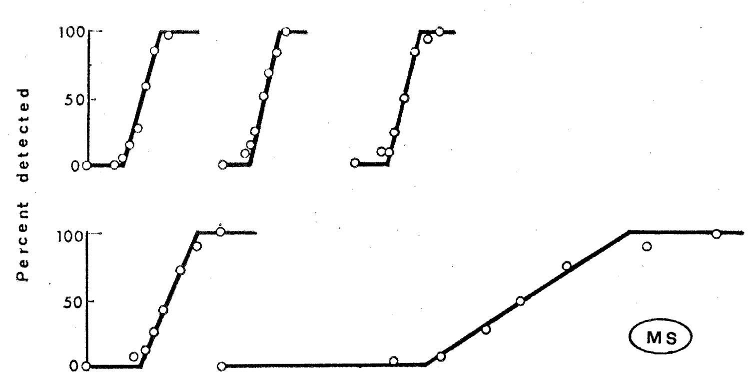


Fig. 20 (right). Poikilitic functions for subject MS with stripe patterns of five different widths, stated as a number of stripes per degree, from upper left to lower right: 1.4, 2.8, 5.6, 11.2, and 22.4. The abscissa scale has been given the same linear modulus for all the NQ functions in order to show that, when the width of the stripes changes, the slope of the poikilitic function changes in inverse ratio to the size of the NQ. [Data from Sachs *et al.* (*23*)] in particular those theories based on the normal probability distribution.

The foregoing data show that a quantal gate function can be demonstrated with a small, brief increment in the fovea (Mueller, *21*) and also with a small, brief increment in the periphery (Blackwell, *22*). A quite different type of incremental target was employed in an experiment by Sachs, Nachmias, and Robson (*23*). The target was a square, 2.25 degrees on a side, and made up of light and dark vertical stripes. The luminance varied sinusoidally across the target, and the amplitude of the sinusoidal variation could be controlled. Specifically, the stripes could be made to appear for a brief period (760 milliseconds) and with any desired degree of contrast. The face of the cathode-ray tube on which the stripes appeared had a luminance of approximately 83 decibels above 10^{-10} lambert. The authors were apparently not interested in the NQ, but their procedure happened to be well suited to show a quantal effect in the observer's responses. The observer pressed a switch to initiate a trial, and he said "yes" if he saw a change from the constant luminance display and "no" if he did not. The size of the increments was randomized, and catch trials were used.

The data shown in Fig. 19, for sinusoidal patterns having 14 cycles per degree, were obtained from two observers. Each point is based on 100 judgments and each function was determined on a different day. The NQ varied by less than a factor of 1.5 from day to day, but it is nevertheless evident that the linearity of the functions would give way to a slightly more sigmoid form if the results for different days were combined. The NQ for observer MS is consistently larger than that for observer MR.

The size of the NQ passed through a minimum as the number of stripes was varied from 1.4 to 22.4 per degree. The variation in the size of the NQ can be seen in the data of observer MS, shown in Fig. 20. The abscissa scale is constant for all five poikilitic functions, and the lines have intercepts in the ratio of 2 to 1, as required by the NQ theory. The NQ is smallest for a target with about 2.8 stripes per degree, and it becomes about seven times larger for a target with stripes as narrow as 22.4 per degree.

As did Mueller before them, Sachs, Nachmias, and Robson assumed that their poikilitic functions could be described by the normal ogive, and they drew S-shaped curves through the data. The normal ogive, as already noted, is more flexible than the NQ function, mainly because there is no restraint on the slope of the ogive. The NQ theory specifies both the form and the slope of the function and in that sense provides the more powerful model.

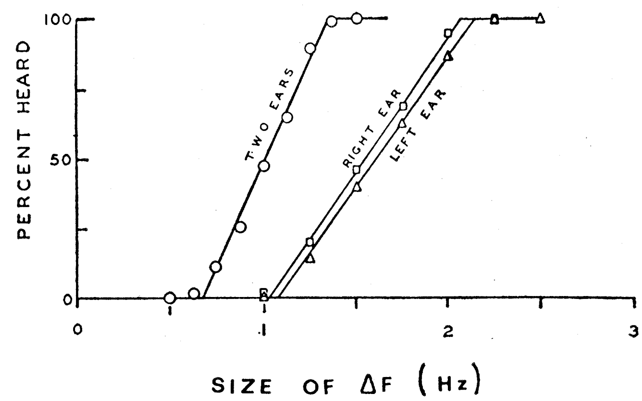


Fig. 21. Monaural and binaural NQ functions for pitch. The NQ was smaller when the tone was delivered to both ears. [From Stevens *et al.* (*8*)]

The Mechanism

Where do we look for the neural response that operates like a gating circuit, storing excitation and firing off in quantal fashion? Quantal action entails, of course, the concept of a holding action, so that, over a finite range below the threshold level, increments can be added with no effect, no response by the observer. Stimulation must build up to a critical level before it triggers a reaction. Actually, synaptic gating mechanisms are a familiar feature of many parts of the nervous system. Indeed, quantal action is so widespread that the all-or-none response is not by itself a guide to the identification of the mechanism for the NQ.

The foregoing examples have demonstrated stepwise discontinuities in three different sensory continua—loudness, pitch, and brightness. Not only has the NQ been found in two different sense modalities, vision and hearing, but in the auditory modality the evidence has appeared equally clear-cut for the metathetic attribute of pitch and for the prothetic attribute of loudness. Pitch is thought to depend on the locus of stimulation along the basilar membrane, whereas loudness is thought to depend on the amount of excitation at whatever locus is activated (*24*). Pitch is based on a substitutive physiological mechanism, loudness on an additive mechanism.

It now seems clear, therefore, that the mechanism of the neural quantum must be sought in a gating action that is sufficiently general to embrace more than a single sense modality and to accommodate at least two different modes of action in the peripheral machinery of the auditory system.

Another fact that may bear on the problem of the physiological mechanism is the change in the size of the NQ for pitch when the mode of listening changes from monaural to binaural. A typical result is shown in Fig. 21. Under binaural listening the NQ was only about two-thirds as large as under monaural listening. However, one of four observers tested showed essentially no difference between monaural and binaural listening. As shown in Fig. 21 the remarkably simple relation between the slopes and the intercepts of the poikilitic functions remains undisturbed when the observer changes from monaural to binaural listening. And the functions remain linear, or nearly so. Those facts set constraints on our theorizing. The functions in Fig. 21 make it appear likely that the neural quantum for pitch probably does not reside in the periphery. A central mechanism seems indicated. In our present state of knowledge, a more explicit statement would lead into speculation, perhaps even into neuromythology.

Summary

The quantal organization of the nervous system, which exhibits itself in the all-or-none aspect of the nerve impulse and in synaptic transmission, leads to the hypothesis that critical points may, under certain conditions, manifest themselves in sensory discrimination. In particular, a step function should appear in the poikilitic function that relates the percentage of increments detected to the size of an increment that is added to a stimulus. The addition of the incre-

ment needs to be nearly instantaneous in order to make the neural quantum, the NQ, maximally visible.

When the increment is added to a steady background stimulus, the observer adopts a 2-quantum criterion. The NQ theory then predicts a rectilinear function whose location determines the slope: the smallest increment that is always detected is two times the largest increment that is never detected. Thus, the slope is inversely proportional to the size of the NQ.

Data fulfilling the NQ prediction have been obtained in a dozen different investigations over a span of four decades. Poikilitic functions having the predicted form have been obtained under a variety of procedures, often by experimenters who did not subscribe to the NQ theory. Some 140 NQ functions are presented, illustrating steplike functions for auditory loudness and pitch, and for three types of visual patterns. The gating mechanism that produces the NQ function is probably central rather than peripheral.

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The Tropical Rain Forest: A Nonrenewable Resource

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There is a popular opinion that the tropical rain forests because of their exuberant growth, their great number of species, and their wide distribution will never disappear from the face of the earth.

On the other hand, it has often been stated that the tropical rain forests (tall evergreen forests in tropical warm and humid regions) around the world must be protected and conserved for the future generations (*1*). It has also been stated that it is most important that knowledge about the structure, diversity, and function of these ecosystems has priority in future biological research (*2*). Unfortunately, either these voices have not been heard or their arguments have not been convincing enough to promote action in this direction.

It is the purpose of this article to provide a new argument that we think is of utmost importance: the incapacity of the rain forest throughout most of its extent to regenerate under present land-use practices.

Even though the scientific evidence to prove this assertion is incomplete, we think that it is important enough to state and that if we wait for a generation to provide abundant evidence, there probably will not be rain forests left to prove it.

During the last few million years of their evolution, the rain forests of the world have produced their own regeneration system through the process of secondary forest succession. This regeneration system evolved in the many clearings that occurred naturally as a result of river floods, storms, trees that die of age, and the like. The genetic pool available for recolonization was great, and a number of populations and species with characteristics that were advantageous in the rapid colonization of such breaks in the continuity of the primary rain forest were selected. These plants were fast-growing heliophytes, with seeds that have dormancy and long viability, and efficient dispersal mechanisms (*3, 4*). These sets of species played a fundamental role in the complex process of regeneration of the rain forest, and it is astonishing that very little is known about their biology, their behavior in the succession, and their evolution, even though they are the key to understanding the process of secondary succession, which is one of the most important ecological phenomena. The few works on the subject point out that there are certain repetitive patterns that can be predicted and that the species involved are fundamentally different from the primary species (*5–7*).

It is still uncertain how most of the primary species of the rain forest reproduce themselves and how the forest is regenerated, but from the evidence available it seems that there is a very complex system working at different times and in different directions, depending on the local situation and the plants involved (*3*).

One of the most important aspects

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