a result, separate trend analyses were performed for each of the four profiles (Fig. 1). The control profile showed no significant trend, the profile for recalled clues showed a significant cubic and quintic component, that for recognized clues showed a significant cubic component, and the clues of which the subject was unaware showed no trend (*5*). These data suggest that awareness of the clue (as manifested by later recognition or recall) is reflected in a cardiac profile with a pronounced cubic component (two inflections); as such, the profile shows a good approximation to the cubic curves reported by Roessler *et al.* (*6*) for cardiac response to random tones, and to the curves reported by Schwartz and Higgins (*7*) for cardiac reactions to a simple motor response or to its ideational equivalent. All four profiles show an accelerative component after stimulus onset; this component is followed by a decelerative drop. When subjects in the present experiment were aware that a meaningful verbal clue was present in the protocol, their cardiac change closely followed the pattern shown by other subjects in response to explicit sounds or warning lights.

Our data support the work of Lacey (*2*) and his colleagues to the extent that attention to an external stimulus is reflected in a drop in mean heart rate. We would add that cubic change in rate is a good predictor of later recall; such a rate change seems to be a sign that the stimulus is being converted into long-term storage. Other, more subtle aspects of the cardiac profile seem to parallel changes in amount of attention being invested in the stimulus, and may pick up variations that are not reflected in later conscious report.

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Electroencephalographic Spectra and Reaction Time in Disorders of Higher Nervous Function

Abstract. *Cerebral electrical abnormalities associated with variability of attention and responsivity were sought in individuals with schizophrenia and epilepsy. Experimental and control subjects were given stimulus-response tasks, and average power spectra for brief electroencephalographic epochs preceding responses of short and long latency were compared. Spectra that precede long-latency or erroneous responses resemble the "ramp" configuration of spectra computed from scalp electroencephalograms for 1-second epochs triggered by (time-locked to) focal subcortical spikes.*

Extraordinary variability of attention, mood, and activity are characteristics of the stream of thought or behavior in a number of neurological and psychiatric disorders and suggest frequent and abrupt fluctuations in the regulation of underlying neural processes. The hypothesis tested in this study was that such variability might be temporally associated with the deviations from normal frequency and voltage commonly recorded in the scalp electroencephalogram (EEG) of individuals with a variety of severe behavior disorders and psychoses and in some patients with epilepsy. Examinations of EEG spectra associated with short and long reaction times in normal controls have yielded conflicting results, but in general indicate either no systematic change preceding the stimulus (*1*), or moderate slowing of background rhythms suggestive of "microsleep" (*2*).

Interruptions in the steady stream of thought are characteristic of patients with seizures and schizophrenic thought disorders. Paradoxically, these individuals may make prompt, almost reflexively immediate responses a few moments before or after the unexplained interruption. Scrutiny of simultaneous EEG's from scalp and limited subcortical placements has disclosed no change consistently related to the delayed reaction time or interrupted speech unless a frank seizure coincidentally occurs (*3*). Use of the high-speed digital computer, implanted electrodes, and averaged EEG from intervals immediately preceding or succeeding the stimulus (that is, time-locked to the stimulus) has led to demonstration of significant correlations between poststimulus evoked potentials or power spectra and response direction in trained cats in response to visual or auditory stimuli (*4*). If the wide variations in reaction time associated with certain acute or chronic brain syndromes reflect abnormal neuronal activity that is discernible at the scalp only as nonspecific slow and sharp activity, sorting of spectra time-locked to stimuli and associated with long and short reaction times may distinguish a more specific relation of erratic response to underlying disturbance in physiology.

Three lines of evidence legitimize this endeavor. (i) Although the irregularities of the EEG that occur in nearly half of the subjects with acute psychoses are of a nonspecific type, recordings from subcortical electrodes in such individuals have demonstrated spike activity related to disturbances in mental state (*5*). (ii) One of the few consistent objective psychologic measures in patients with schizophrenia is the considerable variability of reaction time, particularly in the processing of relatively complex verbal information (*6*). (iii) When deviations of both EEG and consciousness are more severe, as during epileptic absence, there is an unmistakable association between reaction time and abnormal discharges recorded in scalp or subcortical EEG's.

An auditory recognition task for verbal stimuli was used, in which the subject was read a list of 50 to 60 one-syllable words, half of which contained the letter G, N, I, or K and half of which did not. The subject was seated with eyes closed in a comfortable reclining chair facing the examiner. Before commencing the test, he was instructed to respond, as quickly as possible after each word, by pressing a response key upward if the designated letters were present or downward if they were not. The series of words was delivered by the experimenter through a voice-operated relay that placed a positive or negative pulse on one channel of the seven-channel FM tape recorder. The positive or negative signal of the patient's response was recorded on a second channel, permitting the computer to tag and store associated EEG spectra with respect to response latency, direction, and congruence of stimulus and response direction (signaling accuracy). Responses delayed more than 10 seconds were scored as no response. The EEG was recorded on the same tape from standard parietal, occipital, and temporal scalp derivations bilaterally. Total test time was usually 15 to 20 minutes, and subjects showed no tendency to drowse. The output of the tape recorder was monitored by an inkwriting oscillograph (Grass model IV EEG). Trials contaminated by movement or other artifact were deleted when the magnetic tape was analyzed.

The data were processed by a program written to our specifications (7) for the PDP 12 (Digital Equipment). The analog EEG was digitized at a sampling rate of 256 per second. The computer detected and displayed the stimulus, response latency, and response direction and indicated whether the response was correct or incorrect. The accuracy of the program was verified by continuous monitor of the original paper record during the computer display of successive trials. Accuracy of the Fourier analysis was verified by operation of the program on waves of known frequency. One-second epochs of digitized analog data were stored before and after each stimulus and before each response. Following digitization, reaction times were displayed and placement of cursors permitted calling up spectral plots for EEG epochs associated with any single or averaged number of reaction times and for correct, incorrect, or nonresponse trials. Although spectra from all artifact-free trials were included in the sample, actual comparison of spectra was made only between short- and long-latency, correct and incorrect, and no-response trials.

Data from 40 subjects, 18 normal controls (age 18 to 40 years), 12 patients with acute psychoses (age 17 to 35 years), and 10 patients with convulsive disorders complicated by interictal psychiatric disturbance (age 17 to 32 years) have been studied. All but three patients were receiving long-term antipsychotic or anticonvulsive medications. All patients and subjects were of normal intelligence and had previous routine EEG's in the laboratory. In order to maximize differences, spectra were averaged for the three to four shortest and longest reaction times.

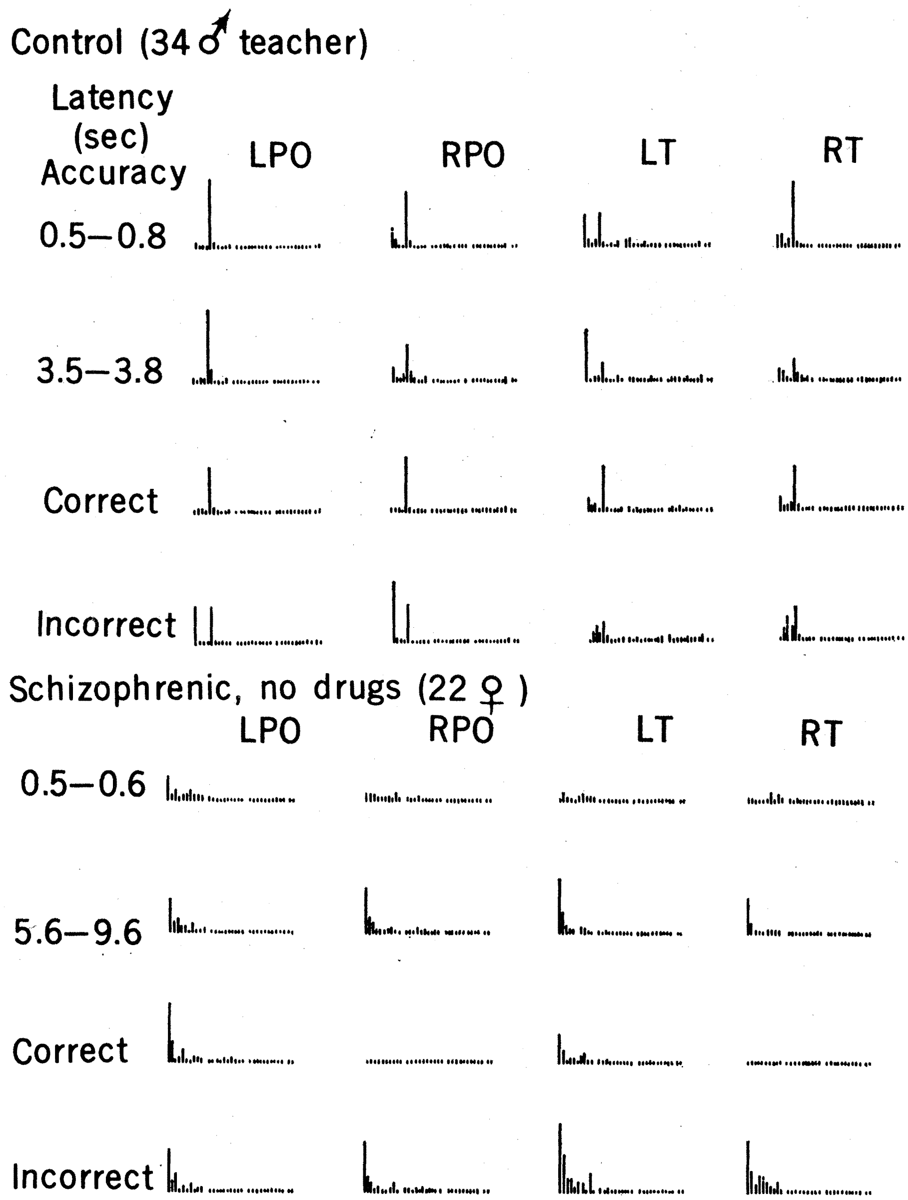

Fig. 1. Prestimulus EEG power spectra from healthy and schizophrenic subjects. Abbreviations are N, the number of epochs averaged; *LPO*, left parieto-occipital; *RPO*, right parieto-occipital; *LT*, left temporal; *RT*, right temporal. (Top) Spectra from a healthy right-handed physics teacher display a strong alpha peak from parieto-occipital regions bilaterally during 0.5-second epochs just preceding stimuli with either short or long reaction times ($N = 3$ in both cases). In contrast, a shift to delta frequencies, predominantly over left temporal region, is seen before stimuli followed by long-latency responses. Before stimuli followed by incorrect responses, a shift to delta frequencies is seen in all regions and is maximum in parieto-occipital montages. Correct and incorrect responses ($N = 4$ in both cases) are matched for latency. Responses with short and long latencies are all correct. Each histogram represents relative power as a function of frequency in half-second prestimulus epochs of the EEG. Columns represent 2-cycle bandwidths from 2 to 64 cycle/sec (left to right). (Bottom) Prestimulus spectra from 1-second EEG epochs are given for a woman with acute schizophrenia dominated by visual and auditory hallucinations and marked psychomotor retardation. Spectra from the right parieto-occipital region and both temporal regions for long-latency ($N = 4$) and incorrect ($N = 3$) responses resemble the ramp pattern (Fig. 2). In contrast, irregular or "noise" spectra precede short-latency ($N = 4$) and correct ($N = 3$) responses. Column heights give relative power at 1-cycle bandwidths from 1 to 32 cycle/sec (left to right).

Variability among spectra comprising the average was examined by inspecting superimposed Polaroid photographs of individual samples. In addition to the reaction time study, spectra were calculated during spontaneous episodes of psychomotor blocking for six of the subjects with schizophrenia or epilepsy and were compared with similar samples obtained during normal speech flow.

In a second phase of the experiment, power spectra were calculated for 10 to 20 1-second epochs of scalp or subcortical EEG that were time-locked to remote spike activity but were themselves free of spike activity discernible to the eye. These spectra were computed for three patients with well-localized spike foci, two with intracranial electrodes, and for a cat with a spike focus in the amygdala induced by carbachol. The spectra from EEG's taken from distant scalp sites immediately before and after focal epileptic spikes were compared with control spectra obtained from the same EEG montage but triggered asynchronously with respect to the spikes by an electronic pulse.

Results for the reaction-time and remote-spike analyses were as follows. Comparison of control subjects with the two patient groups demonstrated a wider range of reaction times and higher error rates for individuals with diagnoses of schizophrenia and epilepsy. The range of latencies for controls was 0.3 to 4 seconds, with a mean of 0.9 second and a standard deviation (S.D.) of 1.4 seconds. Comparable figures for psychotics were a range of 0.1 to 9.8 seconds and a mean of 1.38 seconds (S.D., 1.4 seconds). For subjects with epilepsy, reaction times ranged from 0.3 to 10 seconds, with a mean of 1.85 seconds (S.D., 1.6 seconds). The mean error rates were 4.4 percent for control subjects, 8 percent for those with psychoses, and 10 percent for patients with epilepsy.

Shift to lower frequency bands preceded prolonged response latency in half the control subjects and three-quarters of the patients with either seizures or psychosis (Fig. 1). No consistent localization was noted although right and left temporal regions were most often affected. Localized slow spectra were highly correlated with the site of the epileptic focus in patients with focal seizures and were identified over one or both temporal regions in all patients with generalized epilepsy.

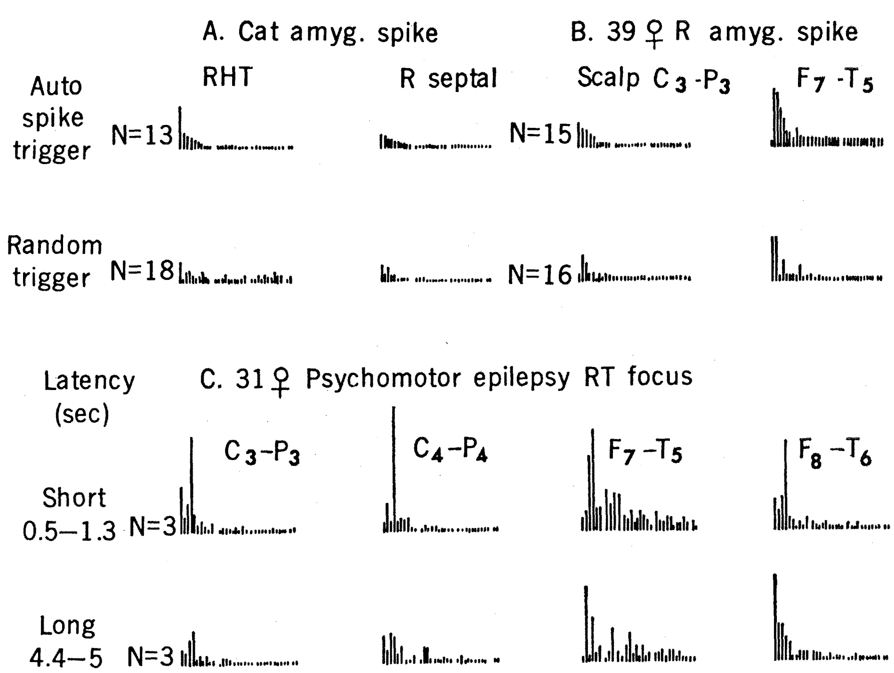

Fig. 2. The ramp configuration in spectra associated with spike activity. Column heights give relative power at 1-cycle bandwidths from 1 to 32 cycle/sec (left to right); *N* is the number of 1-second epochs averaged. (A) Spectra were computed from the right hypothalamus (*RHT*) and right septal nucleus (*R septal*) of a cat with an experimental seizure focus in the right amygdala (*amyg.*). (B) Power spectra from scalp electrodes on the left side (C_3-P_3, left central–parietal; F_7-T_5, left anterior–posterior temporal) were computed for epochs immediately after right amygdala spikes in a woman with psychomotor epilepsy and chronic electrode implants in the amygdala. The ramp configuration is seen in averaged power spectra from 1-second EEG epochs that follow amygdala spikes; no spikes were seen before averaging (A and B, line 1). Spectra associated with random trigger rather than with spikes demonstrate nonspecific noise pattern (A and B, line 2). (C) In power spectra from a woman with psychomotor epilepsy and right temporal (*RT*) spike focus, the ramp configuration is confined to the right temporal (F_8-T_6) scalp region and is seen only during long-latency responses.

A distinct pattern was shown for scalp or subcortical spectra time-locked to distant focal spike activity, compared with spectra triggered by a random control signal artificially generated between spikes (Fig. 2). A smooth ramp-like decrement in power from low to high frequency (Fig. 2, top row) was obtained by averaging EEG samples that did not show spikes but were coincident with focal subcortical spikes. This ramp pattern was easily distinguished from the irregular configuration for spectral envelopes displayed in averaged prestimulus intervals of most subjects and was not a function of the number of epochs comprising the average. This ramp pattern is consistent with the power spectrum from an epoch dominated by a single high-voltage transient, such as the EEG spike. Even though spikes are not detectable by visual inspection of the EEG from scalp or remote subcortical electrodes, averaging spectra from these areas which are coincident with a recognized spike permits emergence of a characteristic spectral pattern, presumably by volume conduction of inphase, common frequency components and canceling of the background noise of the local EEG.

Using this easily recognized ramp pattern as a template, we then searched through the spectral histograms generated by the PDP 12 from EEG's recorded in relation to the word-press task and psychomotor blocking. Unexpectedly, ramp spectra were identified in the prestimulus interval from subjects with seizure disorders or schizophrenia, but from no control subjects. Nine of the ten subjects with epilepsy had such spectra from at least one pair of electrodes in the prestimulus interval for prolonged or erroneous responses, and three of the twelve individuals with diagnoses of schizophrenia had ramp spectra preceding no-response trials or during psychomotor blocking. The ramp spectra were localized to the scalp region corresponding to the seizure focus in patients with psychomotor epilepsy, and were from a left or a right temporal montage in patients with generalized seizures or with a diagnosis of schizophrenia.

With his usual prescience, Grey-Walter forecast the probability of finding hidden out-of-phase spike activity in the interictal EEG's of patients with epilepsy (*8*). Ingenious computer programs have been developed for detection of subcortical spike activity by analysis of surface EEG's coincident with subcortical transients (*9*). By coupling a reaction-time test to examination of brief samples of EEG spectra averaged just before stimuli that precede prolonged or faulty responses, we have found a pattern that resembles power-frequency spectra coincident with known spike activity and is mathematically consistent with such an interpretation. Demonstration of such spectra before prolonged responses from patients with generalized epilepsy confirms evidence that a deep spike focus is not uncommon in this disorder (*10*). If psychologic tasks are developed which permit better discrimination of pathological interruptions in the thought stream, then the ramp spectra preceding delayed or erroneous response may be of some practical use for localizing subcortical abnormality without implantation of intracranial electrodes.

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Sexual Behavior: Ultrasonic Postejaculatory Song of the Male Rat

Abstract. *During the refractory period that follows ejaculation, the male rat regularly emits 22-kilohertz vocalizations. These cease after about three-fourths of the total period has elapsed, and this corresponds to an "absolute refractory period" during which the male cannot spontaneously initiate copulation. Similar 22-kilohertz vocalizations occur in other social contexts, and in general they appear to be desist-contact signals.*

Rats, mice, and many other rodents emit ultrasonic vocalizations (*1, 2*). The ultrasonic cries of newborns have received the greatest attention, but adults too produce and hear (*3*) these sounds. The vocal repertoire for social communication of the adult rat, *Rattus norvegicus*, consists primarily of ultrasonic calls. Sewell has described three such vocalizations: a 22-khz call emitted by defeated or supine subordinate males, a 50-khz pulse associated with aggressive activity, and a 50-khz vocalization that occurs during mounting activity (*2*).

The sexual behavior of the male rat has been exhaustively studied (*4, 5*). In brief, a series of mount bouts that culminate in intromission (penile insertion) leads to ejaculation, a postejaculatory refractory period follows, and a new series begins. This pattern is repeated for several ejaculations and after each, the postejaculatory interval (PEI) grows longer. The female generally does not hop, dart, and ear-wiggle during the PEI, whereas these behaviors are frequent in the copulatory series leading to ejaculation (*6*). The change in the behavior of the females toward refractory males may be influenced by the ultrasonic postejaculatory "song" of the male, the subject of this report.

This call was discovered during a standard observation of sexual behavior, during which ultrasounds were monitored with a Holgate ultrasonic receiver (bat detector) (*7*). Shortly after ejaculation, long, regular pulses were heard from the receiver, which was tuned to about 22 khz. These emissions were also viewed on an oscilloscope and appeared to be quite pure tones of frequency comparable to that indicated by the receiver. The female was removed from the observation chamber and the sound persisted. Later we observed that the calls could be correlated with long exhalations by the languid, refractory male rats.

The call was subsequently observed and recorded from a number of male Long-Evans rats of different ages and experience. Five sexually experienced males (approximately 150 days old), three old breeder males (12 to 18 months old), and three sexually naive male rats (70 to 90 days old) were subjects. Each was observed during at least two mating tests at intervals of approximately a week. Tests were carried out until either four PEI's had been recorded or spontaneous cessation of mating for more than 30 minutes occurred.

Female rats used as stimuli were prepared with injections of estrogen and progesterone (*8*). They were placed into the testing chamber, a 10-gal aquarium (40 by 26 by 29 cm) with cedar shavings on the floor, 5 minutes after introduction of the male; sexual responses—mounts with pelvic thrusting, intromission, and ejaculation—were recorded on a pushbutton-actuated strip chart recorded. Emission of the 22-khz call was monitored both auditorily with the bat detector and visually on an oscilloscope. The overall duration of calling was recorded on another channel of the chart recorder. The criterion for song production was the visible 22-khz signal on the oscilloscope screen.

Ultimately, the vocalization was recorded and characterized (*9*). It was found to consist of pulses of 22 to 23 khz, the duration of which ranged between 1 and 3 seconds. These pulses, emitted about a 0.25-second apart, formed trains of variable lengths (Fig. 1). Amplitude changes were apparent within and between pulses. At times the intensity of the sound was as high as 80 db (referenced to 0.0002 dyne/cm^2) measured 5 to 10 cm from the rat's head.

Each of the 11 males tested was observed to emit the vocalization during the PEI. None was observed to produce it during any other phase of the sexual sequence. There was considerable variation in the quantity and patterning of the calling. Some males called little during the PEI and others called almost continuously for the first three-fourths of the refractory period. Figure 2 shows the periods of vocalization for all of the animals over three PEI's. Calls generally began shortly after ejaculation