out of the tree, or both. Snake alarms were more likely to cause subjects to look down (*9*). The monkeys responded as though each type of alarm call designated different external objects or events.

This view of vervet alarm calls as rudimentary semantic signals contrasts with some earlier interpretations, which regard vervets' alarms, like other forms of animal communication, as manifestations of different levels of arousal that lack clearly defined external referents (*10*). If this were the case, responses to alarms should differ in relation to call features that mirror arousal levels, such as call length or amplitude. Our results indicated that variation in call length and equation of amplitude, as well as variation in the "arousability" of individuals as reflected by age or sex of alarmists, failed to blur distinctions among major response categories. Variation in the acoustical structure of different call types was the only feature both necessary and sufficient to explain response differences (*11*).

By giving alarm calls to some species but not to others, and by giving acoustically distinct alarms to different predators, vervet monkeys effectively categorized other species. More than 100 species of mammals, birds, and reptiles were seen regularly by the monkeys without eliciting alarm calls. When giving alarms, adults were most selective. Adults gave leopard alarms primarily to leopards, eagle alarms primarily to martial eagles, snake alarms to pythons, and baboon alarms to baboons. Sixty-four percent of all well-documented adult alarm calls ($N = 122$) were given to these four species. In contrast with adults, infants gave alarms to a much wider variety of species (two-tailed Mann-Whitney U tests, $P < .05$), and were more likely than adults to give alarms to things that posed no danger to them such as warthogs, pigeons, and falling leaves (*12*). Even for infants, however, the relation between type of alarm call and the stimulus that elicited it was not arbitrary. Infants gave leopard alarms primarily to terrestrial mammals, eagle alarms to birds, and snake alarms to snakes or long thin objects. Age-related differences in alarm-calling behavior (Fig. 1) indicate that while infants distinguished between relatively general predator classes (for example, between a terrestrial mammal and a flying bird), adults distinguished between particular predator species within such classes (for example, between leopards and other terrestrial mammals and between martial eagles and other birds). Evidently as infants grow older they sharpen the association between predator species and the type of alarm call. They behave as though their ability to classify other organisms improves with age and experience. The precise nature of the process of perceptual categorization that is implied and the possible roles of individual experience and adult tutelage in this development remain to be determined.

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3. Vocalizations were recorded at distances of 0.5 to 7 m on either Nagra III or Nagra SNN tape recorders with Sennheiser MKH 804 condenser microphones with foam windscreens.
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6. Beaulieu 5008S or Elmo 350SL Super-8 sound movie cameras were used at a mean distance of 15 m.
7. Long alarms contained a mean of five acoustic units, with a mean duration of 3.7 seconds (standard deviation = 2.5). Short alarms contained a single unit, with a mean duration of 0.3 second (S.D. = 0.2).
8. Sound intensities were measured on a General Radio sound level meter, model 1933, A weighting.
9. In only one trial did a monkey respond to a playback by giving an alarm.
10. See, for example, J. C. Marshall, in *New Horizons in Linguistics*, J. Lyons, Ed. (Penguin, Harmondsworth, England, 1970), p. 234; W. J. Smith, *The Behavior of Communicating* (Harvard Univ. Press, Cambridge, Mass., 1977), p. 181.
11. It has also been argued [for example, by Smith (*10*), pp. 181 and 270] that animal signals encode a limited number of generalized messages, such as attack, escape, or frustration, with the specificity of responses being highly context-dependent. In our experiments, however, context was not a systematic determinant of responses. Different alarms evoked different responses in the same context, and responses to some alarms remained constant despite contextual variation. The most parsimonious interpretation is that each alarm represented a certain class of danger and that monkeys responded according to their vulnerability to that danger at the time.
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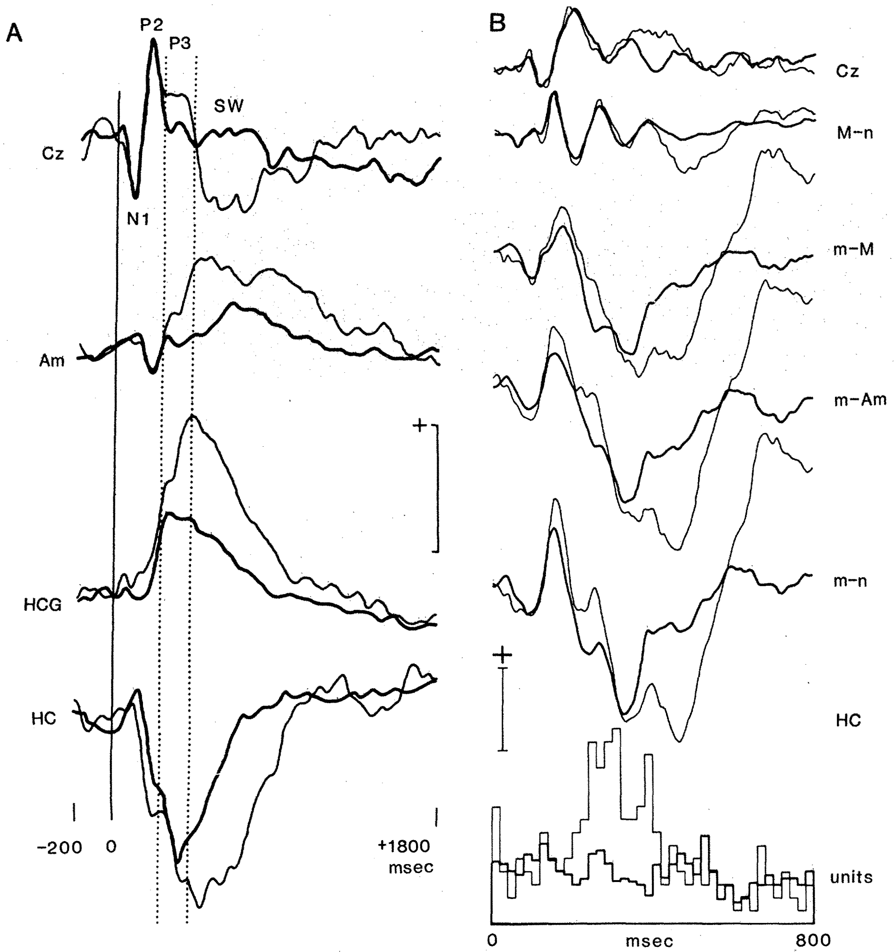
Endogenous Potentials Generated in the Human Hippocampal Formation and Amygdala by Infrequent Events

Abstract. *Infrequent, attended, auditory and visual stimuli evoke large potentials in the human limbic system in tasks that usually evoke endogenous potentials at the scalp. The limbic potentials reverse polarity over small distances and correlate with unit discharges recorded by the same electrodes, indicating that they are locally generated.*

Long-latency potentials that are dependent on the cognitive context in which a stimulus occurs, but are independent of the sensory characteristics of the stimulus and overt motor response required by the task, can be recorded from the human scalp. These potentials (N2, P3, and slow wave) are thus termed endogenous (*1*). Typically, they occur when the subject is actively attending to the stimuli, and the evoking event is infrequent (*2, 3*). Reliable changes in endogenous potentials occur in relation to cognitive variables (*4*) and neurological status, for example, in dementia and retardation (*5*). The functional interpretation of these changes has been limited because the location and nature of neural activity within the human brain during endogenous potentials is unknown (*6*). Here we report that large field-potential and unit responses are evoked in the human hippocampal formation and amygdala by infrequent, attended events.

Recordings were obtained from six adults of normal intelligence and personality with bilateral electrodes implanted in the hippocampus ($N = 20$), hippocampal gyrus ($N = 13$), and amygdala ($N = 8$) to locate epileptic foci for possible surgical removal (*7*). A simple method used to evoke endogenous scalp potentials is to present tone bursts of two different fixed pitches at random intervals. The subject's task is to count silently the number of "rare" tones (20 percent of the total presented) randomly interspersed among the "frequent" tones (*3*). We found that during this task, large potentials may be evoked by rare and by frequent tones in the hippocampal formation and amygdala (Fig. 1A). The limbic potentials were always larger in response to rare tones, even though the rare and frequent tones were of identical intensity and duration (*8*). Similar potentials were evoked by rare visual stimuli (Σ) flashed on a screen for 10 msec, randomly mixed at 2-second intervals with frequent visual stimuli (И) of equal luminance, contour, and contrast (Fig. 1B). The potentials generated in the auditory task were greatly attenuated if the same stimuli were presented while the subject was reading a book and explicitly instructed to ignore the tones (Fig. 2). Thus, long-latency limbic potentials are enhanced when the stimulus is attended and rare, but do not depend on the sensory modality or quality of the stimulus (*9*).

These endogenous limbic potentials (ELP's) presumably reflect widespread extracellular current flows generated by simultaneously activated synapses with a restricted spatial distribution (*6*). Characteristics of the ELP's suggest that they were recorded near the activated synapses where current flows are maximal and change direction over short distances. The amplitude of the ELP's varied with the subject and the electrode site, but was frequently between 100 and 200 μV (Fig. 1A). In 7 of 12 hippocampal, 4 of 7 hippocampal gyrus, and 4 of 6 amygdala sites, amplitudes greater than 40 μV were observed (*10*). This compares with a maximum amplitude for endogenous potentials of about 15 μV at the scalp and 25 μV in the cortex or hemispheric white matter (*11*). The variability in the amplitude of the ELP's is explained by their steep voltage gradients, demonstrated by their presence in bipolar recordings between electrode tips separated by as little as 1.0 mm, and by their varying polarities when recordings were made from nearby electrodes relative to an inactive reference (Fig. 1, A and B). Clear ELP's of both positive and negative polarities were recorded by electrodes directed toward each limbic area. Apparently this occurred because



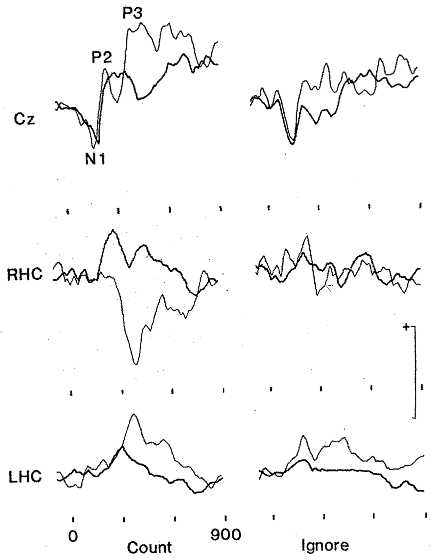


Fig. 1 (left). (A) Characteristic potentials evoked in limbic sites during an auditory paradigm (*3*). The largest negative potential was recorded in the hippocampus (*HC*) after rare tone bursts. Phase reversal occurred 9 mm posteromedial in the hippocampal gyrus (*HCG*) and 26 mm anterior in the amygdala (*Am*). The vertical dotted lines, 265 and 430 msec after stimulus onset, indicate the approximate onsets of the P3 and slow wave (*SW*) at the vertex (*Cz*). In all graphs, the thin lines represent the average of 35 to 45 responses evoked by rare stimuli, and the thick lines the averages to 155 to 165 frequent stimuli (*15*). Scale: 100 μV depth; 25 μV scalp. (B) Neural potentials evoked by rare and frequent stimuli in a visual task. Large field potentials were recorded from the hippocampal microelectrode regardless of whether it was referenced to the (inactive) tip of the nose (*m-n*), to an amygdala microelectrode 26 mm anterior (*m-Am*), or to a hippocampal macroelectrode 5 mm lateral (*m-M*) to the hippocampal microelectrode. Comparison of the field potential recorded by this macroelectrode referenced to the nose (*M-n*) with that recorded by the microelectrode 5 mm medial (*m-n*) indicates that relatively small changes in recording site may produce large changes in response morphology and amplitude. The units recorded by this microelectrode show a large increase in average firing rate (*units*) at the time when the simultaneously recorded potential to rare stimuli has a negative slope, and when a P3 is present at Cz (*16*). The recordings were made from the same electrode in the same subject (CNP 118) as those in (A), but 12 days later. Although morphologies may vary with the task, the polarity and the relative amplitudes of the rare and frequent limbic potentials at one site as compared with another appear to remain constant. The vertical line represents an average rate of seven spikes per second (*units*) and an average amplitude of 25 μV (*Cz*) or 50 μV (all other traces). Fig. 2 (right). Endogenous potentials recorded from the vertex (*Cz*) and hippocampus (*HC*) were greatly attenuated if the tones were ignored while the subject was reading. The right HC (*RHC*) recordings from this subject (CNP 120) illustrate potentials of opposite polarity evoked in the same electrode by rare versus frequent attended tones. In other electrodes they may evoke potentials of the same polarity, but of greatly varying relative amplitude (Fig. 1A); this suggests neural generators that are at least partly independent of one another. The left and right HC (*RHC* and *LHC*) electrodes, although directed toward symmetrical sites, recorded potentials of opposite polarity. In this figure only, one-third of the averaged waveform for Fpz (a midline forehead site) was subtracted from the Cz waveform in order to compensate for contamination of this lead by eye movement potentials. Scale: 40 μV depth; 10 μV scalp.

they fortuitously terminated on different sides of the reversal points in each structure. In addition to phase reversal within each anatomic area, there were consistent differences in polarity between areas. Although ELP's greater than 40 μV were usually negative in the hippocampus (six of seven cases), they were positive in all cases in the hippocampal gyrus and amygdala (*10*). In contrast to these endogenous potentials recorded in the limbic system, those recorded at different scalp sites (*12*) or with successive contacts of probes passing through the parieto-occipital or frontocentral association cortices to the deep hemispheric white matter (*11*) do not show steep voltage gradients or phase reversal.

Direct evidence that current flows generated by local synapses are present in the medial temporal lobe during production of ELP's was obtained from concurrent recordings of limbic unit activity. Behavioral paradigms that evoked ELP's also evoked changes in the firing rates of neurons in the amygdala (three of four electrodes), hippocampus (five of five electrodes), and hippocampal gyrus (five of five electrodes). On occasion, when the field potentials and action potentials recorded simultaneously by the same electrode both changed in response to the stimuli, these changes were correlated, in that they occurred at the same latency and varied in a parallel manner across conditions (Fig. 1B). The neural characteristics that were correlated were different electrodes: either an increase or a decrease in firing rate might be associated with either the slope or amplitude of the ELP. Such variation may be expected, owing to the phase reversals and differing cell populations within the recorded structures. Since the membrane capacitance of neural tissue shunts high-frequency signals, the changes in firing rate must occur in neurons directly adjacent to the recording electrodes. The extraordinary lamination of hippocampal synaptic input makes it unlikely that the synaptic current flows causing these changes in firing rate would cancel. Rather, as when hippocampal synaptic input is activated in animals (*13*), the synaptic current flows probably summate to produce the large amplitudes, steep voltage gradients, and local phase reversals characteristic of ELP's.

Our results do not indicate whether the scalp and limbic endogenous potentials are simply correlated, or whether some component of the scalp potentials is, in fact, a passively volume-conducted reflection of the much larger limbic-generated potentials (*14*). Their correlation, however, may be adequate to infer specific human limbic neural activity during the cognitive, neurological, and developmental conditions that evoke or affect endogenous potentials recorded from the scalp.

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7. Anterior temporal lobectomy is contemplated only when anticonvulsant therapy fails [I. Jensen, *Acta Neurol. Scand.* **52**, 354 (1975)]. Depth electrode recordings are required when the focus cannot be localized with emission computed tomography, pneumoencephalogram, arteriogram, pentothal activation, and 2 weeks of continuous monitoring by video and electroencephalogram. Our studies were conducted during monitoring for spontaneous seizures and provided information on the functional integrity of the recorded structures. Stereotaxic localization was based on direct visualization of limbic structures after injection of contrast medium into the temporal horn of the lateral ventricle and was confirmed by operative radiographs. Stereotaxic accuracy, based on histological examination of lobes removed for reduction of seizures, is approximately 88 percent [E. Halgren, R. D. Walter, D. G. Cherlow, P. H. Crandall, *Brain* **101**, 83 (1978)]. All recordings were with reference to the tip of the nose unless otherwise noted. Limbic field potentials were recorded by microwires 40 μm in diameter (also capable of recording action potentials) [T. L. Babb and P. H. Crandall, *Electroencephalogr. Clin. Neurophysiol.* **40**, 225 (1976)], by the cannulas through which they were placed, or by concentric gross electrodes in comparable sites. Surface recordings were from stainless steel electrodes placed in the outer table of the skull according to a modified 10–20 system [H. Jasper, *Electroencephalogr. Clin. Neurophysiol.* **10**, 371 (1958)]. The bandwidth of the recorded activity was determined by the amplifier and tape recorder characteristics rather than by the electrodes, and was either 1 to 100 Hz or 0.3 to 5000 Hz (half amplitude) in different recordings. Informed consent was obtained in accordance with procedures approved by the Human Subject Protection Committee of the University of California, Los Angeles School of Medicine.
8. Interpretation is confounded by the fact that rare stimuli were counted, whereas frequent stimuli were not. We administered the sequential analysis paradigm [K. C. Squires, C. Wickens, N. K. Squires, E. Donchin, *Science* **193**, 1142 (1976)] to control for this factor. Although only the high tones in a random sequence containing an equal number of high and low tones were counted, limbic potentials occurred in response to either high or low tones preceded by several tones of the opposite pitch. That is, these limbic potentials were in response to a tone that was rare relative to the local structure of the stimulus train, regardless of the covert response elicited by that tone.
9. While field and unit potentials may be evoked by simple or patterned visual stimuli in a task where all stimuli are identical and counted, they are usually confined to the posterior hippocampal formation, are clearly related to stimulus intensity, and are of much shorter latency than the potentials described here [T. L. Babb, E. Halgren, P. H. Crandall, *Neurosci. Abstr.* **2**, 380 (1976); C. L. Wilson, T. L. Babb, E. Halgren, P. H. Crandall, *ibid.* **5**, 285 (1979); unpublished observations]. Auditory stimuli rarely evoked any sensory response in these regions. A further demonstration of the endogenous nature of these potentials is our observation that they occur even in the absence of an evoking sensory stimulus, as when a tone pip is occasionally omitted from a regular series of identical tones. Limbic potentials were recorded when a random one-tenth of the stimuli were omitted from an ongoing train of 50-msec tone pips occurring every 1.1 seconds, with the subject counting stimulus omissions. This is similar to a task that evoked endogenous potentials from the scalp (*2*).
10. This includes data from only three patients: in the other three patients, similar qualitative observations were made, but large epileptic paroxysms prevented reliable ELP amplitude measurements.
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14. The obviously different waveforms of the limbic and the surface-recorded endogenous potentials (Figs. 1 and 2) are not evidence against volume conduction, given the uncertainty as to how the ELP waveforms generated in various lamina or structures will summate and be distorted as they pass through intervening tissue.
15. Subaverages of responses to 40 frequent stimuli demonstrated that the differences in responses to rare and frequent stimuli reported here were not due to differing numbers of trials used in constructing the average.
16. Bursts of action potentials of decreasing amplitude, a characteristic of hippocampal neurons, were recorded by this microelectrode, suggesting that it was located in the pyramidal layer of Ammon's horn [S. E. Fox and J. R. Ranck, Jr., *Exp. Neurol.* **49**, 299 (1975)].
17. Supported by National Science Foundation grant BNS 77-17070, by Public Health Service grant NS02808, and by the Ralph Smith Foundation. We thank T. Sanquist, R. Norman, J. Buchwald, J. Engel, Jr., M. Brazier, E. Carr, and E. Mariani for assistance; S. Hillyard, J. Lieb, L. Paul, K. Squires, and G. Wolfe for useful comments; and our subjects for their active cooperation.

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