XXVI. COMMUNICATIONS BIOPHYSICS[*]

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RESEARCH OBJECTIVES

During the past year publications by members of this group have ranged from certain aspects of applied mathematics[1-4] to certain problems of instrumentation[5]; most of our work has, however, been experimental in character and has reflected our predominant concern with those aspects of the electrical activity of the nervous system which relate to sensory function.

A large number of papers[6-9] have dealt with the application of computer techniques to analytical studies of neuroelectric activity. Six of these papers are part of a forthcoming special supplement to the Journal of Electroencephalography and Clinical Neurophysiology in which the proceedings of a conference organized by Professor M. A. B. Brazier at the Brain Research Institute of the University of California at Los Angeles is summarized.[10]

Several studies of responses[11-20] from the auditory and visual systems have been reported. In some of these papers a particular effort has been made to use the techniques that we have developed in order to examine those aspects of electrical responses that are peculiarly sensitive to an organism's physiological macrostate. A sustained effort is already being made to study sensory discrimination in a given organism by means of compatible electrophysiological and behavioral techniques; during the coming year the first findings of this research should be reported.

Analyses of a variety of biologically significant patterns continue to concern members of this group[21-24]; some of the papers already referred to could have been put

into this category.

Notable progress in research that deals with the behavior of networks of neuronlike elements is reflected in two papers.[25-26]

Our close and fruitful cooperation with the Eaton Peabody Laboratory for Auditory Physiology, at the Massachusetts Eye and Ear Infirmary, continues. The laboratory now constitutes a model experimental facility for whose design Robert M. Brown, and for whose operation, Alan Crist, are largely responsible. Under the able and inspired direction of Dr. Nelson Y-S. Kiang, the past year has been characterized by the accumulation of an impressive catalog of the behavior of neurons in the auditory nerve and in the cochlear nucleus. There is in preparation a highly significant monograph on the coding of acoustic stimulus characteristics.

The always present preoccupation of electrophysiologists with the physical characteristics of the medium, and with methods of recording them, has been expressed in three papers.[27-29]

Finally, the relation of neuroelectric and behavioral events that are concomitant with sensory communication have been examined in two other publications.[30, 31]

<div align="right">W. A. Rosenblith</div>

References

1. M. Eden, On the formalization of handwriting, Proc. Symposia in Applied Mathematics, Vol. 12, Structure of Language and Its Mathematical Aspects (American Mathematical Society, New York, 1961), pp. 83-88.

2. M. Eden, A two-dimensional growth process, Fourth Berkeley Symposium on Mathematical Statistics (University of California Press, Berkeley, in press).

3. R. W. Rodieck, Methods of Studying Spontaneous Activity, S.M. Thesis, Department of Electrical Engineering, M.I.T., 1961.

4. D. D. Rutstein, M. Eden, and M. P. Schützenberger, Report on mathematics in medical sciences, New England Journal of Medicine 265, 172-176 (1961).

5. M. H. Goldstein, Jr. and L. Nicotra, Spectral analyzer for EEG, EEG Clin. Neurophysiol. 13, 475-477 (1961).

6. N. Y-S. Kiang, The use of computers in studies of auditory neurophysiology, Trans. Amer. Acad. Opthalmol. Otolaryngol. 65, 735-747 (1961).

7. M. A. B. Brazier, Detection of evoked responses, Methods in Medical Research, edited by J. H. Quastel (Yearbook Medical Publishers, Chicago, 1961), pp. 423-432.

8. M. A. B. Brazier, Editor, Conference on Computer Techniques in EEG Analysis (Elsevier Publishing Company, Amsterdam, in press); included are the following papers:
    J. S. Barlow, Correlation techniques in EEG analysis;
    W. A. Clark, Jr., Digital averaging techniques;
    B. Farley, Recognition of patterns in the EEG;
    G. L. Gerstein, Neuron firing patterns and the slow potentials;
    M. H. Goldstein, Jr., Averaging techniques applied to evoked responses; and
    W. A. Rosenblith, Commentary.

9. B. G. Farley, L. S. Frishkopf, W. A. Clark, Jr., and J. T. Gilmore, Computer techniques for the study of patterns in the EEG, Trans. IRE, PGME (in press).

10. Publication of the teaching materials used in the special, intensive course on "Computer Techniques for Biological Scientists," is not contemplated at this time; this course, which was sponsored by the National Science Foundation, was organized during the summer of 1961, and taught by a committee composed of T. T. Sandel (Chairman), J. B. Dennis, W. M. Siebert, W. A. Clark, Jr., and M. Eden.

11. M. A. B. Brazier, Paired sensory modality stimulation studied by computer analysis, Pavlovian Conference, Ann. New York Acad. Sci. 93, Art. 3, 1054-1063 (1961).

12. M. A. B. Brazier, Keith F. Killam, and A. James Hance, The reactivity of the nervous system in the light of the past history of the organism, Sensory Communication, edited by W. A. Rosenblith (The M.I.T. Press, Cambridge, Mass., and John Wiley and Sons, Inc., New York, 1961), pp. 699-716.

13. G. L. Gerstein, Firing patterns of neurons in auditory cortex, Brain and Behavior Conference (Brain Research Institute, U.C.L.A., February 1961, in press).

14. N. Y-S. Kiang and T. T. Sandel, Off-responses from the auditory cortex of unanesthetized cats, Arch. Ital. Biol. (Pisa) 99, 121-134 (1961).

15. T. T. Sandel and N. Y-S. Kiang, Off-responses from the auditory cortex of anesthetized cats: effects of stimulus parameters, Arch. Ital. Biol. (Pisa) 99, 105-120 (1961).

16. N. Y-S. Kiang, J. H. Neame, and Louise F. Clark, Evoked cortical activity from auditory cortex in anesthetized and unanesthetized cats, Science 133, 1927-1928 (1961).

17. A. Arduini and M. H. Goldstein, Jr., Enhancement of cortical responses to shocks delivered to lateral geniculate body: Localization and mechanism of the effects, Arch. Ital. Biol. (Pisa) (in press).

18. N. Y-S. Kiang, M. H. Goldstein, Jr., and W. T. Peake, Temporal coding of neural responses to acoustic stimuli, Trans. IRE, PGIT (in press).

19. W. T. Peake and N. Y-S. Kiang, Cochlear responses to condensation and rarefaction clicks, Biophys. J. (in press).

20. D. C. Teas and N. Y-S. Kiang, Evoked cortical responses as a function of 'state' variables, Quarterly Progress Report No. 59, Research Laboratory of Electronics, M.I.T., October 15, 1961, pp. 171-176.

21. C. F. Ehert and J. S. Barlow, Toward a realistic model of a biological period-measuring mechanism, Cold Spring Harbor Symposia on Quantitative Biology, XXV, Biological Clocks (Long Island Biological Association, New York, 1961); see also Discussion, pp. 54, 85, 86, 196.

22. M. Eden and M. Halle, A characterization of cursive writing, Information Theory, edited by C. Cherry (Butterworths Scientific Publications, London, in press).

23. J. S. Barlow, A phase-comparator model for the diurnal rhythm of emergence of Drosophila, Ann. New York Acad. Sci. (in press).

24. S. L. Levine, The Electroencephalogram of Identical Twins, S.M. Thesis, Department of Electrical Engineering, M.I.T., 1961.

25. B. G. Farley, Simulation of nerve nets, Fed. Proc. (in press).

26. B. G. Farley and W. A. Clark, Activity in networks on neuron-like elements, Information Theory, edited by C. Cherry (Butterworths Scientific Publications, London, in press).

27. M. A. B. Brazier, Electrical fields in a conducting medium, Methods in Medical Research, edited by J. H. Quastel (Yearbook Medical Publishers, Chicago, 1961) pp. 416-423.

28. M. A. B. Brazier, Recordings from large electrodes, Methods in Medical Research, edited by J. H. Quastel (Yearbook Medical Publishers, Chicago, 1961), pp. 423-432.

29. C. D. Geisler and G. L. Gerstein, The surface EEG in relation to its sources, EEG Clin. Neurophysiol. (in press).

30. W. A. Rosenblith and Eda Berger Vidale, A quantitative view of neuroelectric events in relation to sensory communication, Psychology: A Study of a Science, Vol. 4, edited by Sigmund Koch (McGraw-Hill Publishing Company, New York, 1962), pp. 334-379.

31. W. A. Rosenblith, Editor's Comment, Sensory Communication (The M.I.T. Press, Cambridge, Mass., and John Wiley and Sons, Inc., New York, 1961), Chapter 40, pp. 815-826.

A. MODELS FOR THE DYNAMIC BEHAVIOR OF THE COCHLEAR PARTITION

The hydromechanical action of the inner ear plays an important role in almost every theory of audition, and has consequently long been a popular subject for speculation and investigation. The recently celebrated direct observations by George von Békésy[1-8] of the motion of the cochlear partition put an end to most of the speculation and leave little room for doubt, at least about the general nature of cochlear dynamics. But von Békésy's reported results provide only somewhat spotty coverage (particularly with respect to phase characteristics) of low- and medium-frequency response in the middle and apical turns. The difficult nature of von Békésy's experiments has apparently discouraged direct extension of his work; we are left with such deductions as we can make from interpolation and extrapolation, from theory, and from indirect electrophysiological evidence.

The present study is primarily an empirical attempt to extend and complete von Békésy's observations, and was undertaken as part of a continuing effort to understand certain psychophysical phenomena. It differs from the similar (and similarly motivated) work of Flanagan[9, 10] in two respects:

a. We are as much interested in studying the functional structure, interrelationships, and internal consistency of von Békésy's observations, as we are in trying to fit the data accurately with specific analytical functions.

b. Such analytical representations as we shall give explicitly have been constrained by a requirement of extreme simplicity and workability, so as to hamper least the psychophysical analyses for which they are intended. In particular, we have seen no reason to limit our search to rational functions of frequency.

1. Von Békésy's Observations

We assume that the behavior of the cochlear system would be adequately described for our purposes by giving the volume displacement of the cochlear partition (in cc/mm) of each point, x (in centimeters measured from the stapes), at each time, t (in seconds), in response to an arbitrary dynamic volume displacement (in cubic centimeters) of the stapes. Since the evidence supports the further assumptions that the cochlear system is — at least for small displacements — both linear and

(essentially) time-invariant, it is sufficient to give both the amplitude and phase of the sinusoidal response at each point, x, to a sinusoidal stimulus of the stapes at an arbitrary frequency, f, (in cps). Symbolically we can represent this stimulus-response relationship by the complex function $F(f, x)$, which is to be interpreted as implying that, if the volume displacement of the stapes is $A \cos[2\pi ft + \theta]$, then the volume displacement of any point on the partition is given by

$$\text{Re}\left[F(f, x) A e^{j[2\pi ft + \theta]} \right]$$

where $\text{Re}[\ ]$ stands for "real part of $[\ ]$."

The measurement of a reasonably smooth function of two variables is usually most easily carried out by fixing one variable and determining the behavior of the function with respect to the other variable. This was the scheme adopted by von Békésy. His principal reported results[1-8] are shown in Figs. XXVI-1 - XXVI-4 (the scales of Figs. XXVI-1 and XXVI-2 are rather unconventional as we shall explain). Figure XXVI-1 is, in our notation, a plot of the magnitude of

$$\frac{F(f, x)}{|F[f_{max}(x), x]|} = H_x(f) \tag{1}$$

considered as a function of f for various fixed x. Two sets of data are shown; the later data[2] consist of only one curve, but the corresponding value of x and of the phase angle of $F(f, x)$ are given, whereas neither the phase nor the position are available for the earlier results.[3] Similarly the curves of Fig. XXVI-2 are plots of the magnitude and phase of

$$\frac{F(f, x)}{|F[f, x_{max}(f)]|} = G_f(x) \tag{2}$$

considered as functions of x for fixed f. Again, two sets of data are shown. The 1943 set[4] covers a relatively wide range of frequencies, but no corresponding phase measurements were made. The 1947 results[5] include phase measurements, but data are given only for quite low frequencies. It is obvious from Fig. XXVI-2 that although these two sets of curves are qualitatively similar they are quantitatively quite different — the spread along the partition of the response to a given frequency is perhaps twice as wide for the earlier observations as for the later.

Figure XXVI-3 is a "cochlear map" — a plot of $x_{max}(f)$. Three sets of points are shown, one from 1942 measurements[6] of this function alone and the others from the peak locations of Fig. XXVI-2. It is important, at least in principle, to observe that we should not necessarily expect to get the same relationship between x and f if we seek to determine the frequency that maximally stimulates a given spot rather than
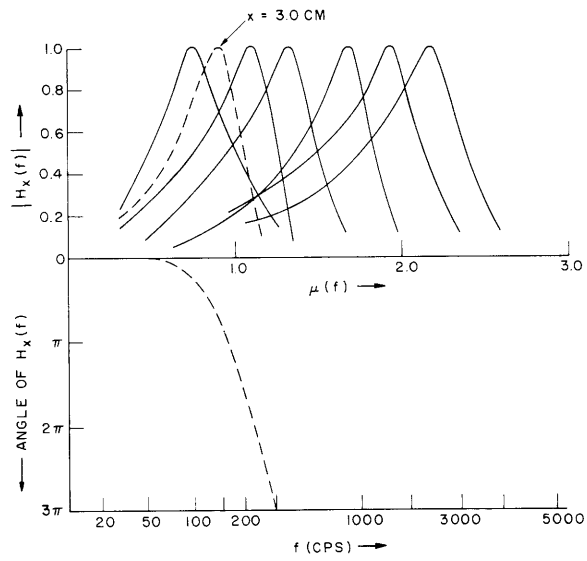
Fig. XXVI-1. **Freq**uency responses for various positions **along the** cochlear
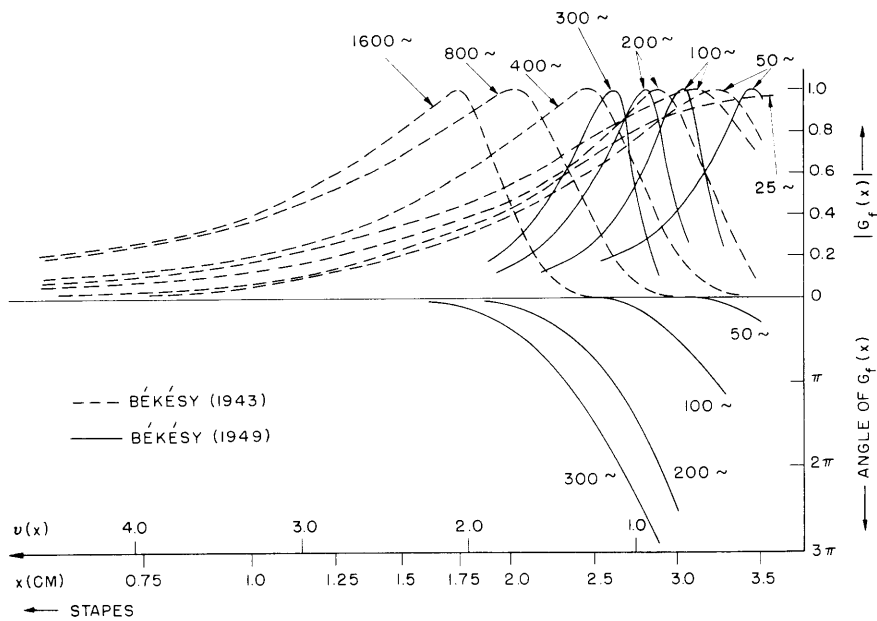partition. Solid curves, von Békésy (1943); dotted curves,
von Békésy (1947).

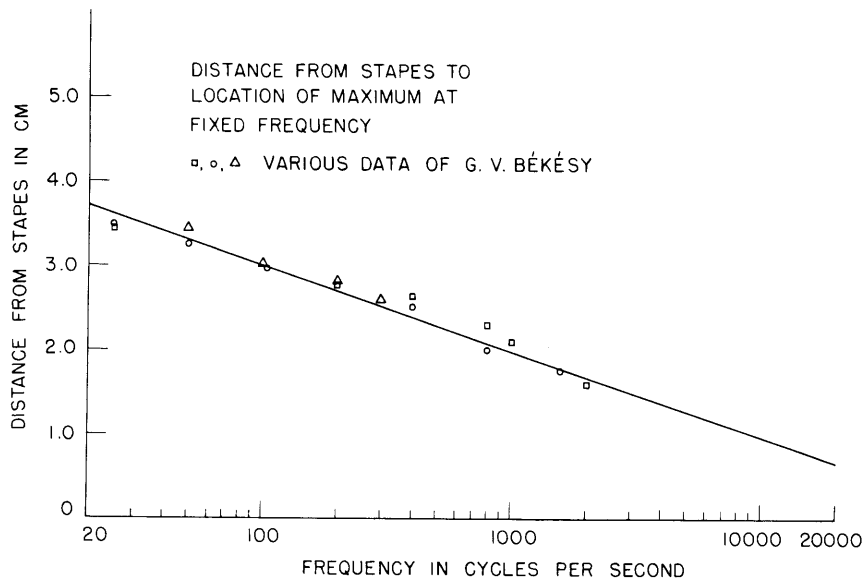Fig. XXVI-2. Volume displacement for various fixed frequencies.
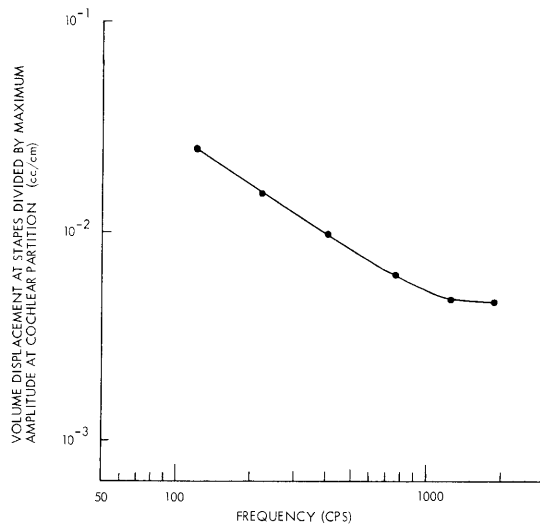
Fig. XXVI-3. A "cochlear map" — plot of $x_{max}(f)$.

Fig. XXVI-4. Amplitude factor (after von Békésy, 1947).

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(as von Békésy did) to locate the position of maximum response to a given frequency. The first, $f_{max}(x)$, is the solution of

$$\frac{\partial |F(f, x)|}{\partial f} = 0,$$ (3)

whereas the second, $x_{max}(f)$, is the solution of

$$\frac{\partial |F(f, x)|}{\partial x} = 0.$$ (4)

There would not seem to be any special experimental difficulty in determining $f_{max}(x)$ rather than $x_{max}(f)$ (position labels for the curves of Fig. XXVI-1, if available, would permit construction of such a curve), and indeed some indirect methods of making coch-lear maps yield one function and some the other. Thus the locations of lesions in the basilar membrane which are produced by intense stimulation should give $x_{max}(f)$, where-as the measurement of the frequency at which fixed damage causes maximum hearing loss presumably relates to $f_{max}(x)$. It is probable that experimental difficulties and differences between individuals and species would preclude observation of any small discrepancy between $x_{max}(f)$ and $f_{max}(x)$, but a large difference would certainly have been noticed by von Békésy if it were present. The absence of such a large effect — at least at low and medium frequencies — is of considerable importance to our study.

Von Békésy's results, as in Figs. XXVI-1 and XXVI-2, are characteristically plotted as "relative amplitudes." To determine $F(f, x)$ from these results, it would be neces-sary to be given separately the amplitude factors

$$h(x) = |F[f_{max}(x), x]|$$ (5)

and/or

$$g(f) = |F[f, x_{max}(f)]|.$$ (6)

These are, of course, different functions; there is, at least formally, no reason to suppose that they are related in any simple way such as $g(f) = h[x_{max}(f)]$. In this respect the one amplitude-factor plot[7] given by von Békésy (Fig. XXVI-4) is somewhat con-fusing. From von Békésy's description, Fig. XXVI-4 is based on the same data as the 1943 curves of Fig. XXVI-1, and is the volume displacement per millimeter at a given point on the partition for a unit volume displacement of the stapes at the frequency to which the given point is maximally sensitive; that is, Fig. XXVI-4 is a plot of $h(x)$. But the abscissa of the curve is frequency. Apparently what is really being plotted is $h[x_{max}(f)]$, with $x_{max}(f)$ given by some unspecified cochlear map. However, it seems likely that the difference between $g(f)$ and $h[x_{max}(f)]$ over at least the frequency region considered is not likely to be very large or again von Békésy could hardly have failed

to detect it. We shall see shortly that perhaps the best evidence that this is indeed the case is provided by the data of Fig. XXVI-4 itself, which show that the maximum amplitude is only approximately 4 times greater at a point 2.0 cm from the stapes than it is at the helicotrema. As von Békésy points out this is "relatively flat," at least when compared with the 60 db or more variation in the auditory threshold for the corresponding frequencies. And it is quite flat enough to make any differences in the low- and medium-frequency region between the plots of $x_{max}(f)$ and $f_{max}(x)$ or between $g(f)$ and $h[x_{max}(f)]$ entirely academic, as we shall see.

2. Deductions and Models

It should be clear from Figs. XXVI-1 - XXVI-4 and the preceding discussion that von Békésy does not provide sufficient observations to define $F(f, x)$ directly, even at low frequencies and in the apical region. The most nearly complete description results from the earlier data of Fig. XXVI-1 in combination with the amplitude factor of Fig. XXVI-4, but this provides no phase information, the values of position are not given in Fig. XXVI-1, and the range of frequencies covered is limited. Some additional information — particularly about phase characteristics — could be derived from Fig. XXVI-2, if the questions of consistency, which arise because the observations were made on separate preparations, could be resolved. To test for consistency as well as to extrapolate in a reasonable way we shall need various principles that we shall now develop.

First we observe that we must have, for consistent data,

$$F(f, x) = h(x) H_x(f) = g(f) G_f(x) \tag{7}$$

and hence

$$h(x) = g(f) \frac{G_f(x)}{H_x(f)} \tag{8}$$

or in particular

$$h(x) \sim \frac{|G_f(x)|}{|H_x(f)|} \tag{9}$$

for each fixed frequency. If the values of $|G_f(x)|$ and $|H_x(f)|$ are taken from the curves of Figs. XXVI-1 and XXVI-2 for common values of x and f, then the values of the ratio for each f should form a smooth curve and the curves for various f should be part of one over-all curve, h(x), except for scale factors (which determine g(f)). This procedure is easily carried out for the data of Figs. XXVI-1 and XXVI-2 except for one thing — the values of x to associate with each curve in Fig. XXVI-1 are unknown. If
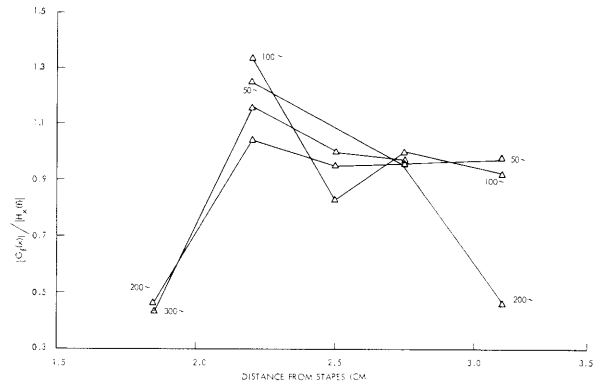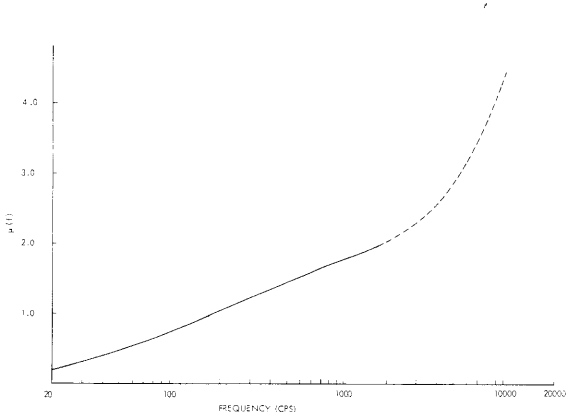
Fig. XXVI-5.   Consistency check.

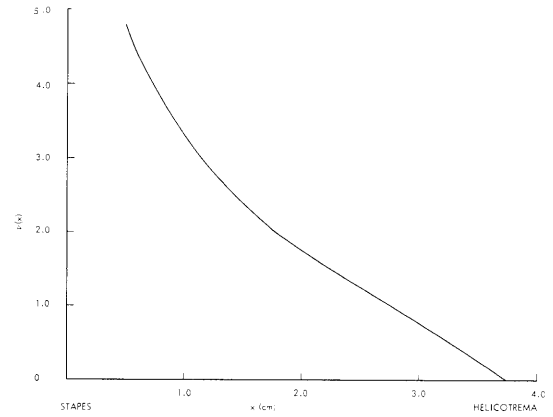

Fig. XXVI-6.   Frequency scale.
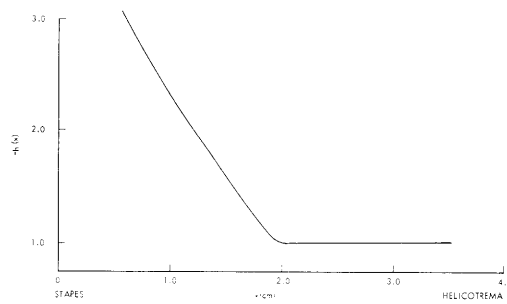

Fig. XXVI-7.   Position scale.

Fig. XXVI-8. Amplitude factor. $L(x) = \nu'(x)$.

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we assume, tentatively, that $x_{max}(f)$ and $f_{max}(x)$ determine the same curve so that the parameter values for Fig. XXVI-1 can be determined from Fig. XXVI-3, it is easy to show (see Fig. XXVI-5) that the curves of Fig. XXVI-1 and the 1947 curves of Fig. XXVI-2 are astonishingly consistent and yield $h(x) \approx g(f) \approx 1$ for apical positions and low frequencies — a result that we consider not inconsistent with the "relatively flat" amplitude factor of Fig. XXVI-4. We have, however, been unable to find any way of assigning positions to the curves of Fig. XXVI-1 which will yield consistency with the 1943 curves of Fig. XXVI-2.

There is, moreover, another and independent way in which we can arrive at similar conclusions to those given above. This procedure depends on two observations — one an induction from von Békésy's data and the other of a more theoretical nature. Von Békésy observed[3] in his paper of 1943 that, when plotted on a logarithmic frequency scale, the curves of Fig. XXVI-1 "could be brought into tolerably good coincidence by parallel displacement along the abscissa" except at low frequencies at which there was a progressive "flattening" or broadening. This "flattening" can be largely eliminated by choosing a low-frequency scale somewhat more compressed than logarithmic (Figs. XXVI-1 and XXVI-6). Von Békésy's data are not given for frequencies higher than 2-3 kc, but it is at least plausible that similar performance would continue for higher frequencies; that is, when plotted on an appropriate scale the response curves would be similar except for displacement of their maxima. But of course there is no special reason to assume that the "appropriate scale" is, even approximately, logarithmic. One series of experiments which both suggests that this extrapolation is reasonable and also provides a possible form for the scale is the electrophysiological observation by Kiang and Watanabe[11] of the tuning curves for first-order single units in the cat. These results suggest that the bandwidths of the response curves continue to increase as the frequency of the maximum increases, but at a <u>less</u> than proportional rate so that a scale somewhat more expanded than logarithmic is required to yield similar curves. The dotted extension of the scale of Fig. XXVI-6 is highly conjectural, of course, but, as we shall see, it is partially checked by a requirement for consistency.

Let us represent the scale that gives displaced but similar response curves (Fig. XXVI-6) by $\mu(f)$. Then the assumption that the curves are indeed similar when plotted on this scale is equivalent to assuming that

$$\left| H_x(f) \right| = \left| H[\mu(f) - \nu(x)] \right| \tag{10}$$

where $\left| H[y] \right|$ is a function giving the shape of any one curve and, if we arbitrarily choose the maximum of $\left| H[y] \right|$ to occur at $y = 0$, then $\nu(x) = \mu(f)$ determines the location of the peaks; that is,

$$\nu(x) = \mu[f_{max}(x)] \quad \text{or} \quad f_{max}(x) = \mu^{-1}[\nu(x)]. \tag{11}$$

In addition, and tentatively, we are going to make the still stronger assumption that not just the magnitude curves but also the phase curves — when plotted versus $\mu(f)$ — are similar except for displacement so that

$$H_x(f) = H[\mu(f) - \nu(x)]$$ (12)

and

$$F(f, x) = h(x) H[\mu(f) - \nu(x)] .$$ (13)

There are a number of disturbing features to von Békésy's phase curves which make it somewhat difficult to test this assumption. In the first place, his curves uniformly show the phase angle tending to zero as either f or x tends to zero. It seems probable that this is more an extrapolation than a direct observation, since the amplitudes of vibration — remote from the maximum — must have been extremely small. However, Flanagan[10] has suggested on physical grounds that the phase angle should approach $\pi/2$ radians for low frequencies. This argument is, essentially, that at frequencies that are low enough the flow pattern must be principally a streaming through the helicotrema with the velocity at each point proportional to the velocity at the stapes, that is, leading by $\pi/2$ radians the displacement at the stapes. At these frequencies the dominant pressure effects should, moreover, be due to viscosity, that is, in phase with the velocity, and the most important property at the partition should be its elasticity, so that, finally, the displacement at the partition should be in phase with the pressure difference, and thus lead by $\pi/2$ radians the displacement at the stapes. This is a compelling argument — it is hard to see how it can fail to be correct at sufficiently low frequencies.

But at frequencies for which there is substantial motion at the partition there is no reason why the pressure difference must be more or less in phase with either the velocity (as Flanagan suggests) or with the displacement at the stapes (as von Békésy shows). Still, if the principal pressure drop were across the partition, it is plausible that the phase relation between pressure difference and stapes displacement might be almost fixed, independent of frequency, and consequently the phase angle at $F(f, x)$ might appear to be approaching a constant (not necessarily 0 or $\pi/2$) as f tended to zero (even though ultimately it would have to actually approach $\pi/2$ as the effect of the helicotrema became important).

The presence of the helicotrema is thus a dominant element in Flanagan's argument. However, von Békésy's experiments do not show any obvious effects of the helicotrema down to frequencies as low as 50 cps, or even lower. These results suggest that the simplest model — adequate perhaps even for relatively low frequencies — would be to imagine the cochlea as being extended indefinitely beyond the apex with a smooth continuation of the properties that it has in the apex-base region. And for such an extended

cochlea there is no clear reason why the asymptotic phase angle of $F(f, x)$ need be either 0 or $\pi/2$.

The concept of an extended cochlea is most useful for theoretical purposes because if we assume incompressible fluids, tissues, and walls, then the volume displacement of the stapes must at every instant be equal to the integrated volume displacement of the partition. This assumption implies an interrelationship between the amplitude and phase of $F(f, x)$, which permits another test for consistency. It also provides an absolute indication of amplitude which can be checked against the data of von Békésy. Flanagan[10] has already proposed a different consistency check between the amplitude and phase of $F(f, x)$ which is based on the requirement that $F(f, x)$ must, as a linear system for each x, be both realizable and stable. Such a test is not only somewhat awkward to apply but has the disadvantage that it is highly sensitive to minor changes in even the "tails" of $F(f, x)$, which we certainly can not assume to be accurately known. In contrast, the present test is sensitive primarily to regions in which $|F(f, x)|$ is large.

To formulate this test for a sinusoidal drive, from the definition of $F(f, x)$, we have

$$\text{Re}\left[10 \int_0^\infty F(f, x)\, Ae^{j[2\pi ft+\theta]}\, dx\right] = \text{Re}\left[Ae^{j[2\pi ft+\theta]}\right] \tag{14}$$

or simply

$$10 \int_0^\infty F(f, x)\, dx = 1. \tag{15}$$

Here, the factor of 10 comes from the units of $F(f, x)$. Applying this formula to the representation of (13), we have

$$\int_0^\infty h(x)\, H(\mu(f) - \nu(x))\, dx = 1/10 \tag{16}$$

which must be true for all values of f. Recalling the significance of $\nu(x)$ as given by (11) and the shape of $\mu(f)$ as suggested by Fig. XXVI-6, we find that it is reasonable to assume that $\nu(x)$ is a monotonic decreasing function of x with

$$\nu(x) \rightarrow -\infty \quad \text{as} \quad x \rightarrow \infty \tag{17a}$$

and

$$\nu(x) \rightarrow \infty \quad \text{as} \quad x \rightarrow 0. \tag{17b}$$

If we make the change of variable,

$$y = \mu(f) - \nu(x) \tag{18}$$

$$dy = -\nu'(x)\, dx.$$

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Then (16) becomes

$$\int_{-\infty}^{\infty} \left[\frac{h(x)}{\nu'(x)}\right] H(y) \, dy = 1/10 \tag{19}$$

which can only be independent of f if

$$h(x) \sim \nu'(x) . \tag{20}$$

Equation 20 is rather intriguing because it relates the amplitude factor, h(x), to an apparently independent quantity derivable from a cochlear map. Actually, we can go further; if (20) holds, then we know from the properties of cochlear maps that h(x) will be rather slowly varying compared with $|H[\mu(f) - \nu(x)]|$, so that the maximum of $h(x)|H[\mu(f) - \nu(x)]|$ versus x for fixed f will be nearly at the same point as the maximum of $|H[\mu(f) - \nu(x)]|$ alone, that is, at $\nu(x) = \mu(f)$. Or, in other words, the loci of $x_{max}(f)$ and $f_{max}(x)$ will be nearly the same, as is observed experimentally. Furthermore, we must have, then,

$$g(f) \approx h[x_{max}(f)] \tag{21}$$

and

$$G_f(x) \approx H[\mu(f) - \nu(x)] \tag{22}$$

so that the curves of $G_f(x)$ when plotted against the scale $\nu(x)$ should be approximately displaced replicas of the same curve as $H_x(f)$ plotted against $\mu(f)$, except that they would be turned around. The curve of $\nu(x)$ in Fig. XXVI-7 has been obtained by interpreting the plot of $x_{max}(f)$ in Fig. XXVI-3 as a plot of $\mu(f) = \nu(x)$ with $\mu(f)$ given by Fig. XXVI-6. This curve of $\nu(x)$ has then been used as the scale in Fig. XXVI-2; the extent to which each set of data in Fig. XXVI-2 is a family of similar curves and the extent to which the 1947 set, at least, consists of curves similar to those in Fig. XXVI-1 in both magnitude and phase are gratifying checks on our entire procedure. Finally, $\nu'(x) \sim h(x)$ is plotted in Fig. XXVI-8, which shows that, for large x, h(x) is approximately constant, as has already been deduced on other grounds.

We thus suggest that von Békésy's data may be described, interpolated, and (with some caution) extrapolated by representing the sinusoidal response of the partition in the form

$$F(f, x) = \nu'(x) H[\mu(f) - \nu(x)] \tag{23}$$

so that only four curves need to be given — the scales $\mu(f)$ and $\nu(x)$ (or either one of them and a "cochlear map" that can be interpreted as a plot of $\mu(f) = \nu(x)$), and the response curve $H[y]$ (which, of course, is complex and hence requires two curves). We would suggest that $\mu(f)$ and $\nu(x)$ might typically look like Figs. XXVI-6 and XXVI-7 and that $H[y]$ might look like the dotted curve of Fig. XXVI-1 with the origin of the abscissa

moved to the frequency of the peak. (It might be necessary to make minor additions and adjustments to satisfy Eq. 15.) It must be kept in mind, however, that our arguments for (23) are largely empirical. We are unaware of any serious experimental contradictions (the assumptions are largely supported by cochlear microphonic data,[11] for example), but any curve-fitting model such as this one is completely at the mercy of new experimental evidence.

3. An Analytical Model

At low and medium frequencies and in the corresponding apical region, $\mu(f)$ and $\nu(x)$ (from Figs. XXVI-6 and XXVI-7) can be well approximated by

$$\mu(f) = \log_{10} f - 1.25 \tag{24}$$

and

$$\nu(x) = 3.75 - x; \quad \nu'(x) = -1 \tag{25}$$

or

$$\mu(f) - \nu(x) = \log_{10} f + x - 5. \tag{26}$$

The curve $\mu(f) - \nu(x) = 0$ is an excellent fit to the cochlear map of Fig. XXVI-3, as suggested by Greenwood.[12] For many purposes it would be convenient to have a complete analytical representation for $F(f, x) = -H[\mu(f) - \nu(x)]$. For the application that we have in mind it would be especially valuable if $F(f, x)$ could be easily transformed or integrated with respect to either x or f. This fact and the observation that the skirts of $H[\mu(f) - \nu(x)]$, if it is considered as a function of f, are rather steep to be represented easily by a rational function, has led us away from the type of approximation selected by Flanagan.[10] By a long process of cut-and-try we have arrived at the following functional form, which bears a loose relationship to a formula derived by Zwislocki[13] on fundamental grounds:

$$F(f, x) = k_o\left(\frac{f}{10^{5-x}}\right) \exp\left[-k_1\left(\frac{f}{10^{5-x}} - 1\right)^2 - \left(\frac{f}{10^{5-x}} - 1\right) - j2\pi k_2\left(\frac{f}{10^{5-x}}\right)\right]$$

$$-\bar{k}_o\left(\frac{f}{10^{5-x}}\right) \exp\left[-k_1\left(\frac{f}{10^{5-x}} + 1\right)^2 + \left(\frac{f}{10^{5-x}} + 1\right) - j2\pi k_2\left(\frac{f}{10^{5-x}}\right)\right] \tag{27}$$

where k_o is a complex constant, $\bar{k}_o$ is its complex conjugate, and k_1 and k_2 are real constants to be adjusted to approximate the data and to satisfy (15). $F(f, x)$ as given by (27), is a little different in form from that previously assumed and is not as complicated as it looks. For purposes of manipulation it is desirable to extend the

domain of $F(f, x)$ to include negative frequencies and to arrange that

$$F(-f, x) = F(f, x).$$ (28)

This accounts for the presence of the second term; for any interesting positive frequency it is so small that we can safely ignore it and obtain

$$F(f, x) \approx k_0 \left(\frac{f}{10^{5-x}}\right) \exp\left[-k_1 \left(\frac{f}{10^{5-x}} - 1\right)^2 - \left(\frac{f}{10^{5-x}} - 1\right)\right] \exp\left(-j2\pi k_2 \frac{f}{10^{5-x}}\right).$$ (29)

$F(f, x)$ is a function of

$$\frac{f}{10^{5-x}} = 10^{(\log_{10} f + x - 5)}$$ (30)

as desired. The magnitude of $F(f, x)$, from (29), is approximately

$$|F(f, x)| \approx |k_0| \left(\frac{f}{10^{5-x}}\right) \exp\left[-k_1 \left(\frac{f}{10^{5-x}} - 1\right)^2 - \left(\frac{f}{10^{5-x}} - 1\right)\right]$$ (31)

which, as may readily be checked, has its maximum at

$$\frac{f}{10^{5-x}} = 1 \quad \text{or} \quad \log_{10} f + x - 5 = 0$$ (32)

as required, and

$$|F(f_{max}, x)| = h(x) \approx |k_0|$$ (33)

independently of x in accordance with (25) and (20). Comparing $|F(f, x)| / |F(f_{max}, x)|$ with Figs. XXVI-1 and XXVI-2, we find that the best fit seems to be

$$k_1 \approx 2$$ (34)

(see Figs. XXVI-9 and XXVI-10).

To find k_0 and k_2, we must have, from (15),

$$\int_0^\infty F(f, x) \, dx = 1/10$$ (35)

$$\approx \int_0^\infty k_0 \left(\frac{f}{10^{5-x}}\right) \exp\left(-2\left(\frac{f}{10^{5-x}}\right)^2 + \left(3 - j2\pi k_2\right)\left(\frac{f}{10^{5-x}}\right) - 1\right) dx$$ (36)

Let $y = \frac{f}{10^{5-x}}$, $dy = (\ln 10) y \, dx$, and the integral becomes
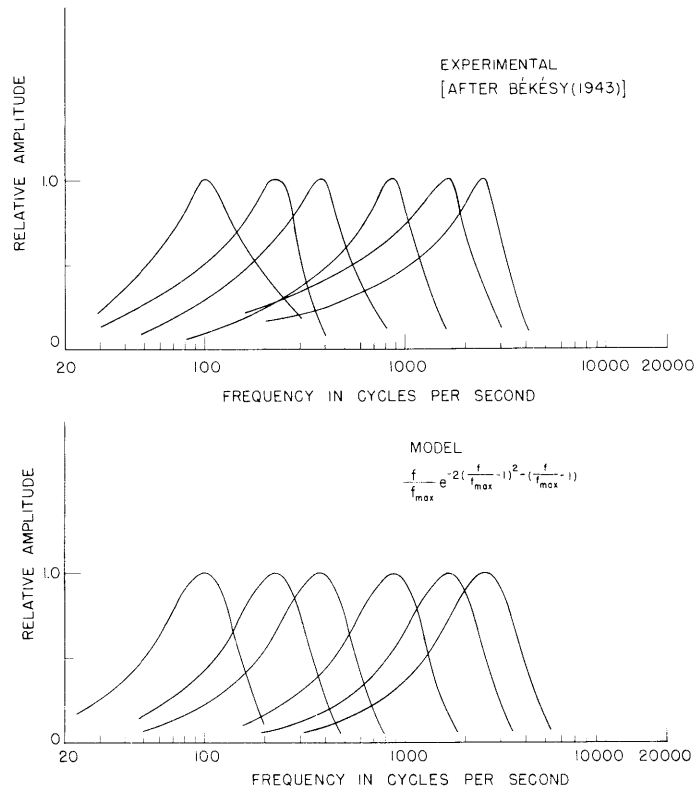
EXPERIMENTAL
[AFTER BÉKÉSY(1943)]

RELATIVE AMPLITUDE

1.0

0

20   100   1000   10000 20000

FREQUENCY IN CYCLES PER SECOND

MODEL

$$\frac{f}{f_{max}} e^{-2(\frac{f}{f_{max}}-1)^2-(\frac{f}{f_{max}}-1)}$$

RELATIVE AMPLITUDE

1.0

0

20   100   1000   10000 20000

FREQUENCY IN CYCLES PER SECOND

Fig. XXVI-9.   Frequency responses for 6 positions along cochlear partition.

RELATIVE VOLUME DISPLACEMENT

--- EXPERIMENTAL (AFTER BÉKÉSY 1947)
—— MODEL

300~   200~   100~   50~

1.0

0

2.0   2.5   3.0   3.5

DISTANCE FROM STAPES (CM)

2.0   2.5   3.0   3.5

π

2π

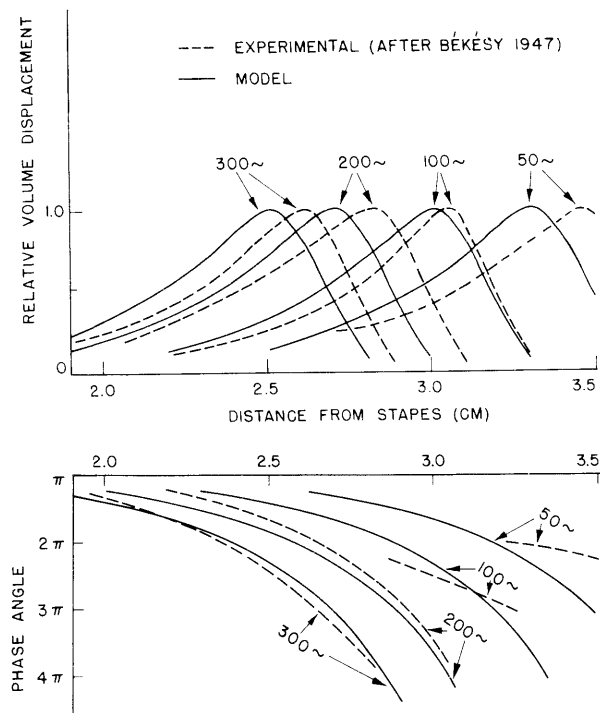3π

4π

PHASE ANGLE

50~

100~

200~

300~

Fig. XXVI-10.   Volume displacement for various fixed frequencies.

255

$$\frac{k_o}{e(\ln 10)} \int_{10^{-5}f}^{\infty} \exp\left(-2y^2 + (3-j2\pi k_2)y\right) dy \tag{37}$$

With an error of less than 10 per cent we may extend the lower limit $\int_{-\infty}$ and evaluate the integral by completing the square in the exponent to obtain

$$\frac{k_o}{e(\ln 10)} \sqrt{\frac{\pi}{2}} \exp\left(+\frac{(3-j2\pi k_2)^2}{8}\right) = \frac{1}{10}. \tag{38}$$

Let

$$k_o = |k_o| e^{j\phi_o} \tag{39}$$

where ϕ_o is the asymptotic phase angle of $F(f,x)$ as f approaches zero for the extended cochlea, as already discussed, and $|k_o|$ is the peak volume displacement per milli-meter per unit stapes volume displacement and has, from von Békésy's data, a value of the order of $1\frac{cc/mm}{cc}$. From (38),

$$|k_o| e^{-\frac{(\pi k_2)^2}{2}} = 0.162 \tag{40}$$

and

$$\phi_o - \frac{3}{2}\pi k_2 = 2\pi n, \tag{41}$$

where n is any integer. If $|k_o|$ is approximately unity, then k_2 can not be much out-side the range

$$\frac{1}{2} < k_2 < \frac{3}{4},$$

which implies a change in phase between $f = 0$ and the frequency at maximum response that is between $-\pi$ and $-3\pi/2$ radians. Since von Békésy's phase measurements are quite precise but might be uncertain by multiples at π, the most reasonable choice for k_2 would seem to be $2/3$, which gives ϕ_o equal, say, to $-\pi$. This choice gives

$$|k_o| = 1.46 \frac{cc/mm}{cc}. \tag{42}$$

The resulting response curves, compared with the data of Figs. XXVI-1 and XXVI-2, are shown in Figs. XXVI-9 and XXVI-10. Multiples of π have been added to von Békésy's phase curves to improve the comparison. The resulting function representing $F(f,x)$
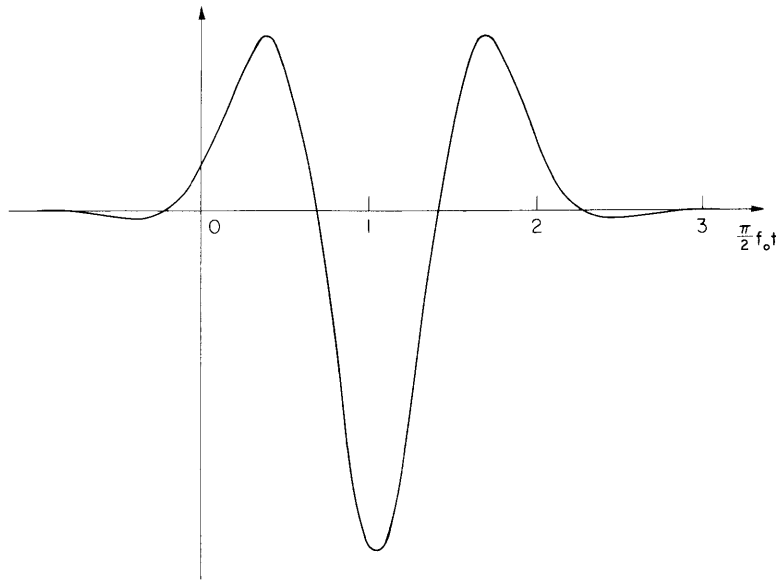
Fig. XXVI-11. Impulse response at point on cochlear partition which responds maximally to frequency f_o. (From Model, normalized.)
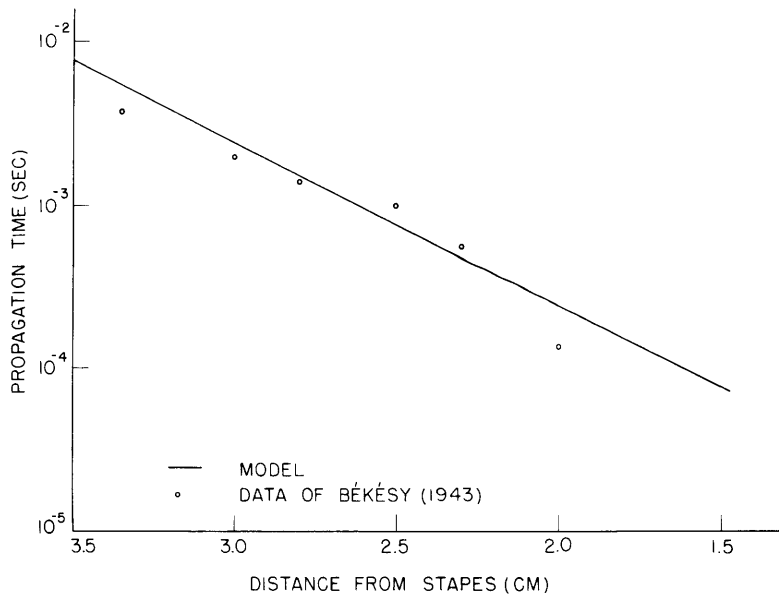

Fig. XXVI-12. Time of propagation of clicks along cochlear partition.

(Eq. 27) can be transformed exactly to yield the response to an impulsive displacement of the stapes.

$$\frac{1}{2\pi} \int_{-\infty}^{\infty} F(f, x)\, e^{j2\pi ft}\, df = -2.03 f_{max}(x)\, e^{-2\xi^2}\, (3/4 \cos 3\xi - \xi \sin 3\xi) \tag{43}$$

where $f_{max}(x) = 10^{5-x}$ and $\xi = \pi\left(\frac{1}{3} - \frac{f_{max}(x)\, t}{2}\right)$. Equation 43 is plotted in normalized form in Fig. XXVI-11. The small "tail" extending into the region $t < 0$ implies that $F(f, x)$ is unrealizable, but this, as we have suggested, is a consequence of the particular form of approximation selected and is not, in our view, very significant.

One final derived quantity is the "travel time for pulses along the cochlear partition." Assuming that the "first deflection" of a given point on the partition as observed by von Békésy corresponds to the time of the first maximum in Fig. XXVI-11, we obtain the delay plot of Fig. XXVI-12 which compares very favorably with his data.[8]

W. M. Siebert

References

1. G. von Békésy's papers have been collected in Experiments in Hearing (McGraw-Hill Book Company, Inc., New York, 1960).

2. Ibid., p. 461.

3. Ibid., p. 454.

4. Ibid., p. 448.

5. Ibid., p. 462.

6. Ibid., p. 442.

7. Ibid., p. 455.

8. Ibid., p. 458.

9. J. L. Flanagan, Bell System Tech. J. 39, 1163 (1960).

10. J. L. Flanagan, personal communication, 1961.

11. N. Y-S. Kiang and T. Watanabe, personal communication, (1961) (to be published).

12. I. Tasaki, H. Davis, and J. P. Legouix, J. Acoust. Soc. Am. 24, 502 (1952).

13. D. D. Greenwood, J. Acoust. Soc. Am. 33, 1344 (1960).

14. J. Zwislocki, Acta Oto-laryngol., Supplement 72 (1948).

B. SOME RESULTS OF COMPUTER SIMULATION OF NEURONLIKE NETS

1. Introduction

There exists little understanding of the behavior of neurons interacting in large numbers. It is true, of course, that experimental knowledge of the behavior of the neuron itself and its relationship with others is still incomplete, particularly in the case

of the dendritic tree. However, enough is known so that reasonable guesses can be made as first approximations. With such approximations as hypotheses we would then like to know if the resulting behavior in any way resembles known experimental findings. Unfortunately, even the simplest and roughest approximations of this kind lead to systems of great complexity and nonlinearity. In such cases it is natural to use a computer for aid in the solution of the problem.

The method used in this study has been to construct, in the Lincoln Laboratory's TX-2 computer, a system of neuronlike elements with specified interactions and connections. These elements or "cells" and their connections have the following properties. Each element has a definite threshold for incoming excitation below which no action occurs, and above which the element "fires." These thresholds are distributed according to a specified distribution (usually normal) over the elements. When an element fires, its threshold immediately rises effectively to infinity, and then, after a short absolutely refractory period, falls exponentially back (relatively refractory) toward its quiescent value. A short time after firing (the situation is the same for every element) an element transmits excitation to all of the other elements to which it is connected. In the present model all of the connections possess the same effectiveness or "weight." The excitation is added to any already present at the succeeding cell, after which the excitation sum decays exponentially to zero. If at any time the excitation exceeds the threshold of the succeeding element, that element performs its own firing cycle and transmits its own excitation. During the firing cycle, the element is said to be "active." Note that, in physiological terms, both "spatial" and "temporal" summation are present, and that the element is "analog," not purely digital. Note also that firing is not forced to be synchronous. External stimuli are introduced by instantaneously adding a large value to the excitation function of each stimulated cell.

The present nets have been given a quasi-planar or sheetlike topology, each cell having a probability of connection with its neighbor which depends on radial distance only. This probability distribution is under the control of the experimenter, and he can select beforehand the type of connection pattern that he wishes to try. The nets used in this study have had 1296 elements, arranged in a 36 × 36 array, and the average number of connections to a cell has varied from 1 to 50, or more.

After the computer program assigns connections according to the desired probability distribution, and other net parameters are fixed, the operator may choose the elements that are to be stimulated initially by means of a photoelectric device on the TX-2 oscilloscope face that displays the array of cells. The computer then proceeds to calculate the resulting activity by using time increments that usually correspond to one-half the absolutely refractory period. Each such time increment actually takes approximately 1 second in computer time for the 36 × 36 -element networks. Decay-time constants of the relatively refractory period have been in the range of from 0 to 10 times

the absolutely refractory period. Activity is indicated for the experimenter by brightening the spots corresponding to fired cells.

2. Tightly Coupled Nets

For qualitative description of observed behaviors, it is convenient to divide the networks roughly into two classes — nets with tightly coupled connections, and loosely coupled nets having relatively long connections. Tightly coupled nets tend to produce well-defined "dense" wave fronts, and the loosely coupled tend to oscillate diffusely.

Nets with tightly coupled connections were the subject of a previous paper,[1] so they will be described only briefly here. If each element of the net is connected only with its immediate neighbors, and a single stimulus is given to a few neighboring cells, a "wave" of activity (fired cells) is generally seen to progress away from the site of the stimulus. As long as only one stimulus is given, or if it is repeated at long intervals, the wave fronts form expanding rings much like those formed by a pebble dropped in a pond. No reflections are observed at the edge of the net. Each wave "pushes" before it a precursor of excitation which has not yet fired cells, and furthermore, leaves behind it a "trough" of refractory cells. Thus if waves interact from a rapidly repeating source or from multiple sources, the interaction will be very nonlinear. A rapidly repeating stimulus may produce, not rings, but a very complex "broken" field of wave fronts, which may continue to re-excite itself after the stimulus stops. If multiple stimuli exist, waves of activities may appear which are not produced when the stimuli are given one by one. This behavior can give the effect of inhibition, since the addition of a stimulus can cause some cells to stop firing. Many different "modes" of self-excited oscillation are possible. A particularly pervasive and striking one consists of one or more continuously rotating spirals. The arms of a spiral maintain such a distance that the refractory trough lies between them.

It has been found possible to obtain a measure of control over the activity by changing the mean threshold of cells by external means. Obviously, if the thresholds in a set of cells are made high enough, no activity can invade it, so that complete inhibition results. Conversely, if thresholds are lower, propagation of activity is made denser and faster. It is therefore possible to exert a control over timing and firing of particular cells or sets of cells. In certain cases the activity circulates repetitively, so that a periodic or nearly periodic firing pattern continues until thresholds are changed.

Beurle[2,3] discussed tightly coupled nets of this general type. He pointed out that in an uncontrolled net, waves of activity tend either to decrease with distance and time or to increase until they become "saturated," that is, activating all of the cells as they pass. We have seen examples of both kinds of behavior.

3. Loosely Coupled Nets

If there are significant numbers of connections that are long enough to reach beyond the refractory trough of a wave, then "backfiring" behind waves can occur. In such a case, the wave fronts become fuzzy, or may not be apparent at all, with activity occurring diffusely over the whole net. The definition of "loosely coupled" thus depends upon the relative values of connection and refractory trough lengths, which in turn depend on connection delay time and refractory time constants. If the net constants are such that the connections are just long enough for backfiring to take place, the whole net will usually oscillate diffusely after a single stimulus. The oscillation may continue indefinitely, or may sometimes stop spontaneously after a burst of a few or many cycles, particularly if the net is on the edge of oscillating. It is easy to understand this behavior qualitatively. A few cells initially stimulated cause more to fire, which in turn fire others in an increasing sequence. This increase continues until a large proportion of the cells are in a refractory state; firing must then decrease progressively until the refractory cells have recovered, and then the cycle recommences if there is still activity in the net. Thus, if the total number of cells that are firing is plotted as a function of time, a roughly periodic function results. The waveform of the oscillation is not sinusoidal, but is considerably smoother than waveforms usually associated with "relaxation" oscillations.

Allanson[4] set up difference equations for a similar net but with completely random interconnections and other simplifications. He was not able to solve the equations because of their nonlinearity, but he was able to predict oscillations and work out some numerical solutions.

There is a number of other features of loosely coupled net behavior which are of considerable interest. Some exist because multiple modes of oscillation are possible. During oscillations activity may be spread diffusely and evenly over the net, and rise and fall more or less in phase everywhere. This "normal" mode gives rise to the large amplitude oscillations just discussed. However, modes in which activity transfers from place to place in the net are also possible. Such modes do not show large amplitude fluctuations on total activity-vs-time plots because many cells are always firing. In fact, the total number of cells firing may remain almost constant, and hence very little change in output is observed. Because the cells that will fire at the next instant depend on the particular cells fired at the present instant, as well as past history, the modes are coupled, and activity can transfer from mode to mode. (This language, borrowed from linear-oscillator terminology, is, of course, only a descriptive analog.) The result of this mode changing upon the total firing-vs-time plot, is that irregular amplitude modulation of the oscillation takes place, but the period remains the same. The net may therefore show irregular "bursts" of rhythmic oscillations,
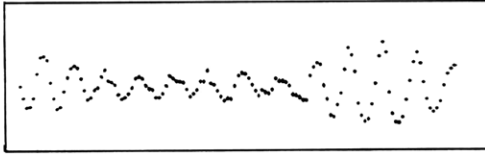
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Fig. XXVI-13.

Network oscillation showing amplitude-modulated rhythmic burst. A single small stimulus was given to start the oscillation that continues indefinitely in this manner.
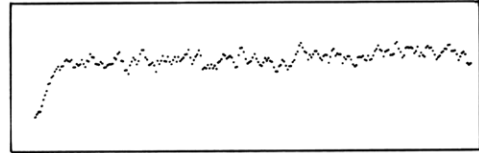

Fig. XXVI-14.

Activity in network without pronounced rhythmicity. A single stimulus, given at the beginning of the trace, produced the initial rise at the left.
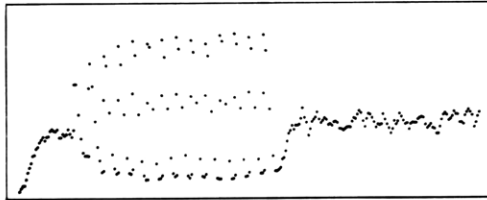

Fig. XXVI-15.

Response of the network shown in Fig. XXVI-14 when stimulated with a burst of 14 stimuli at its "resonant" frequency. The burst starts a short time after the initial stimulus. An expanded time scale is shown in Fig. XXVI-16 for better time resolution.
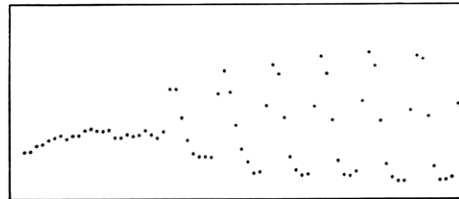

Fig. XXVI-16.

First few responses of Fig. XXVI-15 on an expanded time scale. Note "augmenting" responses.

and this behavior continues indefinitely. Figure XXVI-13 shows a short section of such a graph photographed from the output oscilloscope of the TX-2. The total number of cells firing is plotted vertically, and the discrete time instants horizontally.

For any oscillating system, it is of great interest to know what determines the period of the oscillations. In the present case the period is a complex function of refractory time constant, length of connections, and excitatory time constant, and it has not yet been possible to unravel the details. However, it appears that the following explanation is qualitatively correct. The primary determinant of the period is the refractory period itself. This fact can be demonstrated by eliminating the relative refractory period. Then, if the net oscillates in the normal mode, its period is the same as the absolute refractory period. With the exponentially decaying, relative refractory period in effect, the oscillation period ordinarily lies somewhere between the absolutely refractory period and the end of the relative period. However, the oscillation period will not increase indefinitely as the exponential time constant is increased because, as we have seen, the possibility of "backfiring" will eventually disappear, and the net will fail to continue oscillating. Thus, the connections must be lengthened to obtain a longer period. We have not yet studied the effect of transmission delay time, preferring still to keep the model one in which delay time is small compared with the other times. Thus far, we have assumed an excitatory time constant that is much smaller than the refractory period. If this becomes large, it may have the seemingly paradoxical effect of decreasing the period of oscillation because excitation builds up over all of the net and cells begin to fire earlier upon the decay of their relative refractory period.

Our discussion has indicated that the oscillation period is quite independent of network size and shape, amplitude of oscillation, and initial stimulus, and partly independent of the connection lengths and excitation time constant as long as they are not extreme. These predictions are borne out by observation, at least to a first approximation, although it must be kept in mind that these are conclusions from preliminary data. The period is not precisely constant from peak to peak; in fact it may vary 20 per cent or 30 per cent, and the variation of average frequency over a long period of time has yet to be investigated.

The precise course of the activity during oscillation depends on the cells that are initially stimulated, and small differences in inital stimulus or small changes in net parameters cause large differences in activity pattern, or even in the total activity plot after some time. The assumption is, of course, that there is no "noise" in the system in the form of random firing. If noise is present, as it will be in a real system, the oscillation will eventually lose its dependence on initial stimulus just as it would in any oscillating system. Hence the usefulness of this effect in small-difference detection will depend on the amount of noise present, as well as on the method of detection. The same thing is true if some function of activity is used for classification of stimuli. These

matters require further investigation.

We have been discussing networks that are set in oscillation by a single stimulus. There are also interesting behaviors to be observed if networks (with self-excited activity already started) are given further stimuli. In the first place, it might be expected that an oscillating net can be synchronized or "driven" by a repeated stimulus near its natural period. This is, in fact, the case, if the stimulus is not too small or too large. If it is too small, it will do nothing; if it is too large, the first stimulus may put too many of the cells in a refractory state and stop all activity.

Some nets, if the refractory and excitatory periods are below optimum for normal oscillations, will produce self-excited activity that shows little or no evidence of periodicity (at least to the naked eye). The total activity-vs-time plot of one such net is illustrated in Fig. XXVI-14. If such a net is stimulated periodically with a diffuse constant stimulus, the average amplitude of the responses after the first few varies with frequency in a manner somewhat similar to an ordinary resonance curve, with peak response occurring at a frequency that is determined by the refractory period. The stimulus must be above a certain threshold for this effect to take place. Furthermore, at or near the resonant frequency, the first few responses build up, or augment, to a maximum level, after which the responses may stay more or less constant (especially with large stimulus on-resonance), or they may wax and wane. Figure XXVI-15 shows this in the same net that is illustrated in Fig. XXVI-14. A stimulus train was started soon after the net had achieved its normal level of self-excited activity. Note that although it takes several responses to build up to a maximum, the response in this net ceases immediately after the response to the last stimulus. Figure XXVI-16 shows the first few responses shown in Fig. XXVI-15 which have been expanded in time. At stimulus frequencies that are multiples or submultiples of the resonant frequency, the response may synchronize with the stimulus, may "skip" stimuli, or move from one to another of these modes. Since the second response of a series may be either larger or smaller than the first, the size depending on their separation, as indicated by the type of experiment discussed above, it is of interest to measure the size of the second response as a function of separation when there are only two stimuli in a "train."

In Fig. XXVI-17 are shown the results for one net. The amplitude of the second response relative to the first is plotted as a function of separation. Each point is an average of 10 trials to reduce fluctuations introduced by differing initial conditions in the spontaneously active net. The dotted part of the curve is not well established, because of time-resolution limitations of the present calculation. The second response amplitude performs a decreasing oscillation about the amplitude of the first.

Thus the nets produce at least three interesting results upon stimulation which are related. Their relation may be understood qualitatively as follows. In general, if a large group of cells in an active net is stimulated from outside, not all will fire because
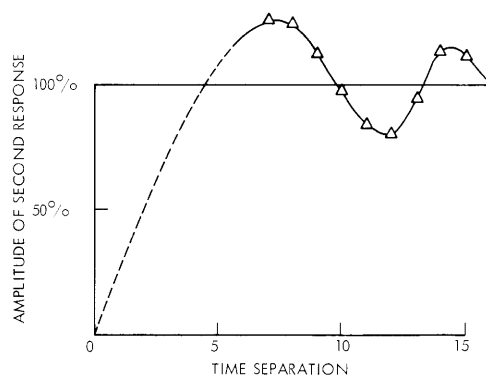
Fig. XXVI-17. Amplitude of response to second stimulus (per cent of first response)
as a function of separation of stimuli. The two stimuli were given to
a spontaneously active net similar to that shown in Fig. XXVI-14.

many will be refractory. After waiting a proper length of time, those cells fired by the
stimulus will have recovered (except for some that may have been refired internally)
and, also, those that were refractory at the stimulus time will be available (except for
some that may have been refired internally). Thus, if the ratio of stimulated cells to
internal average firing rate is large enough, we may expect a second stimulus, given at
the proper time, to fire a larger number of cells than the first. The "transient" intro-
duced by a stimulus may go through several "cycles," which accounts for the variation
of amplitude of a second response with time separation. At the right period, the aug-
mentation of response may last for several responses, whereas at other periods, the
second and later responses may remain smaller than the first. Therefore a peak of
amplitude vs frequency can occur if the first few responses are ignored. The "resonance"
phenomenon, augmenting responses, and two-stimulus response variation, can therefore
all be viewed as consequences of the refractory properties of the units.

4. Discussion

It is clear that the model has interesting and sometimes unexpected properties even
when it is considered solely as an abstract system for study. However, it is also evi-
dent that there are qualitative similarities between the behavior of the model and some
experimental findings in electrophysiology. One's attention is particularly drawn to the
oscillatory and response behavior of the loosely coupled nets which is reminiscent of
several well-known "slow-wave" phenomena, notably the EEG, and the "recruiting"
and "augmenting" responses. That "reverberating" refractory mechanisms of the kind
studied here might account for some of these phenomena is, of course, not a new idea
in physiology. Related ideas have been suggested, for example, by Verzeano, Lindsley,
and Magoun.[5] (See also Walter[6] for a review.) Allanson[4] also suggested that oscillations

of the diffuse type might be related to the EEG. The fact that the nets can exhibit burstlike rhythmic activity and irregular waves, as well as simple oscillations, makes the resemblance even more striking. The synchronizing or "driving" phenomenon may perhaps also be cited as an additional similarity. It is somewhat difficult to separate "driving" behavior from response to stimulation, and this requires more study. This is, of course, also true of EEG driving behavior.

Similarities to aspects of the "augmenting" and "recruiting" responses may also be seen by reference particularly to Jasper,[7] and to Purpura and Housepian.[8] The increase of the first few responses and the sudden cessation of response can occur in both net and electrophysiological experiments. The same is true of waxing and waning of the response under certain conditions. Rosenblith[9] and Freeman[10] have observed physiological "resonance" curves of response amplitude. It is interesting that augmenting and two-stimulus oscillations were also present in the same systems. The two-stimulus experiment is analogous to the "two-click" experiments that have been previously studied in physiological acoustics. Rosenzweig and Rosenblith[11] observed oscillations of the cortical response to the second click of a two-click stimulus as a function of time separation.

In summary, at least the following similarities between the loosely coupled networks and electrophysiological phenomena have been observed:

(a) Oscillations with burstlike amplitude modulation,

(b) "Synchronization" of oscillations,

(c) "Resonance" of response amplitude,

(d) Augmentation of responses — sometimes with amplitude modulation, and

(e) Oscillatory variation of the second of two responses vs time separation.

Some effects observed on stimulation at multiples and submultiples of the resonant frequency may be common to both model and experiment. These similarities are still, for the most part, qualitative, and a great deal more theoretical and experimental work will be required before it can be determined whether systems with the properties of the model exist (among many others) in the brain, or if the similarities are merely remarkable coincidences.

B. G. Farley

References

1. B. G. Farley and W. A. Clark, Jr., Activity in networks of neuron-like elements, Proceedings of the Fourth London Conference on Information Theory, edited by Colin Cherry (in press).

2. R. L. Beurle, Properties of a mass of cells capable of regenerating pulses, Trans. Roy. Soc. (London) B240, 55 (1956).

3. R. L. Beurle, Storage and manipulation of information in the brain, J. Inst. Elec. Engrs. (London), p. 15, February 1959.

4. J. T. Allanson, Some properties of a randomly connected neural network, Information Theory, edited by Colin Cherry, (Academic Press, New York, 1956), p. 303.

5. M. Verzeano, D. B. Lindsley, and H. W. Magoun, Nature of recruiting response, J. Neurophysiol. 16, 183 (1953).

6. W. G. Walter, Intrinsic rhythms of the brain, Handbook of Physiology: Section 1. Neurophysiology, Vol. I (American Physiology Society, Washington, D.C., 1959), p. 279.

7. H. H. Jasper, Unspecific thalamocortical relations, Handbook of Physiology: Section 1. Neurophysiology, Vol. II (American Physiological Society, Washington, D.C., 1960), p. 1307.

8. E. P. Purpura and E. M. Housepian, Alterations in corticospinal neuron activity associated with thalamo-cortical recruiting responses, EEG Clin. Neurophysiol. 13, 365 (1961).

9. W. A. Rosenblith and G. Ricci (unpublished data obtained at the University of California at Los Angeles, 1955).

10. N. S. Freeman, Repetitive electrical stimulation of prepyriform cortex in cat, J. Neurophysiol. 23, 383 (1960).

11. M. R. Rozenzweig and W. A. Rosenblith, Responses to successive auditory stimuli at the cochlea and at the auditory cortex, Psychol. Monogr. 67, 1-26 (1953).

C. A THREE-DIMENSIONAL OPTICAL ILLUSION

This report describes briefly a set of three-dimensional optical illusions that were discovered after consideration of certain properties of the classical plane-figure "illusions" such as the Necker cube, Schröder staircase, and so on.[1] These plane figures share the following properties. (a) They are drawn with certain sets of lines parallel and certain angles as right angles; and (b) they are intended to represent three-dimensional objects with certain geometrical regularities, such as a cube or stairsteps. These figures are not actually illusions, but truly ambivalent; that is, each reading of one of the figures has equal status as a three-dimensional object that might give this plane projection. However, no three-dimensional object with the assumed regularities could project into the plane figure that is usually drawn if a perspective view were made. For example, the forward edges of a cube would be drawn as longer lines than the edges at the back of the cube, so that certain of the lines representing parallel edges of the object can not be parallel in projection. Furthermore, the sets of objects for which the view drawn on the paper could be a perspective view depends on the position of the observer relative to the illustration.

Taking these properties of two-dimensional drawings, together with the fact that observers report these objects as a cube or staircase, and so forth, I would conjecture that the observer has learned to see the regular geometry even in this incorrect (from the point of view of perspective) representation. These factors also suggest that human beings trained to interpret plane illustrations as three-dimensional objects have learned to see pictures without regard to self-localization.
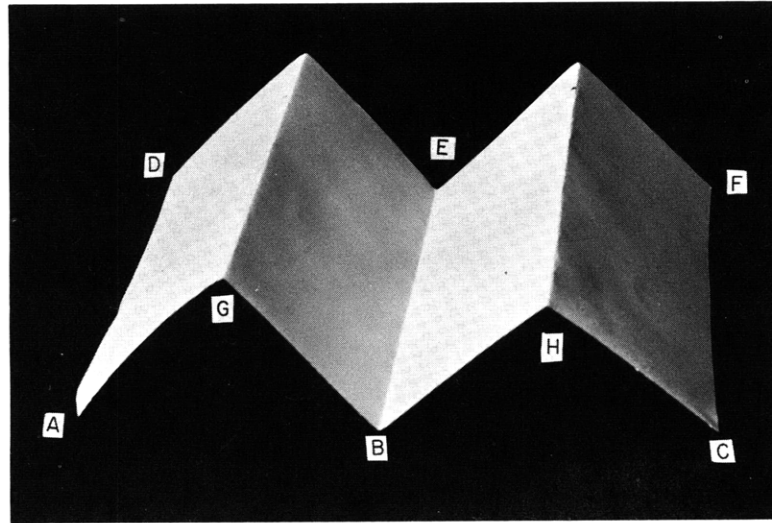
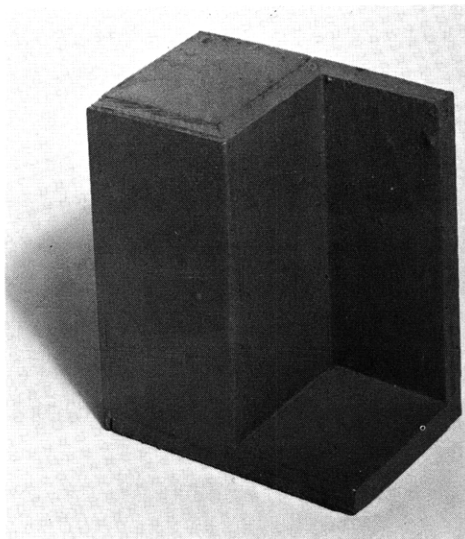Fig. XXVI-18.   The three-dimensional model of the Mach illusion.

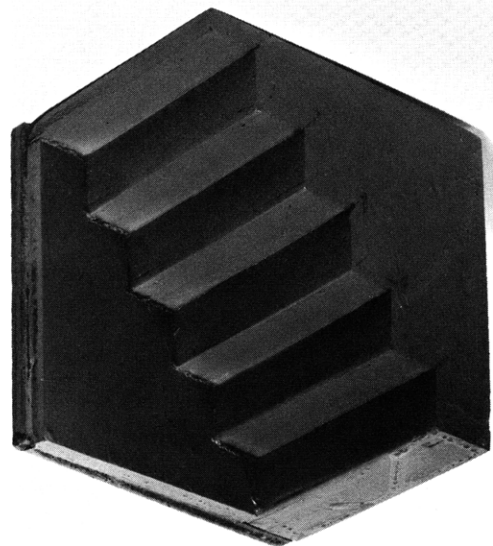Fig. XXVI-19.   The three-dimensional model of the Thiery figure.

Fig. XXVI-20.   The three-dimensional model of the Schröder-Wundt staircase.

These ambiguities can be eliminated by constructing three-dimensional models of the objects that the plane drawings represent. Accordingly models were constructed for some of the figures, and photographs of three of these appear in Figs. XXVI-18, 19, and 20.

Some of the psychologists who have been concerned with the plane figures mentioned above were also aware of the possibility of seeing three-dimensional objects in illusory forms. In large part, their discussions of such illusions are cursory. Mach[2] has the most extensive discussion. The particular illusion that he described is obtained with an object that is essentially one-half of the object shown in Fig. XXVI-18. However, he gave an incomplete description of the properties of the illusion and stated that he found no satisfactory explanation for it.

Since the illusion in Fig. XXVI-18 was the easiest to construct, its properties will be discussed in this report. However, it appears that the others behave in essentially equivalent ways.

To make this figure, take a piece of paper approximately 4 × 10 inches (half a sheet of 8 × 10-inch lined paper is quite suitable). Fold it into four contiguous rectangles, each 4 × 2.5 inches. Set it down on any flat surface and observe it from approximately 2 feet above and 2 feet ahead of the leading edge of the paper. No particular lighting arrangement or background is required.

The subject is asked to close one eye and to concentrate on the central groove. The subsequent instructions have varied slightly, but, most frequently, success has been obtained by asking the subject to imagine that the back corner of the central groove is closer to him than the forward corner.

If the subject sees the illusion he will report that the paper is standing up, usually at a peculiar angle. He is then asked to move his head from side to side or backward-and-forward. At first, he may lose the illusion when he tries to move his head. Usually he will be able to hold it during movement and will generally respond by saying, "It moves," "It wiggles," "It oscillates," or some such remark. It is assumed that if he makes this response he has been seeing the illusion, since the ability to move or dis-tort physical objects by moving one's head is not a common experience.

This illusion has been shown casually to several hundred people. Approximately 80-90 per cent of them reported that they saw the illusion. Some observers report seeing it almost immediately after being instructed. Others take several minutes, although once seen it is quite easy to repeat. Since most demonstrations were done casually, it was not usually possible to investigate the observers who could not see the illusion. However, in approximately one dozen cases, observers were willing to try for many minutes while being given various other instructions and suggestions for eliciting the illusion. Under these circumstances, perhaps two-thirds of this class of observers were able to see the illusion.

The reports of observers indicate the following principal properties for the illusory view. No attempt is made in the following list to report only those that appear to be independent. Indeed it is likely that most of these properties have a common explanation.

(i) The perception of depth is quite compelling.

(ii) The judgment of depth is correct for the three forward points on the table, A, B, and C in Fig. XXVI-18 but incorrect for all of the others; some appear to be closer and some farther than they actually are. If the subject is asked to touch one of the "upper" points with a pencil he will miss the center point, E, and the two sidemost corners D and F (stopping the pencil several inches short of the goal) as well as the second, G, and fourth point, H, on the "bottom" (striking the figure before he would expect to).

(iii) The object distorts when the subject moves his head.

(a) If the head is moved sideways certain points move with the observer, others in a direction opposite to the head movement.

(b) If the head is moved forward, the object seems to bend away, and if the head is moved backward, the object seems to bow toward the observer.

(iv) If the object is moved while the observer's head is still, motion will be observed but it is different from the motion reported by an observer who is not seeing the illusions. For example, a rotation of the object about a horizontal axis normal to the observer's line of sight will be reported as having the upper portion of the figure rotating away while the object would be observed by the experimenter as rotating toward the observer.

The bizarre apparent motion of the illusion is particularly striking when the test object is held in the subject's hand and he is asked to move it. The apparent motion is quite inconsistent with the motions of the hand, although the subject is able to accommo- date to the inconsistency with a few minutes of practice.

(v) If the observer is asked to move his head until the center line is standing per- pendicular to the table, his line of sight to the leading end of the center line makes an angle of approximately 45° with the plane of the table.

(vi) The observer reports that the edges of the object are no longer parallel; that is, the plane surfaces now appear to be rhomboids and not rectangles. This is parti- cularly easy to see if the paper used in making the model is lined parallel to the folds. In this case it is reported that the lines are wider apart at the "bottom" of the object than at the "top."

(vii) Certain objects can be added without destroying the illusion. If one or two pipe cleaners or a rubber band are placed on top of the figure the illusion can still be erected. In this case the pipe cleaners will appear to be floating in mid-air. When the observer moves his head, the object will appear to move while the pipe cleaners stand still.

(viii) If a pair of test objects are placed close to one another, or one above the

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other, then they can be independently inverted. In like manner three such test objects may be observed in any of the eight permutations, although certain of these configurations may be more difficult than others.

(ix) Words, colors, or patterns on the paper do not prevent successful erection of the illusion. The object has been made of newspapers, magazine illustrations, time-tables, and so forth. In each case, an observer who has been successful on the simpler object has no difficulty with these other objects. It should be noted that such objects may be seen entirely in focus; newspapers being as easy to read in the illusory as the real form.

Shadows, whether stationary or moving, are usually insufficient to destroy the illusion or prevent its erection. It was observed by Mach, and it is also observable in this illusion, that the test object in its illusory mode appears to be translucent with the light coming from behind the object. However, this judgment regarding the position of the light source is not necessarily consistent with the shadow pattern.

(x) There is no need for parallelism in the folds or for straight-line edges. Objects have been prepared by tearing a jagged piece out of a newspaper and making three folds at random angles. These objects can be seen in the illusory form as easily as the regular figure by a trained observer. (Training simply consists of permitting a naive subject to practice with the less complicated object for a few minutes.)

(xi) The four principal planes can be broken into many smaller ones without inhibiting the illusion. Thus, the object shown in Fig. XXVI-18 can be crumpled up and straightened partially, as in Fig. XXVI-21. In this circumstance, it is interesting to note that each of the smaller planes invert so that every dimple in the actual object appears to the observer as a protuberance and vice versa. In this instance there appears to be some requirement for keeping some semblance of the original object. Most of the randomly crumpled paper objects are either uninvertible or else only partially invertible.

(xii) An object which can be observed in the illusory mode — but which is more difficult to invert — can be made with no planes at all. The clay object seen in Fig. XXVI-22 was molded into a rough resemblance to the basic test object. In this case the illusion appears to be the mold of a casting with razor-thin edges turned toward the observer. As before, all of the minor, as well as major, contours are inverted and the object appears to move as the observer moves.

(xiii) Saccadic eye movements will generally destroy the illusion. When the subjects are moving their heads and holding the illusion, it would appear that their eyes are in a tracking or pursuit mode exactly as if they were watching an object moving across the field of view.

(xiv) Binocular vision destroys the illusion for almost all of the subjects. Some observers have stated that they could see it with both eyes. It may be that either one
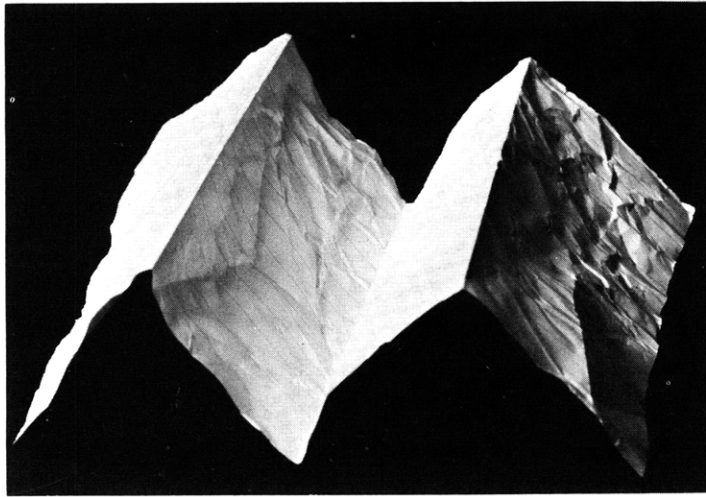
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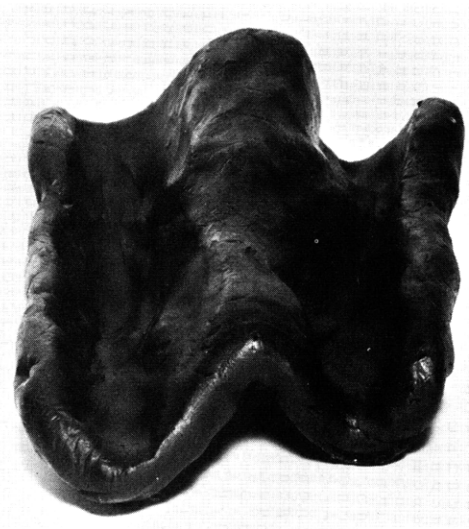Fig. XXVI-21. A crumpled version of Fig. XXVI-18.

Fig. XXVI-22. A clay-model crude approximation to Fig. XXVI-18.

eye is overwhelmingly dominant or else some of these observers defocussed their eyes so that they were seeing two independent and unfused images.

(xv) Observation of some portion of the underside of the object prevents the illusion from being erected and usually destroys the illusion if the observer reaches such a position in moving his head. Presumably this is because such a view requires acceptance of a discontinuity in the surface.

(xvi) Occasionally a subject will report that he has inverted only two planes of the figure. In this case only the inverted planes appear to move. The joint between the two portions of the perceived object appears to stretch and distort "like a rubber sheet."

(xvii) The ease with which such figures can be inverted depends in some way on the surroundings. Thus, a figure that is mounted on a long pin so that it is well above the table is easier to invert. A figure whose corners are tacked to the table does not appear to be invertible.

Although no controlled experiments have been performed yet, the following general comments seem justified. Whatever perceptive cues are responsible for the illusory perception, they can not be any of the more commonly described cues. Thus, the illusion goes counter to perspective, to lighting, to learning (insofar as our familiarity with right angles and parallel lines can be called "learned"), to the presumption that objects stand still, to physical reality at least with regard to the fact that the object rests on the table in highly unstable configurations, and to focusing, since the observer can focus equally well on any part of the surface even though his judgment of relative distance goes counter to the lens adjustment that his eye must make.

The geometrical relation between the real object and the apparent object is subject to experimental investigation. Although these experiments have not been conducted in a quantitative fashion, the following conjecture is proposed as a first approximation to a satisfactory explanation.
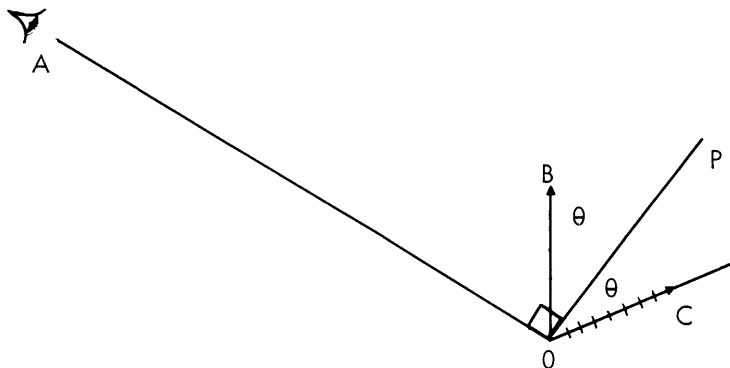

Fig. XXVI-23. Sketch of proposed geometric transformation rule. (AO, line of sight; OB, orientation of one edge of object; OP, perpendicular to line of sight; OC, apparent position in the illusory mode.)

Consider some line element in one surface of the object and in the plane of the line of sight (Fig. XXVI-23). If the perpendicular, OP, to the line of sight, AO, makes an angle θ with the line element, OB, then the line element of the illusion, OC, will make an angle of $90° + \theta$ with the line of sight. Note that the length of each of these line elements is the same. No other transformation will provide this invariance. Note, too, that the line of sight will make different angles with different portions of an extended line on the surface of the object so that the inclination of the illusion must also vary. Finally, if continuity is to be maintained, then only on a single sphere perpendicular to the line of sight can the distance to the eye be correctly judged. Usually this sphere includes the leading point on the central groove. The two other leading points on the table are so close to their correct position in the illusory form that it is doubtful that any errors in judgment could be demonstrated for them.

M. Eden

References

1. E. B. Titchener, Experimental Psychology (Macmillan Company, New York, 1927), Vol. 1, pp. 153-156.

2. E. Mach, Contributions to the Analysis of the Sensations, translated by C. M. Williams (The Open Court Publishing Company, Chicago, 1910); see especially pp. 95-108.

D. THE RELATIONSHIP AMONG "PHOTIC DRIVING," RESPONSES TO SINGLE FLASHES, AND THE RESTING EEG

[Editor's note: This report is based on a paper written by the present author with Dr. Jan Trabka (Visiting Rockefeller Fellow (1959-1960) from the University of Krakow, Poland, with Dr. Mary A. B. Brazier at the Neurophysiology Laboratory of the Neurological Service, Massachusetts General Hospital) and presented at the Fifth International Congress of Electroencephalography and Clinical Neurophysiology, held in Rome, September 7-13, 1961.]

In descriptions of the effect on the EEG of intermittent photic (for example, stroboscopic) stimulation, the terms "photic driving," and "entrainment" have been widely used, but the nature of the phenomena that were being described has not been completely clear. The elucidation of this problem is complicated by the fact that, for some subjects, in response to slowly repeated flashes, there is a rhythmic "afterdischarge," that is, a series of rhythmic waves, the frequency of which may be very close to that of the resting EEG.[1]

In an attempt to clarify further, in the occipital EEG, the distinction between the events specifically evoked by intermittent photic stimulation and entrainment in a strict sense (that is, alteration of the intrinsic frequency of a self-oscillatory system to that of an externally imposed "entraining" signal), EEG recordings were made of a group

of six normal subjects at rest and during stimulation, by means of a stroboscope, at a number of rates between 0.7 and 30 flashes per second. Events in the EEG that were time-locked with the flashes were detected by means of electronic averaging, with the aid of the ARC-1 average-response computer. The average frequency of the resting EEG was determined by means of autocorrelation. The results of the study of recordings from four subjects are reported here.

In Fig. XXVI-24 are shown the results of photic stimulation of one of the subjects (S.L.). The flash rates are indicated in the center of the figure, and 4-second excerpts from the total of 30 seconds of EEG which are analyzed are shown on the left. For the averaging of responses to photic stimulation, the results of which are shown on the right, 75 successive blocks of time of 400 msec each were averaged (the ARC-1 computer being triggered successively by the flash occurring after the end of the preceding epoch). In this way, the number of responses was kept constant, and hence the amplitude calibration remained fixed for all of the flash rates.
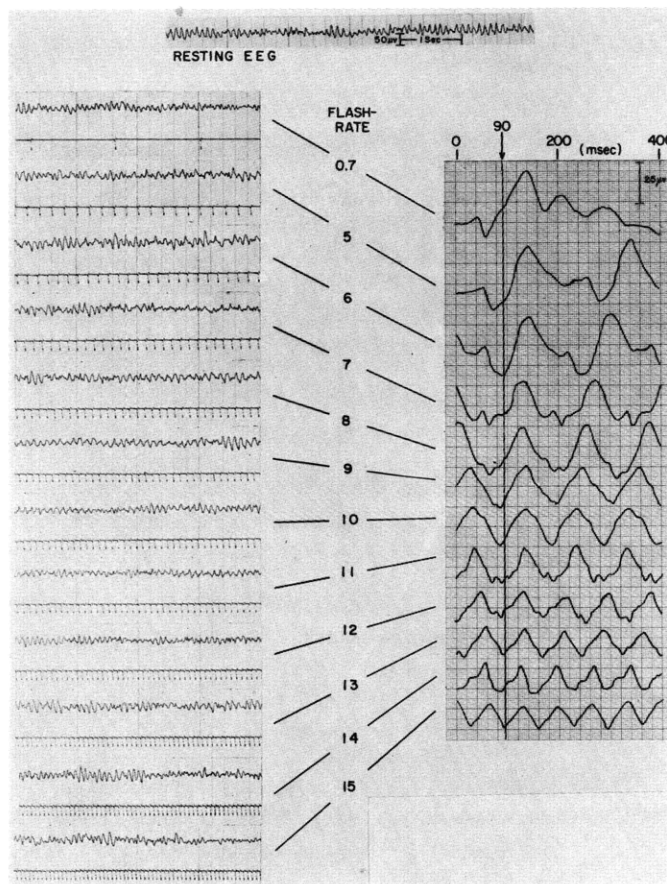

Fig. XXVI-24. Midline parieto-occipital EEG responses to photic stimulation. (Duration of recording analyzed for each flash rate, 30 sec.)

For a flash rate of 0.7 per second, there is a prominent downward (occiput-negative) component with a peak at approximately 60 msec, which is followed by a prominent upward (occiput-positive) deflection, the peak of which occurs at approximately 140 msec. It is evident that the upward deflection, beginning at approximately 90 msec (indicated by the vertical arrow in the figure), and ending at approximately 160 msec is also present for all of the higher flash rates, There is some suggestion that the latency of this event is shortened slightly for flash rates of 7 and 8 per second.

Results from similar recordings for three other normal subjects are shown in Fig. XXVI-25. Vertical lines have been drawn in at the latencies indicated, and these represent, for each subject, the onset of a component of the averaged response that is present for all flash rates. For these three subjects, there is also a suggestion of a slight advance in latency of the onset of the constantly appearing component; for subject D.G. the suggestive advance occurs at flash frequencies of 9 and 10 per second; for subject J.T., at 10, 11, and 12 per second; for subject E.G., at 10 and 11 per second. For subject E.G. there is also a slight suggestion of an alteration in the latency of the onset of the constantly appearing event for flash rates of 18 and 20 per second.

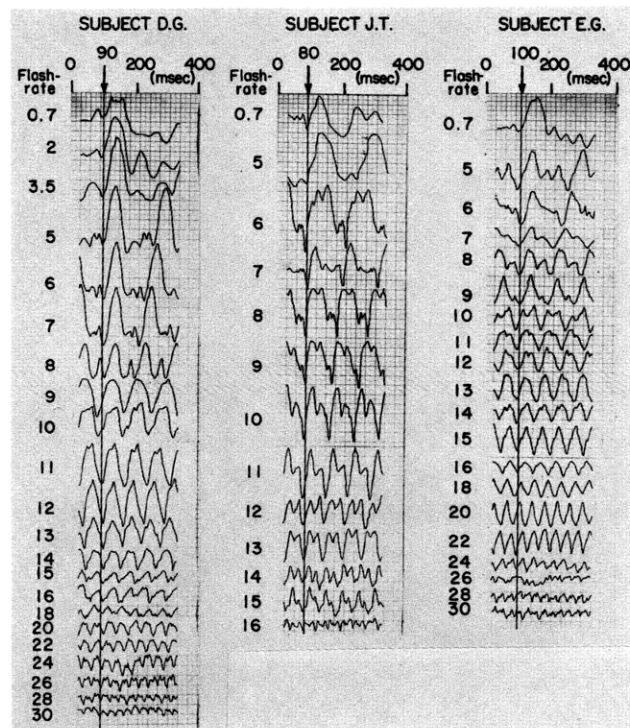These results suggest that for the higher flash rates there is a relatively fixed delay,

Fig. XXVI-25. Midline parieto-occipital EEG responses to photic stimulation for three normal subjects. (Duration of recording analyzed for each flash rate, 30 sec.)

of some nature, of approximately 90 msec before the appearance at the cortex of the major part of the effect of the flash. Neurophysiologically speaking, because of this relatively long latency, it would appear that this component is probably related to non-specific pathways in the visual system, rather than to specific ones.

In an attempt to gain some impression of the dependence upon frequency of the amplitude of the averaged responses, the peak-to-peak amplitudes of the "constantly appearing event" referred to above were determined for all frequencies from Figs. XXVI-1 and XXVI-2, and plotted as shown in Fig. XXVI-26. It is emphasized that this particular selection of a measure of amplitude is quite arbitrary. Although there is some slight indication of a peaking in amplitude for flash frequencies within the alpha-frequency range of 8-13 per second (that is, for S.L. at 8; D.G. at 12; J.T. at 10; and E.G. at
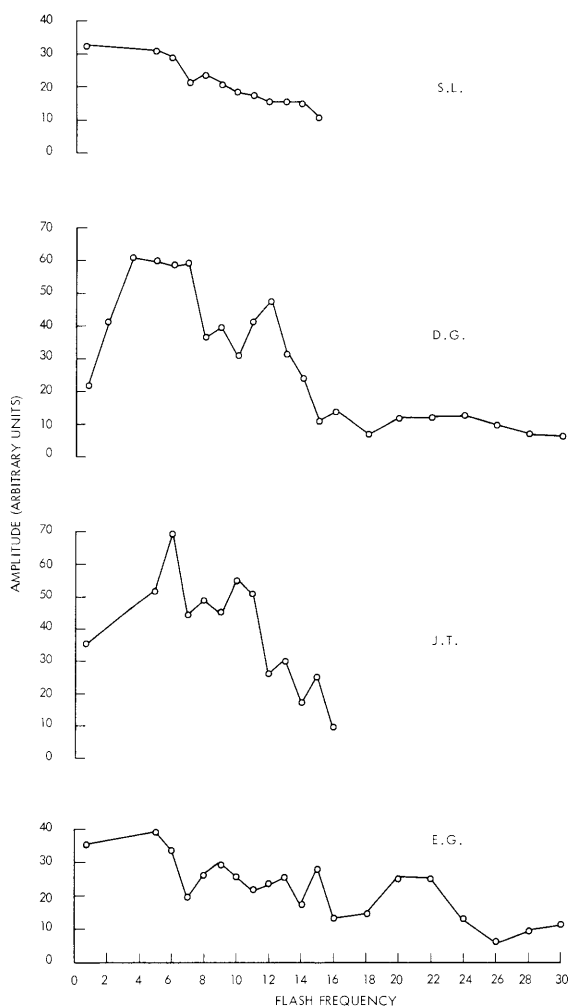

Fig. XXVI-26. Amplitude of response of the "constantly appearing" component as a function of flash frequency.

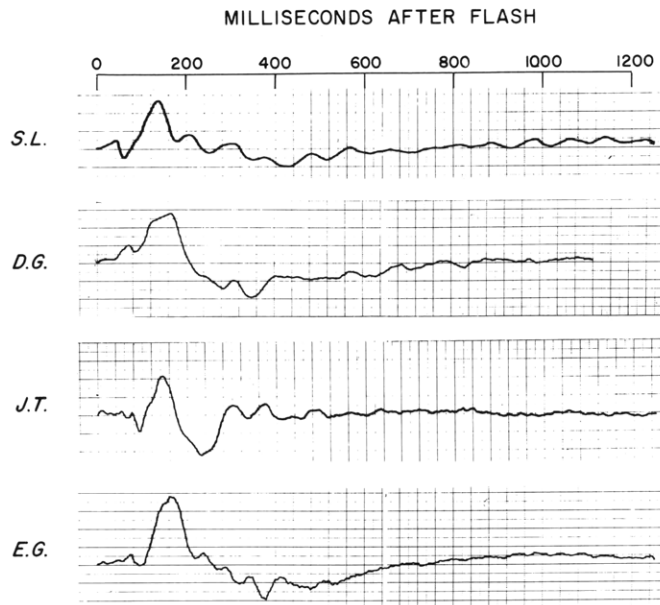MILLISECONDS AFTER FLASH

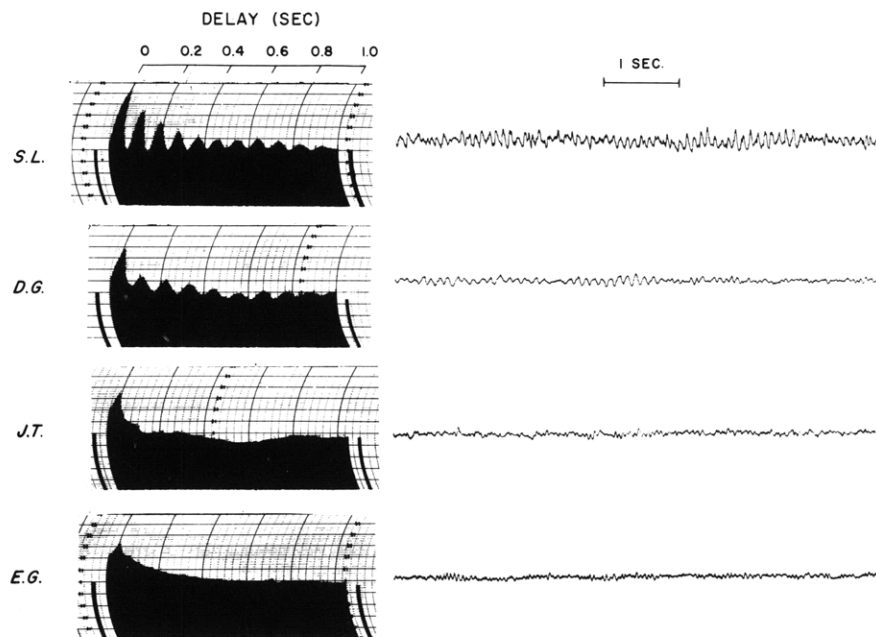Fig. XXVI-27. Averaged responses to 75 flashes at a flash rate of 0.7/sec.

Fig. XXVI-28. Autocorrelograms of resting EEG. (Duration of samples analyzed, 1 minute.)

9 flashes per second), for none of the subjects are these peaks of a clearly outstanding character.

Averaged responses from each of the four subjects to slowly repeated flashes are shown on an expanded scale in Fig. XXVI-27, so that the nature of the sensory after-discharge to photic stimulation can be examined. Of these four subjects, two have a moderately well-defined sensory afterdischarge (S. L. and E. G.). For subject S. L. there are four positive peaks in the interval 210-570 msec; the corresponding average interval between these peaks is 90 msec, and the corresponding frequency is 11 per second. For subject E. G., between 240 and 410 msec there are 3 positive peaks; the corresponding frequency is approximately 17.6 per second. For subjects J. T. and D. G. the after-discharge is not sufficiently rhythmic so that an average frequency can be stated.

Autocorrelograms of the resting EEG are shown in Fig. XXVI-28. For subject S. L., the average resting frequency was 10.8; for subject D. G., 9.1. (For subjects J. T. and E. G. there is no prominent rhythmic activity in the alpha-frequency range.)

The preceding results suggest that for the subjects examined, those components in the EEG that are time-locked to the stimuli (that is, that are reflected in the averaged response) are largely in the nature of responses specifically evoked by the stimuli, rather than a reflection of a self-oscillatory system that is entrained to an external signal (for example, the repetitive photic stimulation). The findings of a slight alteration in the latencies of the above-mentioned constantly appearing components in the averaged responses for certain flash rates suggests, however, that there may be a component representing true entrainment of some components of the EEG.

If an intrinsically oscillating system (or systems) that contribute to the EEG were truly entrained by an external signal, then it would form a component of the average response (since it would then be time-locked with the stimulus) within the frequency limits for which entrainment is possible. However, the relative phase between the external signal and the intrinsic system would be different for different frequencies within the range of entrainability. This point is illustrated in Fig. XXVI-29. In the upper section is shown a schematization of entrainment of the frequency ω of a nonlinear self-oscillatory system, by an externally imposed signal (frequency Ω). In the lower section of the figure, phase relationships between the two are illustrated by mock-up experiments, and schematized in the graph.

The slight shifts in latencies for certain flash frequencies in Figs. XXVI-24 and XXVI-25 thus may be taken as some suggestion that there may be a component in the averaged response which represents true entrainment of the intrinsic rhythmic activity of the brain.

In Table XXVI-1 are summarized for the four subjects the resting EEG frequencies, the frequencies of the sensory afterdischarge, the flash rates for which there was slight decrease in the latency of the "constantly appearing" component, and the flash rates in

Table XXVI-1.

Frequency (flashes/second)	Subject			
	S.L.	D.G.	J.T.	E.G.
Resting EEG	10.8	9.1	-	-
Afterdischarge	11.0	-	-	17.6
Peak in amplitude	8	12	10	20-22
Decrease of latency	7, 8	9, 10	10, 11, 12	10, 11; 18, 20

the alpha-frequency range (and at twice this, for subject E.G.) for which there was a slight peaking of the amplitude of the constantly appearing component.

In general, there is no clear and consistent relationship between the various parameters that are itemized in Table XXVI-1. It is to be noted, from Fig. XXVI-29, that the frequencies for which there would be expected to be a slight advancement in phase (that is, shortening in latency) would be somewhat less than the free-running frequency of the oscillating system (the average resting EEG frequency, in the present discussion). From Table XXVI-1 such a relationship appears for subject S.L., but not for D.G.

From inspection of Figs. XXVI-24 and XXVI-25 it is evident that the sequence in time of events in the EEG following each flash in a train may be quite complex, and at times, from inspection of the inked trace of the EEG, the generation of "harmonic components" of twice or thrice the flash rate may be suggested. Upon close inspection of the averaged waveforms for different flash rates, however, it is evident that description of these phenomena as specific events in time, rather than as "harmonics," may be more appropriate.

An illustrative example is shown in Fig. XXVI-30 for subject J.T. For a flash rate of 8 per sec, in the averaged responses, three separate major events (indicated by the arrows) appear after each flash; these are reflected in the autocorrelogram below by a triangular shape that could suggest the sum of a fundamental at 8 per sec, and a third harmonic at 24 per sec. For a flash rate of 11/sec, however, the successive flashes are so close together that the third event is now no longer present, and the remaining two which follow at the same latency after each flash as before. These are reflected in the corresponding autocorrelogram by a notched shape that could suggest the presence of a fundamental at 11 per sec and a second harmonic at 22 per second. (A frequency analyzer of sufficiently wide range was not available with which to demonstrate this point for these recordings, but it is apparent that the presence in the EEG of "harmonic components" would also have been indicated by automatic frequency analyzers of the type commonly employed in electroencephalography).
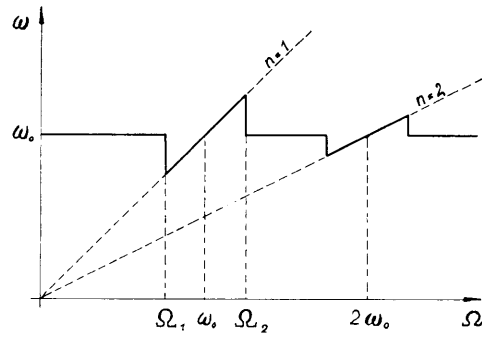
Fig. XXVI-29(a).   Frequency Ω of forced oscillations in systems capable of auto-oscillations, according to frequency Ω of the driving agent (n = 1, first-order entrainment; n = 2, subharmonic entrainment). [Reproduced from Fig. 2 of Klotter,[2] 1960, with permission.]
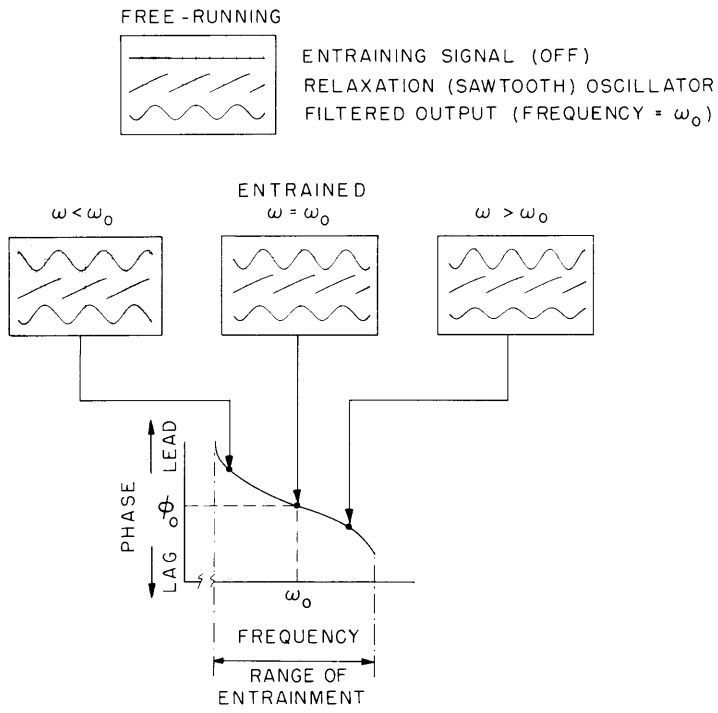

Fig. XXVI-29(b).   Phase relations between a nonlinear oscillator and a sinusoidal entraining signal.
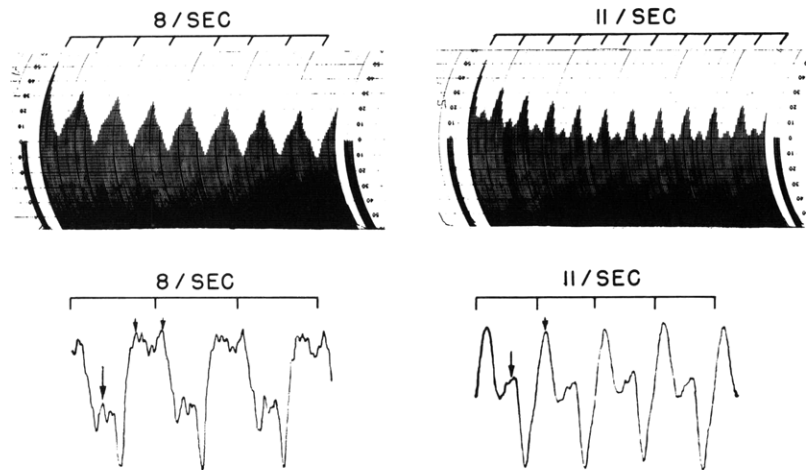
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Fig. XXVI-30. Autocorrelograms and averaged responses for flash rates 8/sec and 11/sec (Subject, J. T.). (Analysis of 30-sec midline parieto-occipital recordings.)

The results reported here indicate that the effect on the EEG of repetitive photic stimulation is indeed complex. There appear to be no simple and direct relationships between the responses to photic stimulation, the average frequency of the resting EEG and the frequency of the sensory afterdischarge (if one is present). There is only minimal and indirect evidence in these results to indicate that there was true entrainment (as defined in this report) of the occipital EEG by intermittent photic stimulation, with the flash rates that were employed.

Further examination of the question of entrainment could appropriately be undertaken with direct power-spectrum analysis of the EEG recordings, and with the utilization of a series of flash rates close to (that is, within 1 or 2 cps) the resting alpha frequency.

In the specific technique of averaging that was used, it was assumed implicitly that all of the evoked responses were equivalent; any alternation in the amplitude of successive responses that might have occurred would thus be completely obscured. It would, therefore, be appropriate to repeat these studies with the use of "bursts" or trains of stimuli at the various frequencies; the identity of the average response to each successive flash in the train would thereby be retained. It would particularly be of interest to explore further the nature of the "constantly appearing" component, with stimuli of this nature.

J. S. Barlow

References

1. J. S. Barlow, Rhythmic activity induced by photic stimulation in relation to intrinsic alpha activity of the brain in man, EEG Clin. Neurophysiol. 12, 317-326 (1960).

2. K. Klotter, General properties of oscillating systems, Cold Spring Harbor Symposia on Quantitative Biology, XXV: Biological Clocks (The Biological Laboratory, Cold Spring Harbor, Long Island, N.Y., 1960), pp. 185-187.