have transformed the goggles into effective blindfolds.

In six of the experiments described, three bats carrying radios were released simultaneously, one with blindfold, one with goggles, and one without a mask. The behavior of bats released singly or in groups of three was indistinguishable; there was no evidence that one bat followed another.

The difference between the behavior of the blindfolded group and that of the bats which could see indicates the importance of vision for rapid orientation of these animals at the release point. We do not yet know which aspects of the visual environment are important for this oriented behavior. The visual acuity of *P. hastatus* as measured by Suthers (*4*) lies between 0.7° and 3.0°. This visual acuity would allow the bats to distinguish from the release points such features of the terrain as the northern range of mountains in which they live. The bats might conceivably use celestial cues, but some of the accurate headings shown in Fig. 1 were observed on moonless nights or under overcast skies.

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References and Notes

1. T. C. Williams, J. M. Williams, D. R. Griffin, *Animal Behaviour* **14**, 468 (1966).
2. The transmitters were designed by W. W. Cochran ["Techniques in aerial telemetric studies of nocturnal migration of birds," Prog. Rep. 1, NSF grant GB-3155 (1965)], adapted for use on bats by P. Hartline, and built by the Electronics Laboratory of Rockefeller University. The receiver was constructed by S. Markusen, Esko, Minn.
3. G. V. T. Matthews, *Ibis* **103a**, 211 (1961).
4. R. Suthers, *Science* **152**, 1102 (1966).
5. We thank D. R. Griffin, J. Crane, the staff of the William Beebe Tropical Research Station of the New York Zoological Society in Trinidad, W.I., Robert Loregnard, and the Trinidad Government bat collectors under his supervision for assistance. Research supported by contract Nonr 4857 (00) between the Office of Naval Research and The Rockefeller University.

10 January 1967

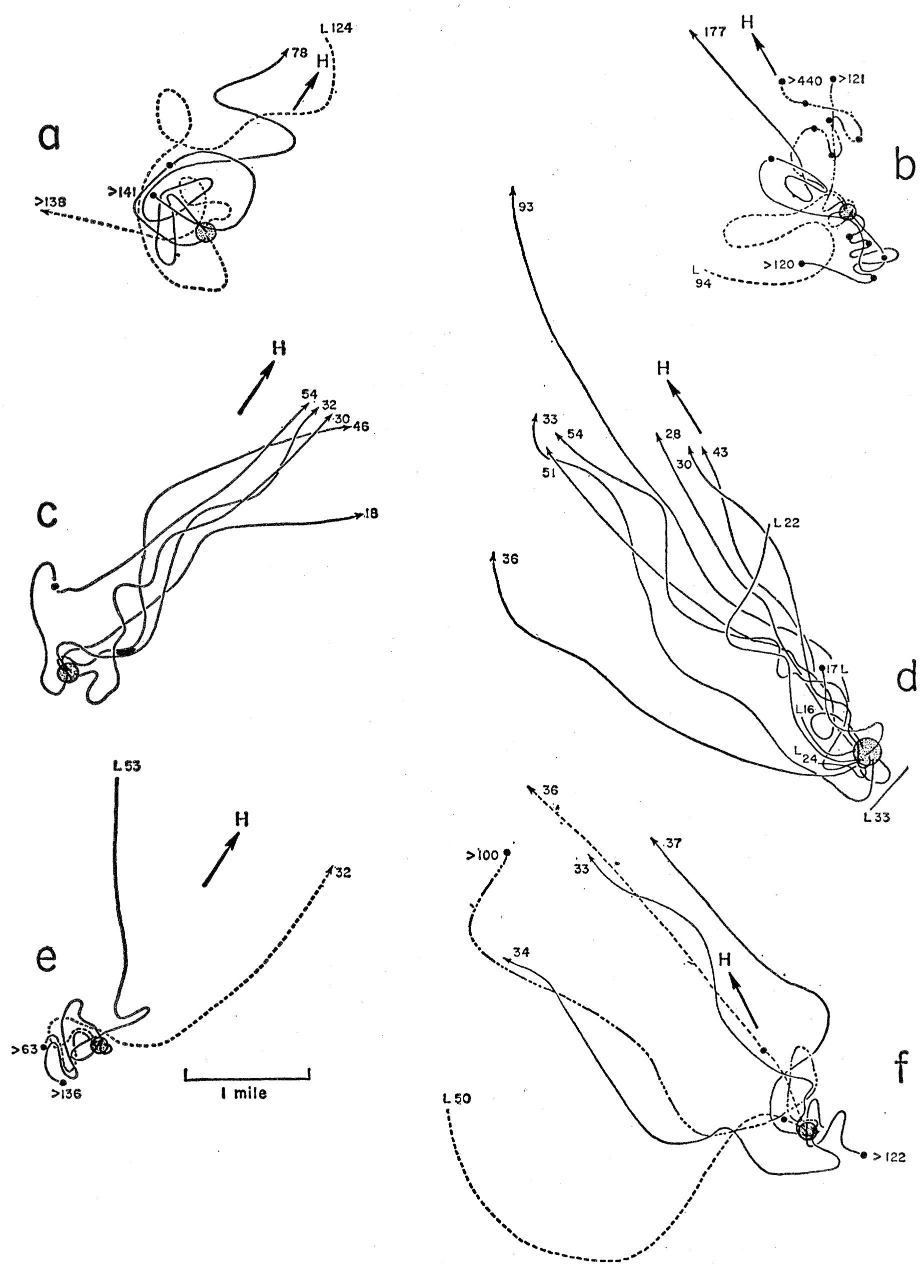

Fig. 1. Approximate flight paths of bats released 10 km from their home cave. Home direction is shown by *H*, release point by large circle, except for one bat in (d) released 0.5 km to the east. Parts (a) and (b) refer to blindfolded bats, (c) and (d) to bats without masks, (e) and (f) to bats equipped with goggles. In (a), (b), (e), and (f) solid lines mean bat returned with mask effectively in place, broken lines that mask was not effective on recovery, and lines containing both dashes and dots refer to bats not recovered at all. Numbers at the end of each line give the elapsed time in minutes from time of release until the signal was lost (> means experiment ended while signal still clear). Arrowheads signify gradual fading of the signal, and *L*, sudden loss of the signal.

Information Delivery and the Sensory Evoked Potential

Abstract. *The waveform of evoked responses recorded from human scalp is not determined solely by the physical eliciting stimulus, but also varies as a function of the effective information provided by the stimulus. There is a positive component whose latency is determined by the point in time at which ambiguity is reduced, and whose shape and amplitude are influenced by whether it is the presence or absence of an external event which delivers the information.*

We presented evidence (*1*) that the evoked potentials recorded from human scalp to simple stimuli, such as clicks or light flashes, are a function of the significance (*2*) of the stimuli to the subject. Responses to stimuli whose occurrence resolved some doubt or uncertainty were generally of larger amplitude and contained a positive-going process which reached peak amplitude at about 300 msec. This process was virtually absent when the occurrence of the stimulus did not resolve any uncertainty, that is, when the subject knew in advance which stimulus was to be presented next.

These and other findings (*1*) are consistent with the interpretation that certain features of the evoked potential waveform are related to the effective information content of the stimulus. Presentation of an anticipated stimulus merely provides information about the time at which it takes place, while an unanticipated stimulus provides information about both the nature of the stimulus and the time at which it occurs. The amount of information is greater for a stimulus with a low probability of occurrence than for one with a high probability. We have shown that the amplitude of the positive process follows stimulus probability. Except for latency, the positive-going process seems to be independent of the sensory modality of the stimulus which delivers the information.

We have been concerned with two other aspects of information, the point in time in a stimulus complex at which information is delivered and the mode of information delivery. In the experiment, the subject was asked to guess verbally, for each trial, which of two alternative stimuli would be presented —a single or a double click. The double-click stimulus consisted of two clicks separated by a brief time interval. Approximately 500 of each stimulus programed in random order were presented 3 to 5 seconds apart during a few hours. Electrodes were attached to vertex and left earlobe, but the precise location of the electrodes is not critical. Recordings were made with Grass P511 amplifiers set to pass a band of frequencies between 0.15 and 100 cycles. Data were recorded on multichannel magnetic tape to facilitate sorting of responses associated with different experimental categories. Approximately 200 responses entered into each average, obtained with a computer of average transients (CAT 400).

All the average response waveforms presented in Fig. 1 were elicited by physically identical single clicks. The first tracing is the response to single clicks when the subject was informed in advance whether the click would be single or double. The second tracing is the response to single clicks presented in the guessing situation. For both the first and the second tracings the alternative stimulus was a double click with a 180-msec interval between the members of the click pair. There is a large positive process (going downward in these tracings) when the subject was uncertain. The third tracing is also the response to single clicks in the guessing situation, but the alternative stimulus was a double click with a 580-msec interval between the members of the click pair. There is a resulting shift in latency of the positive process.

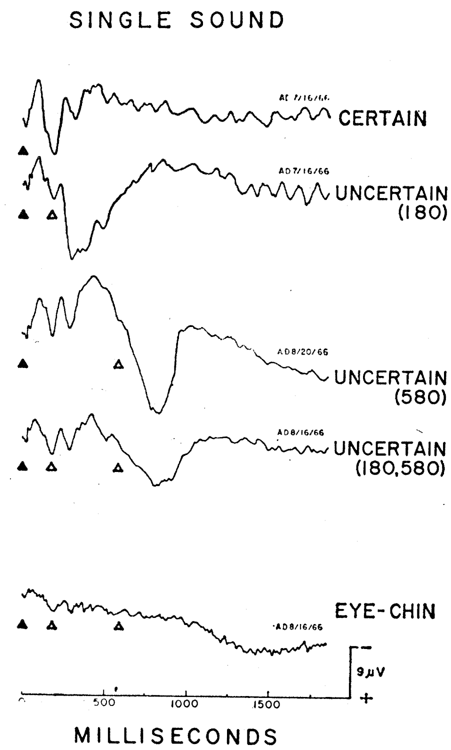

Fig. 1. Average response waveforms to single clicks obtained for one subject under several experimental conditions. ▲, Actual delivery of clicks. △, Points in time when a second click might have occurred but did not.

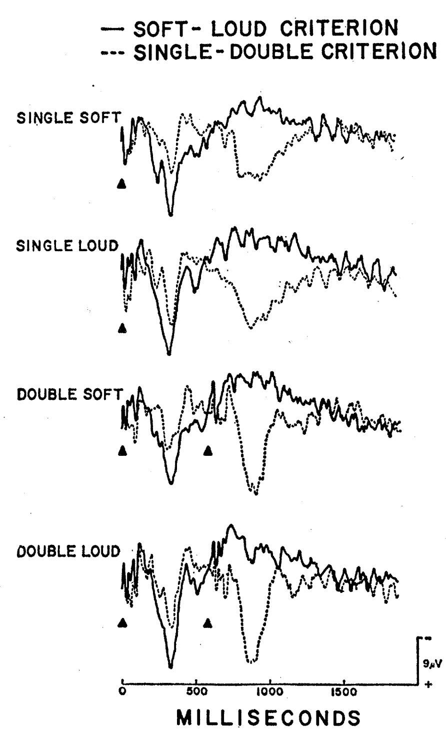

Fig. 2. Average response waveforms obtained to four types of clicks (as labeled) for one subject. ——, Waveforms obtained when the subject is guessing soft versus loud; – – –, waveforms obtained when the subject is guessing single versus double. ▲, Points at which clicks were delivered. Labels at the left specify the physical characteristics of the stimuli.

In the situation of uncertainty, the response to a stimulus is evidently in part a function of the alternative stimulus. This shift in latency of the positive process can be thought of in the following way: When the subject hears a click, he does not yet know whether it will be single or whether it will shortly be followed by a second click. When the alternative stimulus has the second click at 580 msec, this doubt cannot be resolved before this length of time has elapsed. When the alternative stimulus has the second click at 180 msec, the doubt can be resolved earlier. In other words, the latency of the positive deflection is a function of the point in time at which the second click might have occurred, but did not occur. Absence of an external event, or alternatively stated passage of time, evidently can act as an endogenous stimulus (*3*). These findings were replicated in 15 sets of experiments in five subjects.

The large positive process is related to the resolution of uncertainty. To test this assertion we used three stimuli: a single click, a double click with a 180-msec interval, and a double click with a 580-msec interval. The subject was asked to guess only whether the forthcoming stimulus would be single or double. The interval within the double click had no bearing on the correctness of his guess. The response to the single click contained only the late component related to the 580-msec alternative (Fig. 1, tracing 4). Our interpretation is that the absence of a click at 180 msec only partially resolves the uncertainty since the stimulus may still be double if a second click occurs at 580 msec. Therefore, the positive process is delayed until the point at which uncertainty is finally resolved.

The waveform at the bottom of Fig. 1 was obtained with a pair of electrodes so placed as to reflect several major sources of movement artifact. This tracing suggests that muscle activity was not significantly involved in the deflections with which we were concerned.

These conclusions with respect to the time at which uncertainty is resolved are illustrated even more strikingly as follows. The subject on any trial was presented with one of four stimuli: a loud single click, a soft single click, a loud double click, or a soft double click. The interval in the double clicks was 580 msec. The loud clicks were 10 db more intense than the soft clicks. Alternate blocks of trials were conducted under different instructions. In odd blocks of trials the subject was told to guess before each presentation whether the stimulus would be loud or soft. Here the criterion for correctness was intensity; whether the stimulus was single or double was irrelevant. In even blocks of trials, he was told to guess before each presentation whether the stimulus would be single or double; whether it was loud or soft was irrelevant.

For the blocks in which the subject's instructions were to guess single versus double, the response to single-click stimuli included a late positive component with a peak at approximately 900 msec (Fig. 2). As before, this process evidently registers the relevant absence of a second click. This component did not appear in the waveform obtained in response to the identical stimulus when the subject was guessing loud versus soft. For the double-click stimuli, when the subject was guessing loud versus soft, the response to the second click was quite small, and no late positive component of large amplitude can be seen; on the other hand, when he was guessing single versus double, the late positive component is very much in evidence. If we turn to the early portion of the waveforms, we find that for all stimuli a positive process peaking at approximately 300 msec had a larger amplitude when the subject was guessing loud versus soft than when he was guessing single versus double. When taken together, these findings are consistent with the idea that increased amplitude of the positive component is associated with the point in time at which uncertainty is resolved. When the subject is guessing loud versus soft, the first click delivers all the relevant information and resolves the uncertainty. When the subject is guessing single versus double, ambiguity is not resolved until the second click can be noted to be present or absent.

Since the subject was guessing, the occurrence of the stimulus informed the subject whether his guess was wrong or right. We have presented the combined waveforms without separating right and wrong guesses. In our earlier paper, we reported that the waveform obtained in response to a stimulus which signaled a correct guess was different from the waveform obtained in response to an identical stimulus which signaled an incorrect guess. Further experiments were done to ascertain whether different waveforms would be associated with different errors in a situation in which there was more than one way of being wrong. The experimental design is best explained by reference to Fig. 3. In this situation, there were no single clicks presented, but rather three kinds of double clicks. We presented in random order either a double click with a 180-msec interval ($S_{180}S$) between the members of the click pair, a 580-msec interval ($S_{580}S$), or a 980-msec interval ($S_{980}S$). Prior to each stimulus presentation, the subject was asked to guess whether the interval would be "short," "medium," or "long." This design generates a 3 × 3 table with three ways of being right but six ways of being wrong. If we postulate that all right guesses should yield similar waveforms, we can test this by examining the waveforms along the diagonal from the upper left to the lower right. These waveforms are not strikingly similar, nor are they uniformly different from all the wrong guesses. Note the second column, when the subject was presented with the medium (580-msec) interval. The waveforms for the two ways of being wrong in relation to this stimulus are quite different. Furthermore, it is quite striking that neither the physical stimuli, looking down the columns, nor the guesses, looking across the rows, impose uniformity on these waveforms.

These findings can be understood by considering the two ways in which information is delivered in this situation. The occurrence of the second click may be the earliest point in time at which the subject can discover whether his guess was wrong or right. For example, consider a trial in which the stimulus contained a short interval (180 msec) but the subject had guessed that the interval would be long (980 msec). The subject would discover that he was wrong at the occurrence of the second click at 180 msec. By contrast, consider the opposite case in which the stimulus contained a long interval (980 msec) but the subject had guessed that the interval would be short (180 msec). Prior to the actual occurrence of the second click at 980 msec, the subject would discover that he was wrong by noting the ab-

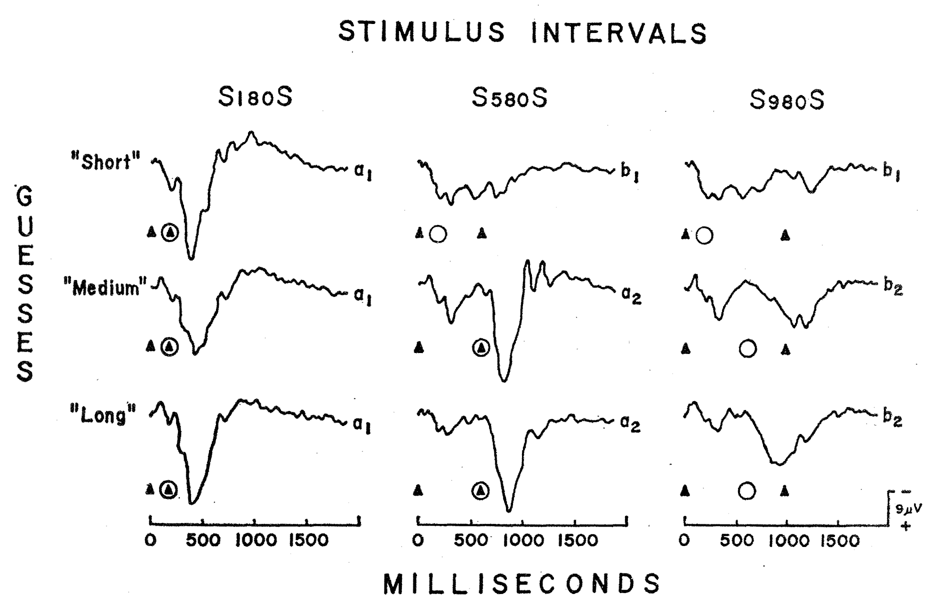

Fig. 3. Average response waveforms to three types of double clicks for one subject. Waveforms in the same column are obtained in response to physically identical stimuli but are associated with different guesses. Waveforms in the same row are obtained in response to physically different stimuli but are associated with the same guess. ▲, Points at which clicks were delivered. ○, Point at which ambiguity vanishes. (*a*) Cases where the occurrence of the second click provides the information, so that the triangle and circle coincide; the positive-going waveform has a larger amplitude and is relatively peaked. (*b*) Absence of the sound click provides the information (○ earlier than ▲), and the waveforms appear flattened. Subscripts 1 and 2 mark corresponding subgroups with respect to the relationship between the delivery of information and the occurrence of the second click.

sence of the second click at 180 msec. Even had he been right (guessed long) for this trial in which the second click was delivered at 980 msec, absence of the second click at 180 and 580 would have delivered all the information. The actual occurrence of the second click at 980 msec would be redundant.

In all the cases where the occurrence of the second click delivers the information (labeled *a*), the positive-going component has a larger amplitude and is relatively peaked. In all the cases where the absence of the second click delivers the information (labeled *b*), the waveforms appear flattened.

In the *a*1 group, information delivery and the occurrence of the second click are both at 180 msec. In the *a*2 group, the second click and information delivery also coincide, but this point in time is now 580 msec. Therefore, these resemble the *a*1 group except for a time displacement. In the *b*1 group, ambiguity is reduced after a short interval and they resemble each other more than they do the *b*2 group, in which ambiguity is reduced after a medium interval. These findings have been replicated several times in one subject and repeated in two other subjects.

It is conceivable that both the peaked and flattened waveforms reflect the same underlying process. Perhaps the delivery of information releases an identical waveform whether information is delivered by the presence or absence of an external event. However, when the information is provided by the occurrence of an external event, precise phase-locking of the positive process to time of presentation can be achieved. This would result in larger amplitude, more peaked waveforms in the average response. When the absence of an external event delivers information, the point in time at which information is obtained can only be specified by the subject's internal time sense. In this experiment, unlike the situations described in Figs. 1 and 2, there are three time intervals which the subject must internalize. Therefore, it seems possible that this would create some inaccuracy in time estimation and, we believe, consequent time jitter of the positive component. Averaging would make this time jitter appear as a flattening of the waveform. (These differences in the positive process in relation to the presence or absence of the second event may also be seen in the data of Fig. 2.) These conclusions might be tested by finding an effective way of fractionating populations of individual waveforms into like structured subgroups.

It seems unlikely that these findings merely reflect generalized fluctuations of arousal or activation, although the conditions which produce larger response amplitudes may be considered to raise the arousal level. The long latency of the positive process, its independence of the eliciting sensory modality, and the fact that it is best recorded from the vertex would seem to implicate the diffuse projection system. Yet there are features of the data which indicate that the increased responsiveness is differential and selective. The situations we have described are not characterized by generalized arousal so that the occurrence of *any* stimulus releases higher amplitude activity. Rather, the experimental conditions are devised to attach specific meaning to a particular type of stimulus. The mechanism which mediates the amplitude of the late positive component is capable of fine discriminations, and can be preset for release by a stimulus with a particular significance. Under certain conditions, the releasing external stimulus may be absent. In other words, the late positive process may be initiated endogenously. These considerations lead us to interpret the fluctuations in the late positive component of the evoked potential as a reflection of the information content of the stimulus.

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References and Notes

1. S. Sutton, M. Braren, J. Zubin, E. R. John, *Science* **150**, 1187 (1965).
2. The use of the word "significance" is an attempt to summarize the underlying relationship between a variety of complex psychological factors which influence the evoked potential. See also R. Herandez-Péon and M. Donoso, in *First International Congress of Neurological Sciences*, L. van Bogaert and J. Radermecker, Eds. (Pergamon, New York, 1957); M. Jouvet and J. Courjon, *Rev. Neurol.* **99**, 177 (1958); M. W. van Hof, J. van Hof-van Duin, I. van der Mark, W. J. Rietveld, *Acta Physiol. Pharmacol. Neerl.* **11**, 485 (1962); E. Garcia-Austt, *Electroencephalogr. Clin. Neurophysiol.* Suppl. 24, 76 (1963); R. M. Chapman and H. R. Bragdon, *Nature* **203**, 1155 (1964); H. Davis, *Science* **145**, 182 (1964); W. Grey Walter, R. Cooper, V. J. Aldridge, W. C. McCallum, A. L. Winter, *Nature* **203**, 380 (1964); R. Guerrero-Figueroa and R. G. Heath, *Arch. Neurol.* **10**, 74 (1964); M. Haider, P. Spong, D. B. Lindsley, *Science* **145**, 180 (1964); J. H. Satterfield, *Electroencephalogr. Clin. Neurophysiol.* **19**, 470 (1965); H. Begleiter, M. M. Gross, B. Kissin, *Psychophysiol.*, in press; J. Cohen and W. Grey Walter, *Psychophysiol.* **2**, 187 (1966); K. Lifshitz, *Psychophysiol.* **153**, 55 (1966); M. D. Low, R. P. Borda, J. D. Frost, P. Kellaway, *Neurology* **16**, 772 (1966); D. W. McAdam, *Electroencephalogr. Clin. Neurophysiol.* **21**, 194 (1966).
3. Responses to physically absent stimuli have been reported in various experimental contexts. For findings in humans, see V. S. Rusinov in *The Central Nervous System and Behavior* (Transactions of the Second Conference), M. A. B. Brazier, Ed. (Josiah Macy Jr. Foundation, New York, 1959); and J. S. Barlow, L. Morrell, F. Morrell, in *International Colloquium on Mechanisms of Orienting Reaction in Man* (Smolenici and Bratislava, Czechoslovakia, in press). For findings in cat, see E. R. John, *Mechanisms of Memory* (Academic Press, in press). Also relevant are observations on the contingent negative variation by W. G. Walter, R. Cooper, V. J. Aldridge, W. C. McCallum, A. L. Winter, *Nature* **203**, 380 (1964).
4. Supported in part by grant MH 07776 (S.S.) and MH 08579 (E.R.J.) from the National Institute of Mental Health, USPHS. P.T. is a USPHS trainee supported under grant MH 07997. We thank M. Braren, S. Hobson, and N. Lieberman for assistance with various aspects of this work; R. Laupheimer and R. Simon for instrumentation; and Dr. N. Beckenstein, Director of Brooklyn State Hospital, for providing the facilities for carrying out this research.

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Effects of Visual Form on the Evoked Response

Abstract. *The average visual evoked potentials elicited from relaxed human subjects are different for a blank visual field and one containing a geometric form, are different for different geometric forms of* equal *area, are similar for versions of the same geometric form of* unequal *area, and are different for two printed words equated for total letter area. These findings suggest that the waveform of evoked responses is not determined solely by the set of peripheral receptors which is stimulated, but it also reflects the perceptual content of the stimulus.*

Systematic relations between certain features of the visual evoked potential and such stimulus features as intensity, area, or color have been reported (*1*). However, the waveshape of the evoked response is not solely determined by the physical characteristics of the stimulus; it can be changed by procedures which direct attention to specific visual (*2*) or auditory (*3*) stimuli, or which alter subjective expectancy (*4*). Further, correlations between features of