

STIMULUS INTENSITY AND MODULATION OF BRAIN OUTPUT

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ABSTRACT In accordance with the implications of a previously proposed mathematical model of modulation of bioelectric response in the brain, it is found that a single free coefficient predicts the observed modulation periods over a range of stimulus intensities. This coefficient is shown to be a computable function of stimulus intensity. Change in the mean modulation period of evoked bioelectric output at the visual cortex of the rat can be described as a power function of the intensity of photic stimulation.

INTRODUCTION

When narrow band-pass-filtered electroencephalogram recordings are taken from scalp electrodes over the occipital cortex of humans, the bioelectric output shows a characteristic modulation of its amplitude envelope with a systematic distribution of time intervals between troughs in the amplitude envelope. These intertrough intervals, or modulation periods, form distributions over time which reveal a consistent shift to longer periods when the subject is exposed to photic flicker tuned to the center frequency of the band-pass filter (Trehub, 1965).

A theoretical explanation of these basic brain modulation phenomena has been proposed, and based upon the theory, a mathematical model has been constructed which fits the empirical findings that were obtained with humans under the conditions of no stimulation and moderately intense photic stimulation (Trehub, 1969). Later studies with rats having chronically implanted recording electrodes in the visual cortex and the dorsal lateral geniculate nucleus provided additional confirmation of the proposed theory and the mathematical model (Trehub, 1971 *a*). In the latter studies, tests were again made under the two conditions of no stimulation and moderately intense photic stimulation. However, the theory and its associated mathematical equations contain a single free coefficient (c) predicting the bioelectric brain modulation distributions. The coefficient c may be thought of as a value inversely related to the number of neurons potentially dischargeable in response to stimulation and, if the underlying theoretical formulations hold, should be a system-

atic function of stimulus intensity. This relationship has not been demonstrated before the present report in which I describe the functional relationship between the coefficient of stimulation (c) and intensity of photic stimulation.

THEORY OF MODULATION

The general theory of endogenous brain modulation is based upon a concept of kinetic and potential neuronal collectives. A *neuronal collective* is defined as a subset of neurons which is characterized by a temporally coherent discharge pattern. Two kinds of neuronal collectives are postulated: (a) *kinetic collectives* which are defined as neuronal collectives in the process of discharge; and (b) *potential collectives* defined as the *maximal* number of neurons in a neural mass which can coherently discharge under a specified condition. In real neuronal systems, the kinetic collective (which is measured in the signal channel) is almost invariably smaller than the potential collective because the probability of a stimulus discharging any given neuron at any particular time is less than unity and where large numbers of neurons are involved there is always a high probability that some potentially dischargeable neurons will not fire when stimulated.

It is assumed that the bioelectric output of the brain derived under our experimental conditions can be treated as an ordinal step time series computable as a Markov process (Trehub, 1969). It is theorized that the larger the ratio of the kinetic collective to the potential collective during any moment the greater is the probability of a decrease in the kinetic collective in the succeeding moment, and the smaller the ratio of the kinetic collective to potential collective, the greater the probability of an increase in the succeeding moment. Consistent with this, we assume that on the average, the probability of a transition to a larger kinetic collective will decrease at a rate inversely proportional to the magnitude of the kinetic collective relative to its potential collective. Thus a negative exponential function is taken as a generator for the set of transition probabilities in a Markov lattice model of brain output.

The Markov model can be expressed as a Monte Carlo algorithm in which a set of transition probabilities is given by the equation

$$P_{k_t} = \exp(-ck_t),$$

where k_t is any amplitude at time t expressed in unit ordinal terms, and P_{k_t} is the probability of transition to a unit higher on the ordinal amplitude scale at the immediately succeeding observation point ($t + 1$). The probability of transition to a unit lower in amplitude at $t + 1$ is simply $1 - P_{k_t}$. The parameter c , called the coefficient of stimulation, is the only free term in the model (Trehub, 1969). In the work presented below, it is shown that the value of c may be estimated on the basis of intensity of stimulation.

Simulations of the model on a digital computer yield time series which can be

analyzed for period distributions in the same manner as the subject's actual brain output and a direct comparison can be made between the theoretical predictions and the empirical data.

METHOD

In the present investigation, narrow band-pass-filtered measures of bioelectric brain output were taken from monopolar electrodes chronically implanted in the right visual cortex of unanesthetized adult albino rats ($N = 5$). Flickering photic stimulation tuned to the filter frequency was presented to the contralateral eye of each rat. During each experimental session, stimulus intensity was increased sequentially from 0 to 440 lx in equal intensity steps of 55 lx; the stimulus was similarly decreased in steps of 55 lx from 440 to 0 lx. Stimulation was presented for 30 s at each intensity step with a 1 min dark period interposed between each pair of intensity steps. The entire experimental procedure was repeated on each of 6 separate days. Thus on each of the days, each rat received 9 different stimulus conditions over 18 trials, 9 in a rising series and 9 in a falling series.

One branch of a bifurcated fiber-optic tube was used to conduct the photic stimulation through the wall of an electrically shielded sound-isolation chamber to the left eye of the rat within. The other optically matched branch of the tube terminated outside the enclosure at a light meter which provided a continuous measure of the intensity of light falling on the eye of the animal.

Modulation periods of filtered brain output were determined by measuring the time intervals between successive positive inflections in the amplitude envelope and classifying each period to its nearest second. The number of periods falling in each duration class was multiplied by the duration and the percentage of total time occupied by each class of cycles was computed under each condition for each animal. Average modulation distributions were plotted separately for each level of stimulation intensity.

RESULTS

Fig. 1 shows the average empirical and theoretically predicted distributions of modulation periods for each level of photic intensity together with the standard deviations of the mean values. Also shown in this figure are the values of the coefficient of stimulation (c) associated with each theoretical distribution. It can be seen from these data that our experimental results are well fitted by the proposed (Trehub, 1969) mathematical model. Analysis of these distributions reveals an average mean *square* difference of 4.4 between empirical and theoretical points.

Shifts in mean modulation period of the visual cortex ($\Delta\bar{W}$) are computed by subtracting the mean modulation period under the condition of no stimulation (\bar{W}_0) from the mean modulation periods during the various stimulus conditions (\bar{W}_{s_i}). Thus: $\Delta\bar{W}_{s_i} = \bar{W}_{s_i} - \bar{W}_0$. Fig. 2 shows the empirical and theoretically predicted shifts in mean modulation period over the full range of stimulation. Deviations of the theoretical points from their least squares trend line can be expected to occur because of the stochastic properties of the model. It can be seen that the relationship between change in mean modulation period and intensity of photic stimulation is described by the power function $y = ax^b$, where $a = 0.015$, $b = 0.571$, and x is stimulus intensity measured in lux.

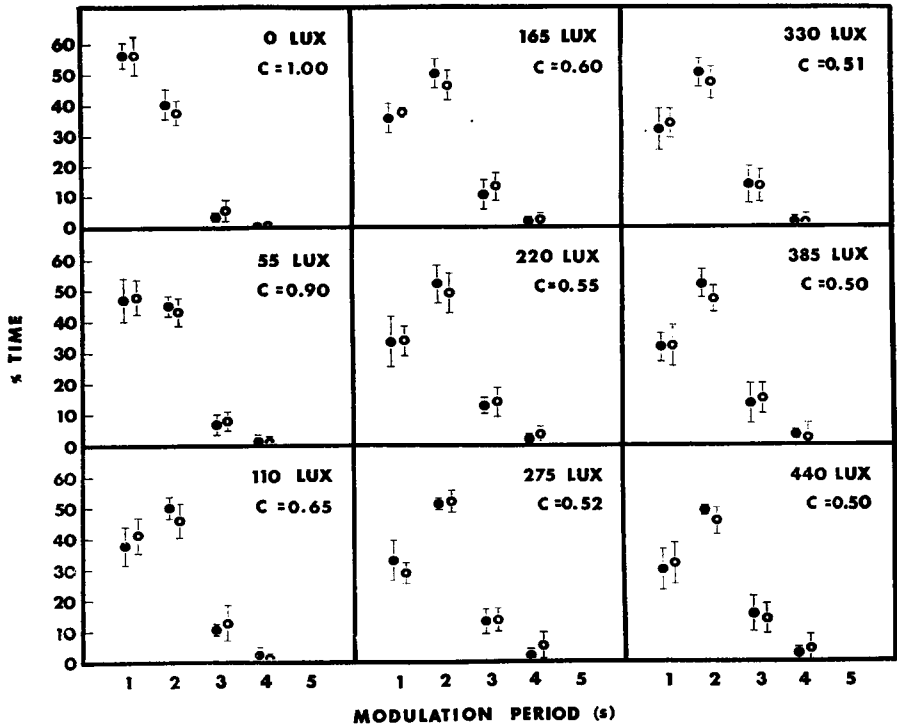


FIGURE 1 Empirical and theoretical plots of percent time incidence for the indicated modulation periods in the visual cortex. Closed circles, empirical. Open circles, theoretical. Means ± 1 SD shown. Upper right value in each frame represents intensity of stimulation in lux (lux = lumen per square meter). c in each frame represents value of coefficient of stimulation yielding associated theoretical distribution.

Figs. 3 *a* and *b* show how the coefficient of stimulation (c) varies as a function of the level of light intensity. The relationship between c and stimulus intensity is reasonably well described by either an inverse power function or an ordinary hyperbolic function with the latter giving somewhat the better fit. Which of the two functions will ultimately prove the better predictor of c remains an issue for further exploration.

DISCUSSION

In accordance with the implications of the theoretical model for brain modulation (Trehub, 1969), it is now verified that the free coefficient c is indeed a continuous systematic function of the intensity of stimulation impinging upon the animal. Thus in the case of the rat, under the conditions of our experiment, if we know the intensity of photic stimulation, we can specify the distribution of modulation periods in the multineuronal bioelectric output of its visual cortex.

A number of neuroelectric studies have indicated that single unit and multi-

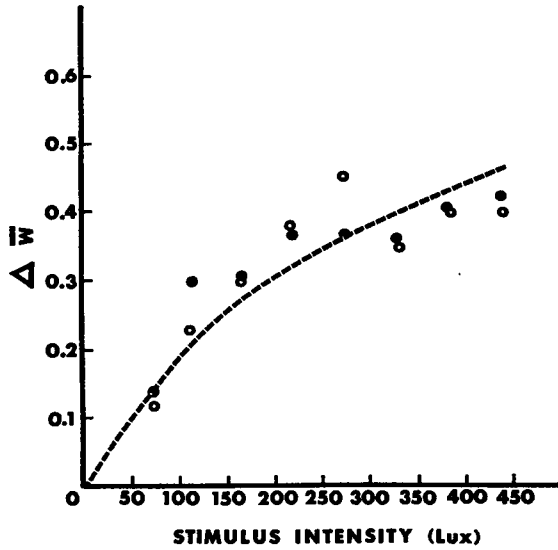


FIGURE 2 Empirical and theoretical plots of shift in mean modulation period ($\Delta\bar{W}$) as a function of stimulus intensity. Closed circles, empirical. Open circles, theoretical. Dashed line, least squares trend line of theoretical points; $y = 0.015 x^{0.671}$. x is the stimulus intensity in lux.

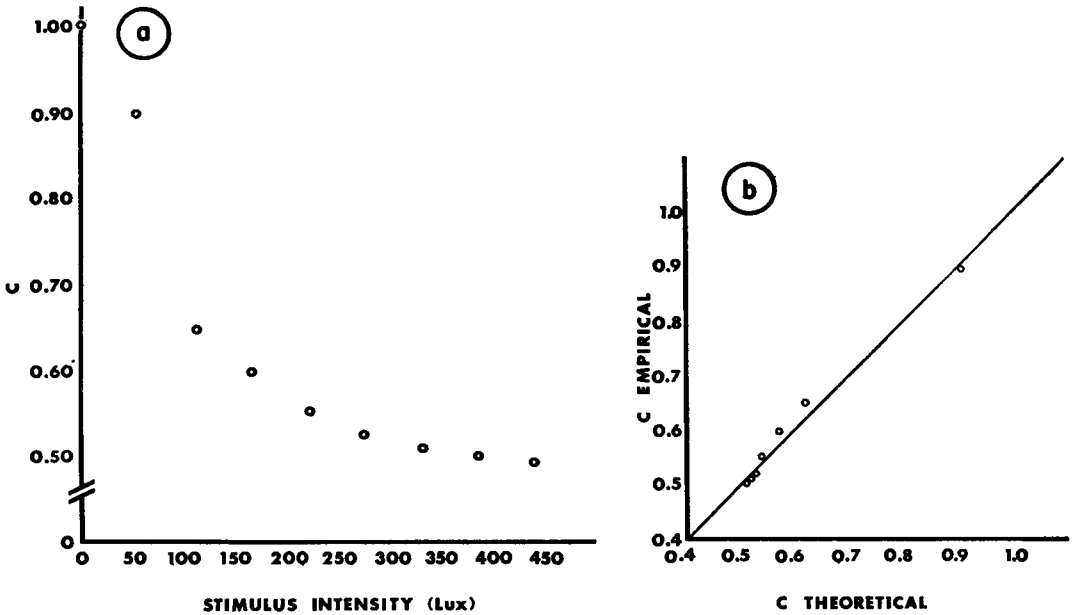


FIGURE 3 (a) Plot of applied coefficients of stimulation (c) against associated intensities of photic stimulation. (b) Plot of empirically applied c against theoretically predicted c derived from least squares hyperbolic function $c = x/(-55.5 + 2.1 x)$, where x is stimulus intensity measured in lux. Diagonal, line of perfect fit between empirical and theoretical values of c .

neuronal response magnitudes may be power functions of stimulus intensity (Donchin and Lindsley, 1969; Mountcastle et al., 1969; Stevens, 1970). The findings presented in this report reveal a *temporal* aspect of bioelectric signal processing in the brain (shift in mean modulation period) which is also characterized by a power function. The fact that power functions may describe both response magnitude and shifts in modulation of brain output does not necessarily imply a common underlying mechanism. This does suggest, however, an area of investigation which might prove to be particularly fruitful.

Investigation of the coefficient of stimulation (c) in relation to the various known anatomical characteristics of other sense modalities and other species may disclose important functional properties of multineuronal systems in the brain. Of specific relevance to the study of evoked potentials and of general significance to the broad effort aimed at understanding the brain as a multineuronal system, is the evidence that apparently complexly generated bioelectric processes in the brain may be quantitatively predicted by models explicitly based upon concepts of coherent neuronal events. At this level of analysis, the present findings concerning modulation of brain output and earlier derivations showing a visual signal system in the brain operating as a parallel coherent detector (Trehub, 1971 *b*) combine integrally to add to our knowledge of the quantitative systematics of brain function.

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