

A MODEL OF NEURON ELECTRICAL ACTIVITY

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1. Every theory is based on some simplifications of observed phenomena. This simplified abstract phenomenon is usually called a "model". Depending on the level of simplification the model enables us to predict more or less accurately the original situation. The scientist who tries to describe a physical phenomenon in terms of mathematical equations, or, more generally, by means of some mathematical algorithm, deals in fact with a particular type of model which, due to its abstract form, is more flexible and in which the number of parameters used is less restricted than in models of a different kind. However, the similarity between the original and model phenomena is clearer in mathematical models because we never deal with the similarity between two obscure situations and at least one side of the relation, namely the mathematical side, can be fully explained.

Now the form of a model might be very simple, therefore the similarity is very superficial. In the case of a mathematical model such a simple form gives only the possibility of reconstruction of the original phenomenon using the values of several parameters and we usually try to use a minimal number of such parameters. Such a simple model of the electrical activity of the neuron will be described in this paper.

The deeper sense of creating models is to extract such information as enables us to predict behavior: if the model agrees with some actual phenomenon then perhaps a physiological experiment can be designed which will clarify its physical or chemical mechanisms. The procedure described below should be treated as the first step to obtain a more complete model.

2. The information carried by the signals from the sensory unit to the central nervous system is, as it is commonly believed, coded by a pattern of activity. However, we do not know the coding system.

We hope to decipher it on the basis of a correlation with some other physiological phenomena, observing the changes of the signals due to the changes of, e.g. the physical or chemical environment of a sensory unit.

From information of such kind we may assume that:

(a) In some cases (in tonic sensory units) "at any time, except shortly after an abrupt change from one state to another the frequency of the impulse discharge of the unit will depend on the value of physical and chemical function in question" (Gray 1959).

(b) "The responses of phasic units and the adapting part of responses of tonic units are dependent on the time course of the stimulus" (Gray 1959).

In the model described below only the sensory units obeying to (a) are considered and we assume that those physical and chemical factors which are correlated with the monitored discharge might be represented by two functions $to(t)$ and $s(t)$ (see Section 7).

3. Sometimes important information may be obtained from the global characteristics of the electrical activity of a neuron. We have in mind the following characteristics: the time-length of the volley tc , silence period Sp , total number of impulses N , the mean spike frequency $\nu = N/tc$ (or the mean spike interval $\tau = 1/\nu$) and the histogram of spike intervals.

It has been shown that these histograms generally do not obey to either the Poisson or Gaussian distribution (Amassian et al. 1961). A successful model to obtain an appropriate histogram was proposed by Kotov and Cetlin 1966. It is based on the threshold idea. There is some similarity between this model and the model proposed below; in both the process of generation of impulses is treated as a random process. The conceptual differences lie (i) in the fact that in the cited paper there is no attempt to reconstruct the pattern of the volley, (ii) hence no correlation with physical phenomena are considered, (iii) the mathematical approach is quite different.

4. By comparing a number of volleys from an isolated neuron without changing the conditions of its activity, we observe that they differ in some minor details, for example in the total number of impulses, but that the general pattern remained constant.

This observation forms a basis of frequency description of the volleys, a description which is commonly used in many papers. If t is time counted from the beginning of the volley and ν is the "local frequency", that the function $\nu(t)$ for different volleys of the same neuron are all then the frequency description is given by the function $\nu = \nu(t)$. If the local frequency is determined in some reasonable way, then we find

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most the same. One may make the concept of this similarity more precise in a way analogous to that which will be described later for the function $n(t)$. However, the frequency description of the pattern of a volley has two weak points. First, the description may hardly be used for "low-frequency" volleys, i.e. those which consist of a small number of impulses: for this case the notion of "local frequency" loses its sense. The second weak point lies in the determination of what we have to understand as a local frequency at the beginning and the end of the volley. Finally, it is worth mentioning that the frequency curves found in many papers are artificially smoothed. What they look like if we make the picture more accurate can be seen in Fig. 9. The figures are obtained from the "artificial" volleys shown in Fig. 7. The values f_3 and f_5 are the means of 3 respectively of 5 subsequent spike intervals. Usually the mean values are calculated in a slightly different way, namely, the time unit is taken as constant and the number of spikes for this time unit is a basis for determining $\nu = \nu(t)$; however, this change is not essential.

From this figure we may conclude that the differences between frequency curves of similar volleys are quite significant. This may be important if we aim to compare different volleys and to find some measure of the difference between them.

5. The most common method for the quantitative comparison of volleys is based on the analysis of correlation coefficients. In this method we begin with the calculation of the correlation between spike intervals distanced by a given number of impulses. Let τ_i be the spike interval between the $(i - 1)$ -impulse and i -impulse.

The correlation coefficients are given by

$$R_j = \frac{1}{S^2} \sum_{i=1}^{N-j} (\tau_i - \bar{\tau})(\tau_{i+j} - \bar{\tau})$$

where $\bar{\tau} = \frac{1}{N} \sum_{i=1}^N \tau_i$ is the mean interspike interval for a volley

and $S = \frac{1}{N} \sqrt{\sum_{i=1}^N (\tau_i - \bar{\tau})^2}$ is the dispersion.

For all j , $-1 \leq R_j \leq 1$; the correlation is stronger as $|R_j|$ approaches 1.

This type of description gives a method for the comparison of volleys but there are several factors which limit the use of the method. The first is purely technical; sometimes it is difficult to obtain a good record of spike intervals. The second is that for comparison of two volleys we

need a large number of parameters; usually we use the value j up to 10. Thirdly we must adopt some rather conventional criteria of similarity between the two sets of parameters R_j . Finally, this description, unlike that of a frequency description, is given in terms which do not have a direct physiological meaning. Therefore the reconstruction of the volley from R_j is not an intuitive one. More generally it seems that the main weakness of the correlation method lies in the fact that we employ too detailed information. For the purpose of comparison in Table I, we give the values of $\bar{\tau}$, S and R_j for the volleys shown in Fig. 7. It should be noticed that the difference between some of the numbers quoted reached 20%.

TABLE I
Parameters of artificial volleys

Volley number	$\bar{\tau}$	$S \cdot 10^{-3}$	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}
1	0.1395	2.013	0.804	0.619	0.481	0.359	0.266	0.143	0.075	0.041	-0.039	-0.133
2	0.1418	2.073	0.790	0.642	0.546	0.415	0.293	0.200	0.097	-0.027	-0.130	-0.226
3	0.1361	1.780	0.760	0.450	0.476	0.399	0.266	0.186	0.097	-0.027	-0.078	-0.200
4	0.1391	1.771	0.795	0.693	0.529	0.368	0.289	0.136	0.097	-0.011	-0.111	0.182
5	0.1391	1.661	0.796	0.624	0.481	0.319	0.233	0.113	0.002	-0.092	-0.161	-0.224

Key: $\bar{\tau}$, mean interspike interval;

S , standard deviation;

R_j , correlation coefficients.

6. In the proposed model we try to superimpose two components: first, the deterministic one, which governs the pattern of the volley, and the second, stochastic, which gives the fluctuations observed in the experiments. The physiological, chemical or mechanical stimuli which are responsible for the generation of impulses or the receptors responding to them are correlated with the first component, and hence the pattern of the volley is assumed to be a carrier of the biological information. Figure 1 shows the typical position of the volley relative to lung volume which was registered simultaneously.

The biological role of the second component is less obvious, perhaps it may be treated simply as biological noise which in some cases may essentially distort the information. Interestingly enough the observed differences between volleys are small in those cases in which the observed process may be considered as "running in health". It is also possible that these fluctuations provide some "elasticity" in the consignment of information.

The superposition mentioned above cannot be treated as a superposition in the mathematical sense. There is no "adding" of the two processes but, as it will be seen, the function describing the process depends on two parameters. This is clearly seen in the mathematical description of our model.

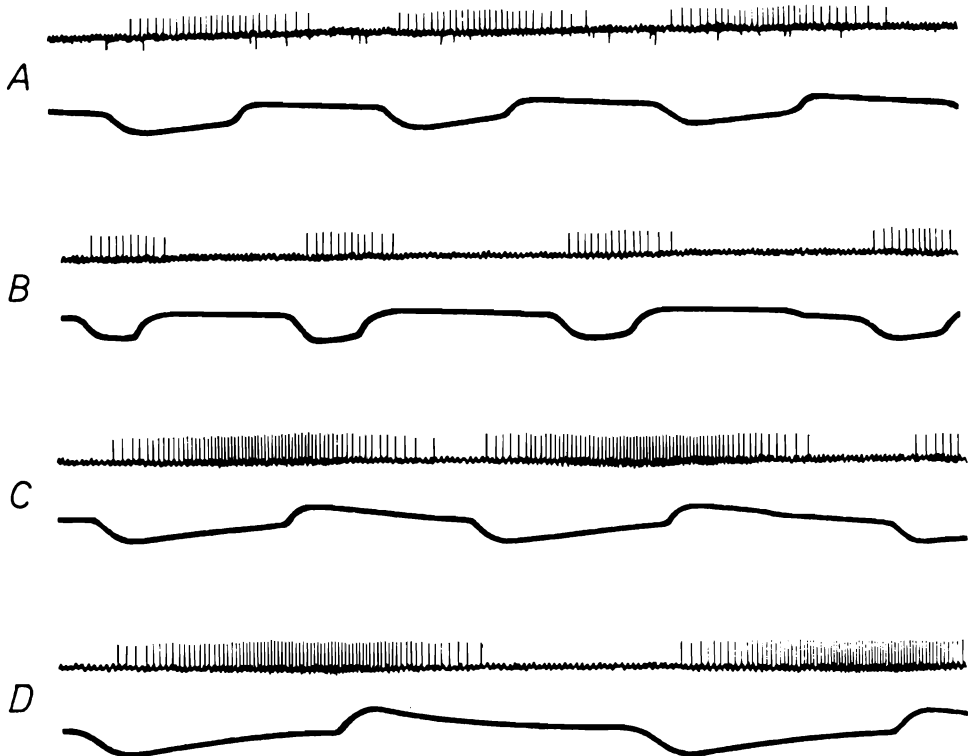


Fig. 1. The position of volleys from pulmonary stretch receptors relative to the curve representing air flow. Upper traces, electrical activity of a slowly adapting stretch receptor; lower traces, air flow. A, control run; B, contralateral vagotomy; C, D, 30 sec and 1 min later, respectively. (Reprinted from Karczewski 1965).

Let the stochastic function ξ of the continuous parameter t (time) permit two values or states: 0 silence, and 1 impulse. The Markovian chain is fully determined by the transition probabilities i.e.

$$P_{ij}(u, t) = P\{\xi(t) = j \mid \xi(u) = i\}, \quad i, j = 0, 1,$$

i.e. by determining the probability that the stochastic function will be at time t , in the state j , provided its state at time u was i . Assuming that the impulse is instantaneous, for a full description of the process we need

where

$$\operatorname{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x \exp(-y^2) dy; \operatorname{erf}(0) = 0; \operatorname{erf}(\infty) = 1.$$

The left hand side of the equation (2) is the monotonic function shown in Fig. 2. The solution of (2) gives us the interval τ we are looking for. It should be noticed that t_0 and s in the previous equation are given numbers because for each step we take t_0 and s in the point t_{k-1} .

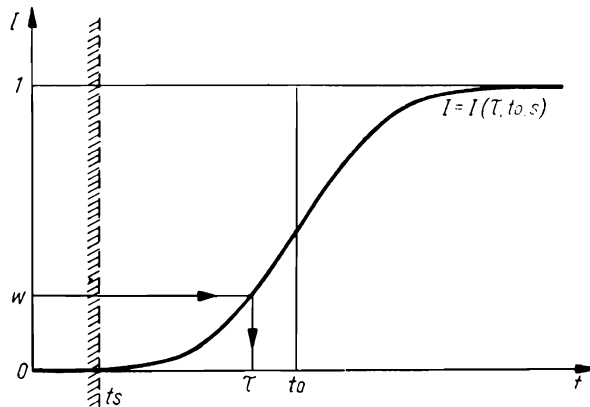


Fig. 2. See text.

In our numerical procedure the solution of the transcendental equation has been done with a given accuracy ε . In practice we limited ourselves to the random number between 0.003 and 0.997, to exclude too small and too great intervals; for ε we choose a value of 0.01.

Further, in our Markovian machine we included a threshold, t_s ; if the resulting value of τ was smaller than t_s the step was not accepted and the procedure was repeated beginning from the choice of the random number.

8. At this stage of our work we did not aim to use an actual correlation between the physiological stimuli or responses and the electrical activity of the neuron, and we limited ourselves to the procedure of generating the volley itself. Therefore we did not use any information concerning stimuli, but simply assumed some form of the functions $t_0(t)$ and $s(t)$. In our experiments we used either triangular or parabolic shapes of these functions. In this paper only "parabolic" experiments are presented.

In order to elucidate the role of the parameters involved, two series of experiments were undertaken. In the first we changed only the function t_0 , keeping $s = \text{const}$. In the second $t_0 = \text{const}$ and the changes in the pattern of volleys were due only to the functional behavior of s (and to the role played by the threshold t_s).

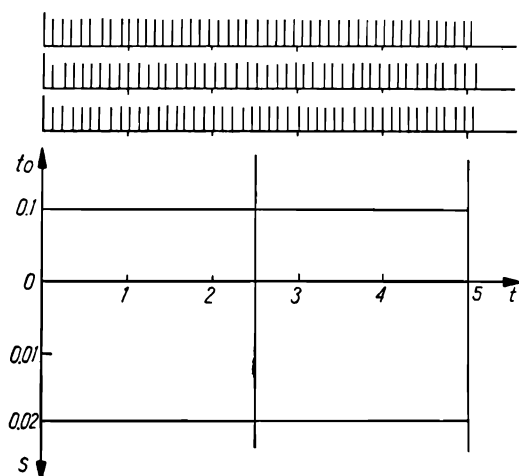


Fig. 3. For $t_0 = \text{const}$ we obtain uniform volleys; the differences between spike intervals and between the volleys are due only to the dispersion s , taken in this case as constant.

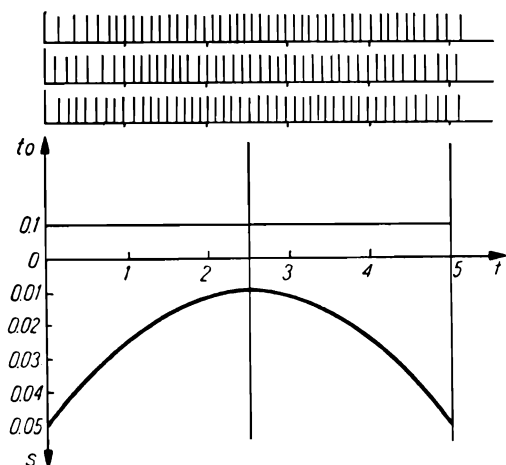


Fig. 4. If s is assumed in a parabolic form ($0.01 \leq s \leq 0.05$) and $t_0 = \text{const}$ the resulting volley is only slightly non-uniform.

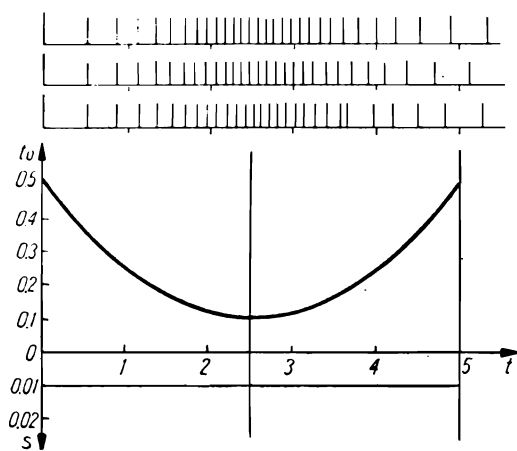


Fig. 5. Assuming t_0 in a parabolic form ($0.1 \leq t_0 \leq 0.5$) and $s = 0.01$ we obtain symmetric volleys with a marked density peak at $t = 2.5$.

Fig. 6. The change (see Fig. 5) of the value of s (now $s = 0.05$) causes a great variability of spike intervals.

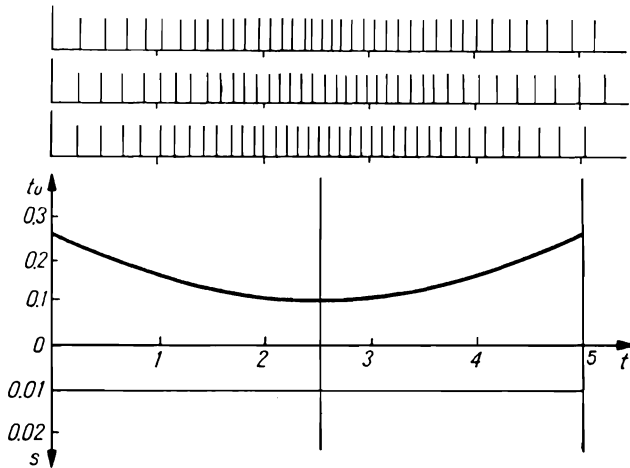
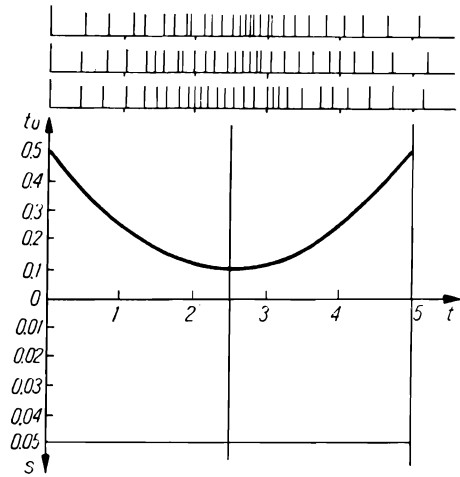


Fig. 7. A case similar to that presented in Fig. 5 but for the more flat function $t_0 = t_0(t)$. The peak in the middle of the valley is less marked.

In Figures 3–8 we present the assumed shapes of the functions t_0 and s together with the results obtained for several cases. In all these pictures we took $t_c = 5$ (arbitrary time units). Short comments on different results are given below the pictures. Generally in all cases for which we took $s = \text{const}$ we got volleys similar to those obtained in physiological experiments if $\max t_0 / \min t_0 \sim 3$ and $(\max t_0 + \min t_0) / s \sim 15$. However, this cannot be treated as a general indication because of the variety of patterns found in physiological experiments. Therefore all results presented must be treated only as an illustration.

9. Some more detailed analysis of the results will be shown for the volleys presented in Fig. 7.

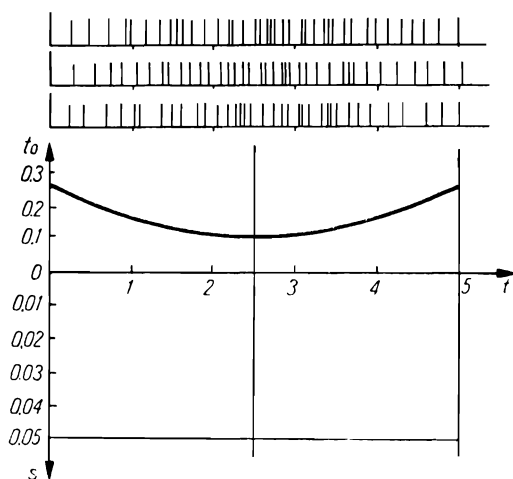


Fig. 8. The case similar to that presented in Fig. 6 but for the more flat function $t_o = t_o(t)$.

First of all we calculated local frequencies f_3 and f_5 defined as

$$f_3(i) = (\tau_{i-1} + \tau_i + \tau_{i+1})/3,$$

$$f_5(i) = (3 \cdot f_3 + \tau_{i-2} + \tau_{i+2})/5.$$

The curves f_3 and f_5 (together with the t_o -curve for the sake of comparison) are given in Fig. 9. Both f_3 and f_5 follow the assumed t_o -curve, but the randomness of the procedure causes their fluctuations; as expected f_5 is smoother than f_3 .

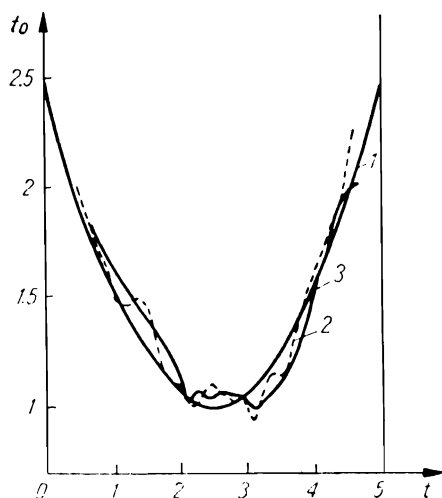


Fig. 9. The frequency curves: 1, represents the assumed parabolic curve $t_o = t_o(t)$; 2, the mean value for three subsequent intervals; 3, the mean value for five subsequent intervals.

The histogram of the spike intervals (Fig. 10) is similar to those obtained in the original experiments. As it was noticed before the com-

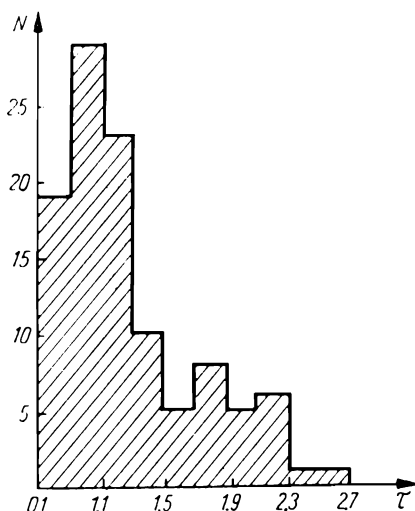


Fig. 10. Histogram of the interval lengths for five volleys obtained in the same way as shown in Fig. 7.

parison of volleys using the frequency curves has some weak points, so it was interesting to find a simple method of comparison of the volleys. It seems that for such measure the nondimensional value:

$$\delta = \int_0^T |n^1(t) - n^2(t)| dt / \frac{1}{2} \int_0^T (n^1(t) + n^2(t)) dt \quad (3)$$

may be used, where $n^1(t)$ and $n^2(t)$ are numbers of spikes for the two volleys which we compared. The denominator of this formula is simply a mean value of the area below the curves $n^1(t)$ and $n^2(t)$. The mathematical sense of numerator is seen in Fig. 11 represented by the shaded area. In the case when the time of the volley T^1 differs substantially from T^2 we may use the same formula, but after the transformation

$$\frac{t}{T} = t' \cdot Tc/T,$$

which gives us the same basic interval (namely tc) for both compared volleys.

For the volley which we analysed the values of $R_1, R_2, \dots, R_{10}$ are shown in Table I.

10. It seems that the class of volleys which may be obtained with the assumption that $s = \text{const}$ is large enough. Even with this limitation the problem of deriving analytically the function t_0 from the volley obtained from physiological experiments seems to be a difficult stati-

stical problem. However, we convinced ourselves that it is rather easy to obtain a given volley by means of a method of trial and error. The comparison between two volleys either through the functions $n(t)$ as

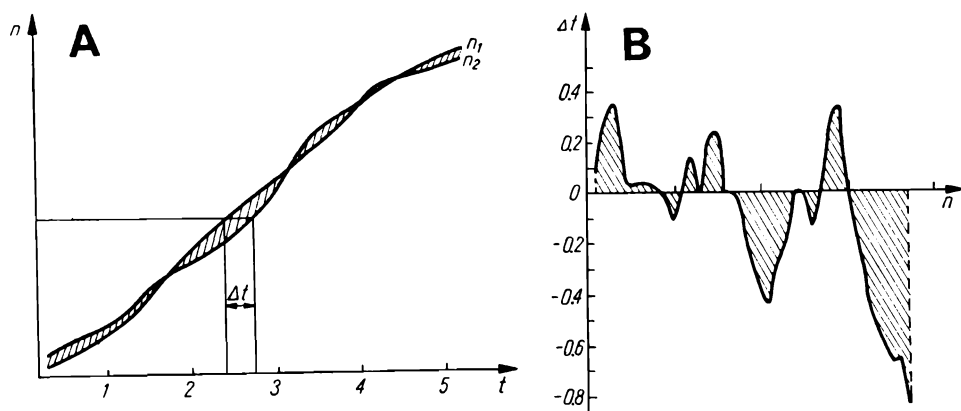


Fig. 11. A, scheme showing the sense of the formula (3); the shaded area represents the nominator. B, the actual values of Δt and n for two volleys on Fig. 7.

described above or by similar comparison of to -curves seems to be promising; both methods are based on simple physiological concepts.

Work on the use the physiological data concerning stimuli or responses is in progress.

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Received 16 June 1970