

XIII. COMMUNICATIONS BIOPHYSICS*

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A. RHYTHMIC AFTERDISCHARGE TO FLASHES

In response to slowly repeated flashes of light, the parieto-occipital EEG of human subjects with closed eyes frequently exhibits a series of rhythmic voltage fluctuations, a phenomenon that has been called the rhythmic sensory afterdischarge (references have been given elsewhere¹). This rhythmicity is usually not evident upon visual inspection of the EEG inked trace, but becomes detectable by the use of averaging techniques. The frequency of the rhythmic afterdischarge may be quite close to, if not identical with, the predominant frequency of alpha activity. Therefore components of the EEG might appear in the averaged responses merely as sampling artefact and would not represent a true afterdischarge. Results from a series of mock-up experiments to illustrate this point have been described elsewhere.² Although the possibility of such an occurrence is greater the smaller the number of responses averaged, it cannot be eliminated even for averages of as many as 200 stimuli.

Several types of controls to test the validity of such averaged responses were described previously.^{3,4} These include the use of arrhythmically as well as rhythmically repeated stimuli, the use of several slightly different flash rates for periodically repeated

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flashes, and the use of an opaque cover on the flash source so that no light reaches the subject's eyes. It should be noted that when no stimuli are applied it is assumed that all the statistical characteristics of the EEG are the same as they are when stimuli are presented. Such an assumption is not made, however, if the "control average traces" are carried out on the same recordings that were used to determine the averaged evoked responses. For these controls the averaging computer can be triggered at times that are shifted with respect to the actual instant of stimulation. When the stimuli are presented at random intervals, triggering the computer after a fixed initial delay, which is several times the average interval between stimuli, provides one such control.³ This procedure, however, does not eliminate the possibility that there might be remnants of stimulus-locked activity in the EEG after such large delays. On the other hand, triggering the computer at a fixed interval of time before the occurrence of a stimulus entirely eliminates this possibility.

For periodic stimuli, the averaged response is simply repeated for integral positive or negative multiples of the interstimulus interval; hence this procedure does not provide a control for a sampling artifact. For periodic stimuli, however, the computer can be triggered by repeated pulses separated by intervals that differ slightly from the interflash interval. Alternatively, the computer can be triggered with randomly recurring pulses whose average interval is approximately the interstimulus interval.

Illustrations of these controls for averaged evoked responses are shown in Figs. XIII-1, XIII-2, and XIII-3. The visual stimuli produced by a stroboscope (Grass Model PS-2, intensity setting 4, peak flash intensity 4,000,000 lumens). The stroboscope was triggered by means of a repetitive-pulse generator (Tektronix Type 162). For randomly recurring stimuli, the latter was triggered by random low-frequency electrical noise from a noise generator (Elgenco Model 312A). The minimum interstimulus interval was 0.8 sec; the average interval was 1.2 sec.

The averaged evoked responses were computed with the aid of the Analog Computer for Neurophysiology,^{5,6} modified for the simultaneous averaging of two channels on identical or on different time bases.⁷ The autocorrelograms, which were computed with the Analog Correlator for Brain Potentials,⁸ and the averaged responses were evaluated simultaneously. The two results were written out on the same time scale by a two-channel ink-writing galvanometer (Texas Instruments Dual Rectiriter). From the display of such a write-out (Fig. XIII-3), the time structure of the averaged response and the period of the rhythmic afterdischarge can be compared directly with the time structure of the EEG from which the average was obtained (for example, its average period and degree of rhythmicity). Such a direct comparison of the averaged evoked response with the EEG from which it is derived would not be possible, of course, if the summary analysis of the EEG were displayed as a spectrum.

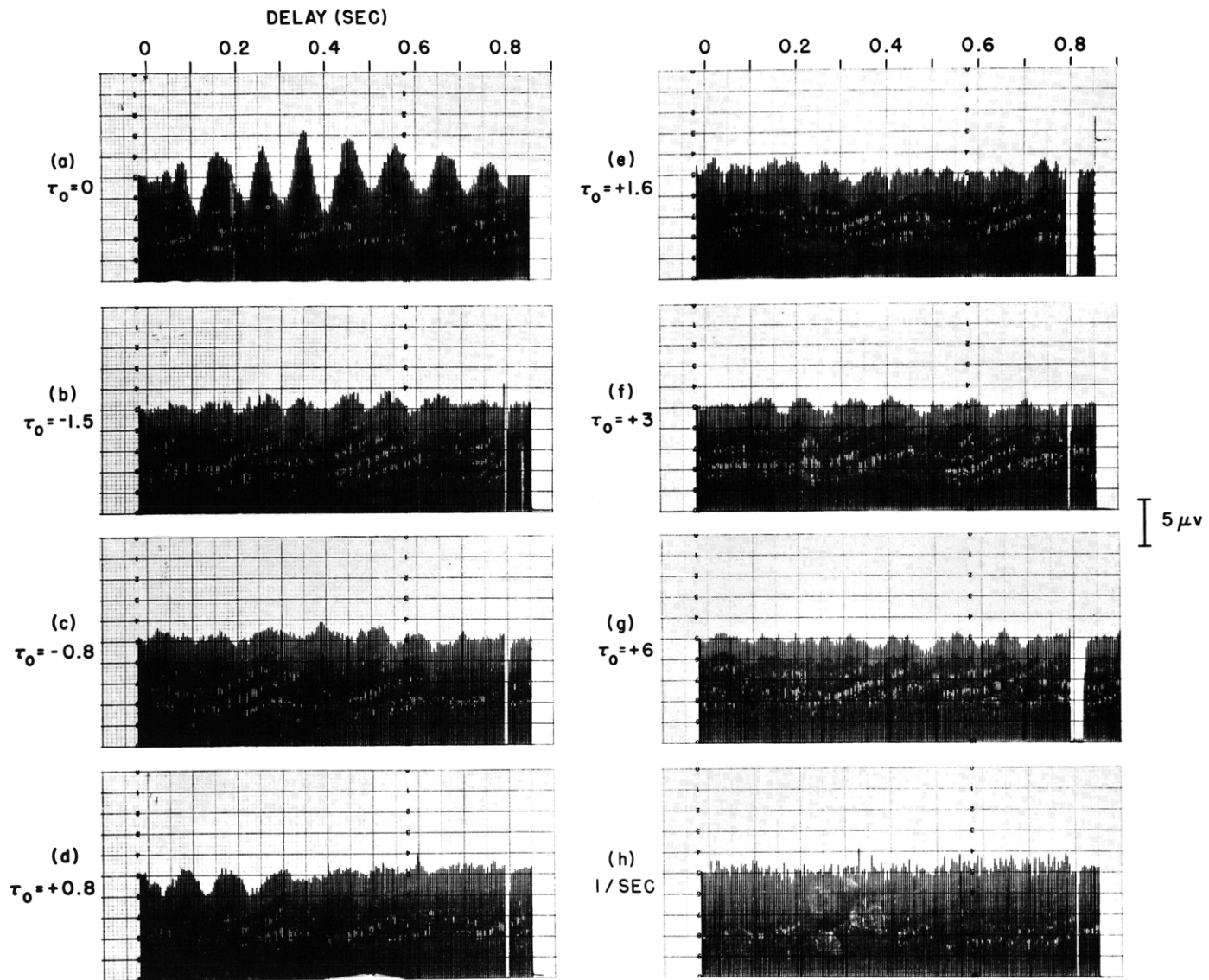


Fig. XIII-1. Averaged responses with different initial delays for a 4-minute parieto-occipital EEG recording. Aperiodic flashing, eyes closed. Subject: W. A. R.

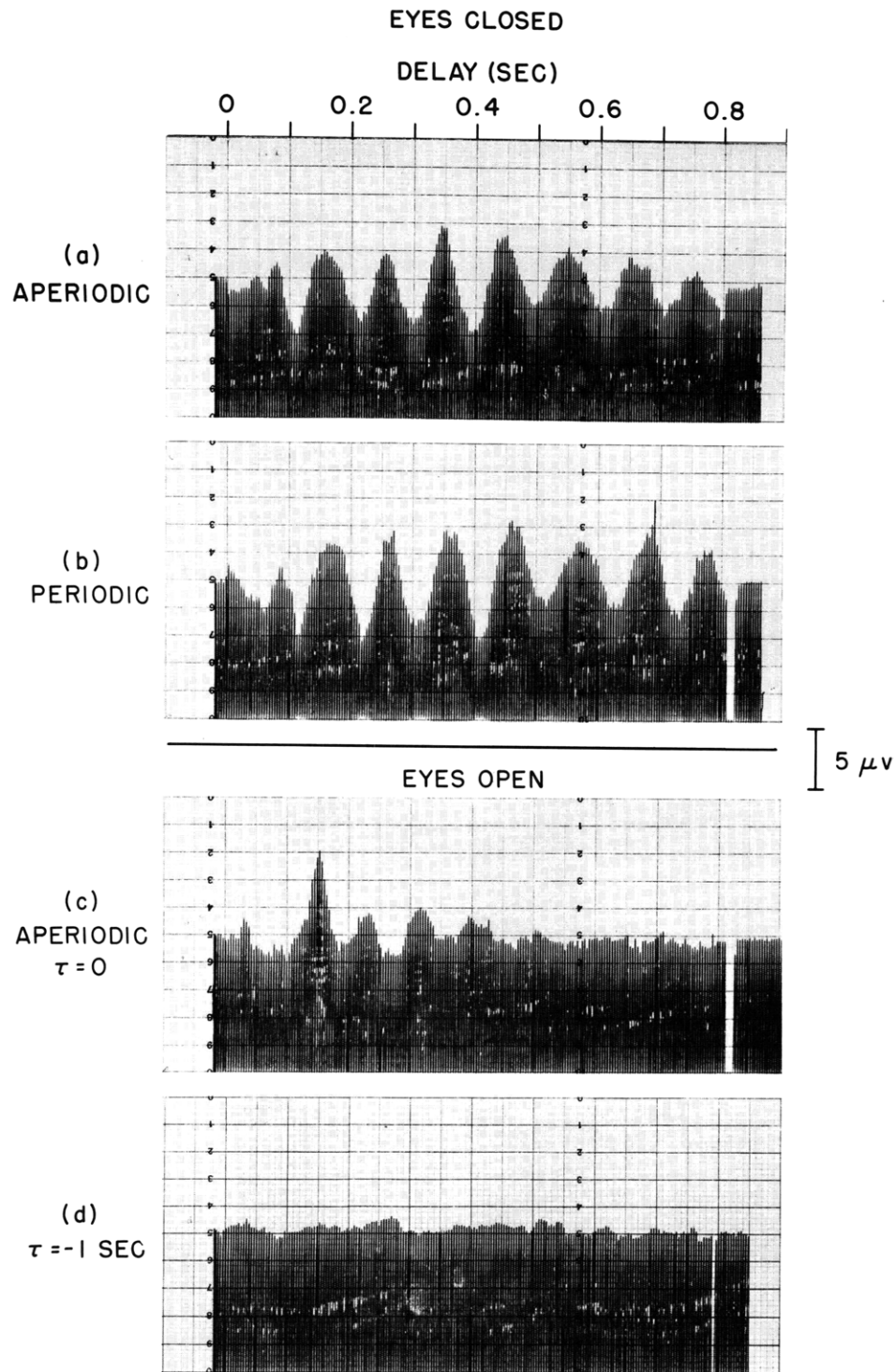


Fig. XIII-2. Averaged responses for aperiodic and periodic flashing with eyes closed and open. Subject: W. A. R.

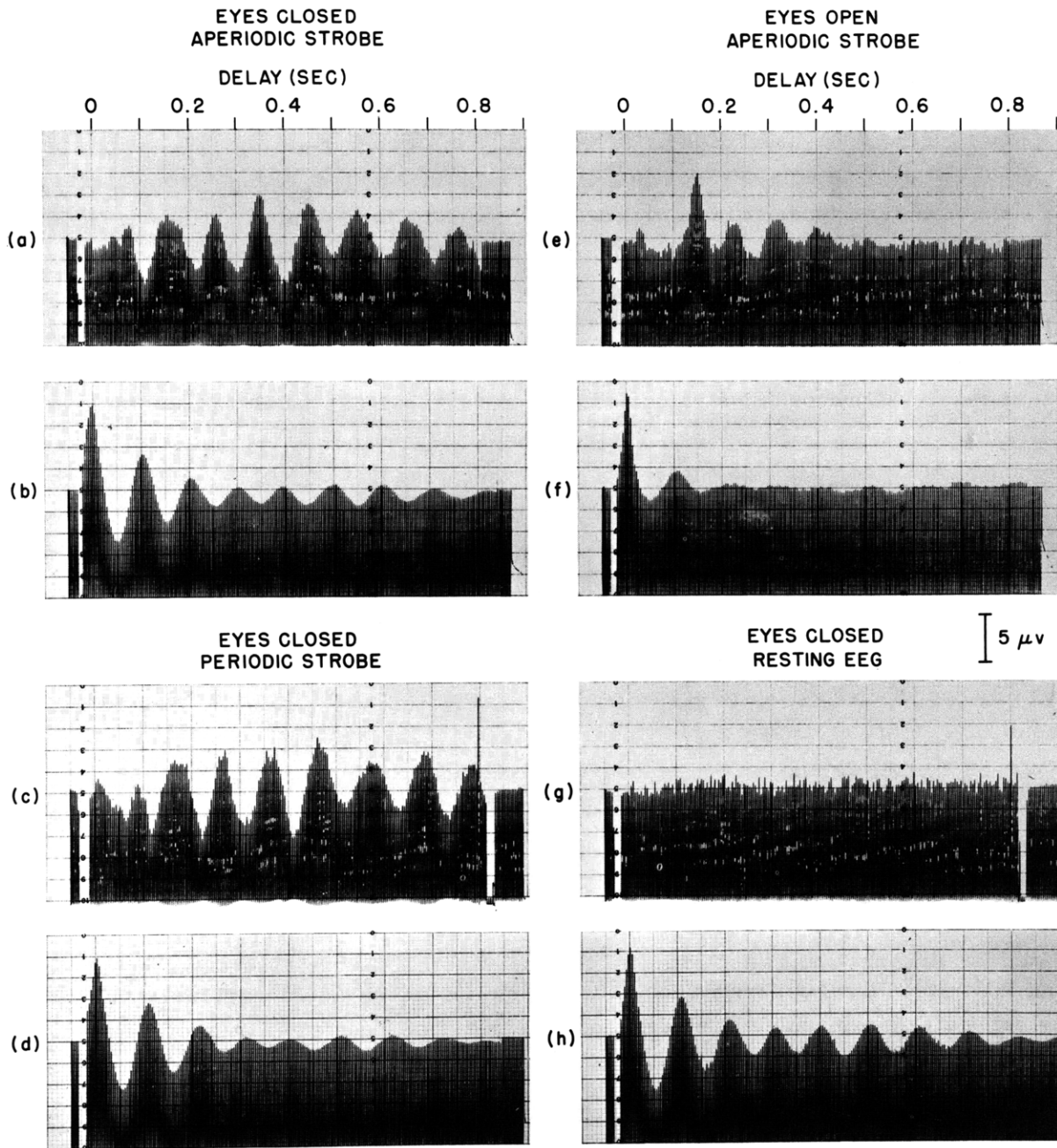


Fig. XIII-3. Averaged responses and autocorrelograms for the midline parieto-occipital EEG under various conditions. Subject: W. A. R.

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In Fig. XIII-1a, the averaged evoked response from a 4-minute midline parieto-occipital EEG recording (eyes closed) is shown for randomly recurring flashes. Two hundred responses were averaged. There is a very prominent rhythmic afterdischarge with a frequency of $\sim 10/\text{sec}$. The peak-to-peak amplitude of individual waves ranges from 5 to 10 μv . The averaged responses shown in Fig. XIII-1b through h were computed as controls for this result. The results of b through g in Fig. XIII-1 may be considered as an ensemble of averages whose initial delays (τ_0) range from -1.5 sec to +6 sec. The departures from a flat baseline indicate the extent of artifact in the averaging process due to sampling error. The maximum peak-to-peak of these random excursions in any one average is approximately 2.5 μv , or approximately 1/4 the maximum peak-to-peak amplitude of the "real" response shown in Fig. XIII-1a. For the result shown in Fig. XIII-1h, the computer was triggered completely independently of the original EEG recording by a periodically recurring pulse which had an effective repetition rate of 1/sec. Because of this complete independence of computer triggering and original EEG recording, the successive pen excursions in Fig. XIII-1h are also independent, in contrast to those in Figs. XIII-1b through g. The peak-to-peak amplitude of the sampling-artifact error in Fig. XIII-1h is approximately 2.5 μv , which is in agreement with that shown in Figs. XIII-1b through g. (A similar computation for the resting EEG is shown in Fig. XIII-3g.)

After consideration of the results described above, there is little question about the significance of the rhythmic afterdischarge shown in Fig. XIII-1a; it is clearly not a result of a sampling artifact.

In Figs. XIII-2a and b, the responses evoked by arrhythmic and by rhythmic stimulation (flash-rate 1/sec) are compared, and it is evident that the two are quite similar. In Fig. XIII-2c the evoked response for arrhythmic stimulation for open eyes is shown. The initial delay of the control for this computation was set at -1 sec (Fig. XIII-2d). It is evident that an afterdischarge is definitely present when the eyes are open, although it is neither as great in amplitude nor as long in duration as that for eyes closed (see Fig. XIII-2a). The frequency of the afterdischarge in the two instances is very much the same. Comparison of the corresponding peaks of the waves for averages for eyes open and for eyes closed indicates that the latency of the afterdischarge is decreased by approximately 30 msec if the eyes are open. Alternatively, this apparent difference in latency could be ascribed to an initiation of the afterdischarge in an earlier phase if the eyes are open. Whether this effect is due wholly, or only in part, to the removal of the filtering effect of the eyelids cannot be stated from these results alone.

In Figs. XIII-3a and b, c and d, e and f, the averaged evoked responses for aperiodic stimulation with eyes closed, for periodic stimulation with eyes closed, and for aperiodic stimulation with eyes open are compared with the autocorrelograms of the corresponding EEG recordings from which the averaged evoked responses were

computed. For the averaged response shown in Fig. XIII-3g, and computed from the resting EEG recording, the computer was triggered entirely independently of the EEG recording by a pulse whose effective repetition rate was 1/sec.

From the autocorrelograms in Fig. XIII-3 it is evident that the average or dominant frequency is ~ 10 /sec in all cases. The degree of rhythmicity, as evidenced by the rate of decrement of the amplitude of the envelope of the correlogram, is highest for the resting EEG recording, and lowest for photic stimulation with open eyes. It is of particular interest that the shorter persistence of rhythmicity in the autocorrelogram for eyes open is paralleled by a shorter duration of the sensory afterdischarge for the same recording (Figs. XIII-3e and f).

These results confirm and extend earlier reports⁴ of the extent to which the rhythmic sensory afterdischarge and the intrinsic alpha activity exhibit parallel behavior in the parieto-occipital region of the cortex in man. Additional statistical tests have been carried out as a part of the computation in order to establish the validity of the phenomenon of the rhythmic afterdischarge. It is hoped that further study of the rhythmic afterdischarge may shed some light on the still unsolved problem of the exact origin and nature of intrinsic alpha activity.

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