Archiv für Psychiatrie und Zeitschrift f. d. ges. Neurologie 206, 309—322 (1964)

Burden Neurological Institute, Bristol

Slow Potential Waves in the Human Brain Associated with Expectancy, Attention and Decision

By

W. GREY WALTER

With 5 Figures in the Text

(Received August 8, 1964)

When stimuli in any modality are presented to a normal human subject electric responses appear over wide regions of frontal cortex (WALTER 1964). However, these responses decline after about 50 repetitions if the stimuli are monotonous and given at regular intervals, a phenomenon generally referred to as "habituation". Any change in the character of the stimulus may restore the responses and the most effective change is to associate them with some other event, such as a subsequent stimulus in another modality. When this is done there is gradually established a "contingency" between the stimuli, that is, the probability of association between them grows steadily with repeated pairing. In such conditions the brain responses to the first of each pair of stimuli tend to recover their original size and extent while those to the second tend to decline. This effect has been called contingent amplification and contingent attenuation.

Such effects suggest that the brain responses reflect a probabilistic analysis of the stimulus situation in terms of its information content. Habituation may be considered as indicating the steady reduction in information conveyed by a monotonous stimulus which becomes increasingly *probable.* Conversely, contingent amplification is the effect of increasing *probability of association,* that is the accretion of meaning, when the occurrence of the first stimulus always implies the arrival of the second.

Even when two stimuli are regularly associated, the responses tend to decline if their only significance is in their mere association; the brain responses reflect their subjective rather than objective significance. This can be seen clearly when the first stimulus is assigned conditional importance, either by association with a subsequent stimulus with an unconditional reflex effect (such as a mechanical irritation of the cornea), or by pairing with another stimulus to which the subject is instructed to make an operant response, for example by pressing a button to terminate a loud noise. In the conditions it is convenient to refer to the first stimulus as "conditional" and the second as "imperative"; in effect the experimenter is communicating with the subject in an elementary physiological language. In a typical situation the experimenter is saying: "*If* there is a click, there *will be* flashes so *press the button!*" In these terms the "habituation" to meaningless stimuli would be seen as due to the weakness of such repeated "Indicative" statements as "There are clicks".

When conditional and imperative stimuli are presented in this way a remarkable change appears in the frontal brain responses; a negative potential appears immediately after the conditional response and endures until the imperative response, when it declines rapidly to zero or becomes positive. This has been described as the "Contingent Negative Variation" or *Expectancy Wave* (WALTER et al. 1964). In conditions such as those described the E-wave is the most constant and stable of all electro-cerebral phenomena in normal adults. It does not depend on the character of the intrinsic normal rhythms and is as large and extensive with the eyes open as shut. In children, however, and in mentally disturbed patients, the E-wave is often elusive and variable; above all, it is extremely sensitive to social influences.

The amplitude of the E-wave is rarely more than $20 \mu v$ as recorded between an electrode on the vertex and one on the mastoid process. For this reason it is difficult to detect without some means of clarification such as average computation or cross-correlation with the conditional stimuli, but it can usually be seen in the primary records as a small hump following the conditional stimulus. Needless to say, this effect, which may persist for several seconds, cannot be recorded at all with the short time-conts generally used for conventional EEG; either direct coupling or time-constants of 5—10 sec are essential. No doubt this is why the E-wave has not been noticed before by the large number of experimenters who have been studying human evoked potentials with the aid of computers. Similar waves and slow potential changes have been reported in animals during conditioning and arousal (CASPERS 1961, ROWLAND and GOLDSTONE 1963; RUSINOV 1960; SHVETS 1958).

Comparisons have been made between the amplitude and extent of the E-wave as recorded on the scalp with its representation on cortex and within the brain, using the chronic implanted electrodes designed for progressive leucotomy and the investigations of epilepsy (WALTER and CROW 1964). These have yielded some very interesting information about the effect of the superficial tissues on the EEG (COOPER, WINTER, CROW and WALTER 1964). In general, the amplitude of brain activity as seen on the scalp depends on the degree of synchronisation and area of cortex involved. The E-wave is remarkable in being almost synchronous over a very wide extent of frontal cortex, and is thus little attenuated by the intervening tissues (Fig. 1). In fact the amplitude of the E-wave as recorded directly from cortex is only about twice as great as that on the scalp. This observation applies to the particular conditions of these experiments, in which synchronised stimuli and prompt responses are involved; the less co-ordinated experiences and actions of everyday life evoke more intricate and irregular E-waves, which are accordingly more difficult to detect. These probably constitute a great part of the familiar irregular background activity of the EEG.

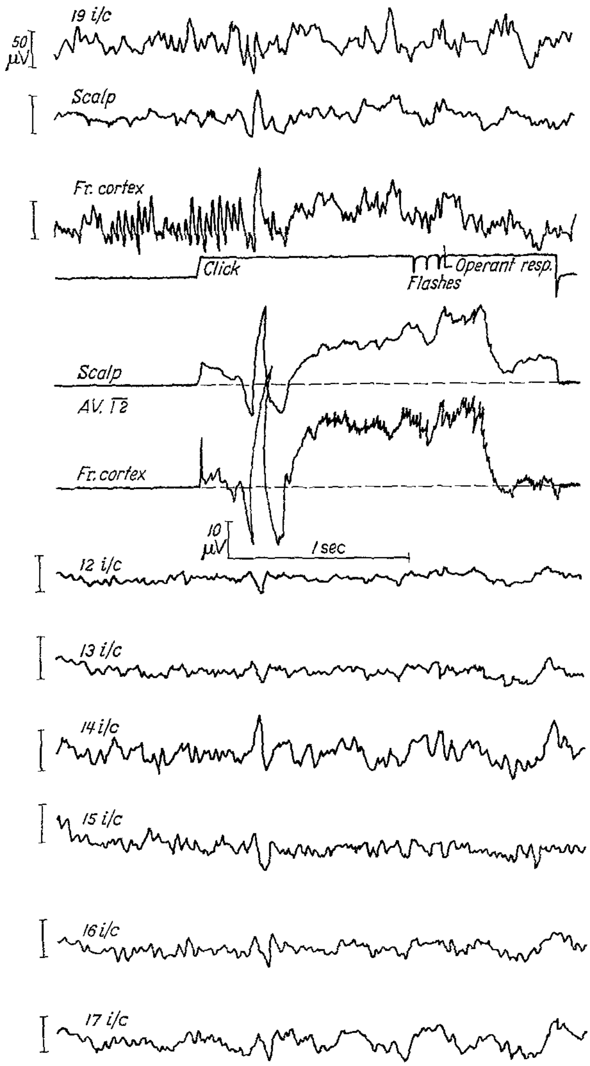

Fig. 1. Comparison of intra-cerebral, cortical and scalp representations of E-wave. Electrodes 19, 12, 13, 14, 15, 16, 17 and 20 are within various regions of frontal cortex. All these show the primary components of responses evoked by conditional clicks. The second channel is from scalp and the third from an epicortical electrode directly beneath it. The latter shows beta rhythm not seen on the scalp, but scalp and cortex both show the E-wave linking conditional and imperative responses. The cortical derivation is only about twice as large as the scalp for the widespread features. All electrodes are referred to intra-cerebral average reference

Attempts have been made to identify the E-wave with multiple intracerebral electrodes, but an elementary physical difficulty is encountered here—the intrinsic time-constant of all non-toxic electrodes. Any metal which makes direct electric contact with living tissue tends to poison it, and the metal of choice fpr DC recording, silver and its chloride, is particularly poisonous. The gold electrodes used for chronic implants have an intrinsic time-constant of about 0.1 sec when coupled to an amplifier with an input impedance of about 5 megohms. The E-wave is inevitably grossly attenuated by such a system and an input impedance of 50 megohms would be necessary to obtain records comparable with those from silver epicortical or scalp electrodes. However, such measurements as are possible suggest that the E-wave originates in the superficial plexiform layers of cortex, that is, from the feltwork of apical dendrites. This is in accord with the interpretations offered by experimenters with animals. The cortical surface certainly becomes electronegative with respect to the depths of the brain, and usually (again in the conditions of these experiments) the wave seems to spread from the prefrontal back toward the motor cortex, with topologic discontinuities to be expected from the convoluted nature of human cortex.

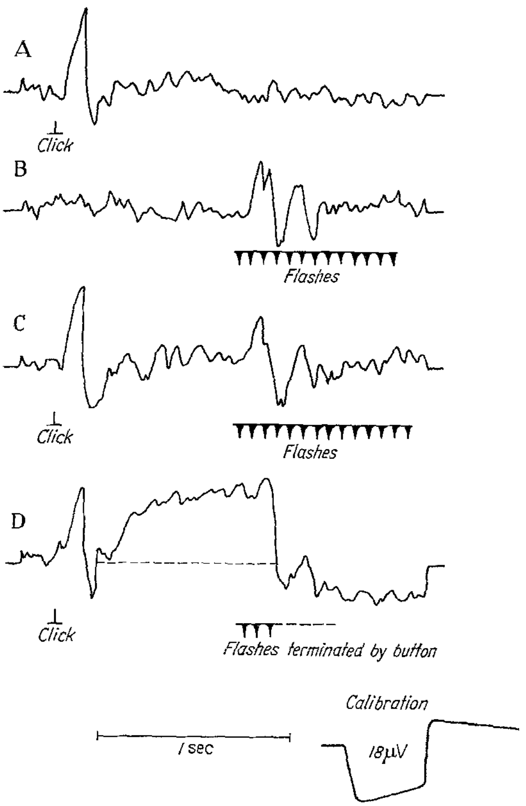

Fig. 2 A—D. Typical development of E-wave in normal adult subject. Vertico-mastoid derivation. A Average of 12 responses to clicks; B Responses to flashes; C Responses to clicks followed by flashes; D Appearance of E-wave following clicks when subject is instructed to respond to flashes one second later (from Nature 1964)

As already mentioned the E-wave arises always and only during sensory-motor association, but both the sensation and the motion may be of quite a subtle nature. In the simplest case the presentation of a conditional stimulus in any modality, followed by an imperative stimulus in another modality, evokes an E-wave following the primary conditional responses and lasting until the moment when the imperative response would have occurred (Fig. 2). The striking feature of the E-wave is that it appears, as it were, to submerge the imperative response, and terminates very abruptly at the instant when the latter would have subsided. The typical saw-tooth waveform of this phenomenon is remarkably like that of the time-base of an oscilloscope, rising steadily toward a maximum value over a time determined by the established stimulus interval, and dropping suddenly to zero. The duration of the E-wave as studied systematically so far is several seconds, but in some subjects the potential difference seems to be sustained much longer during "extinction" trials when there is no imperative stimulus to act as a "fly-back" trigger. Sometimes there is even a suggestion of a staircase or "Treppen" effect when conditional stimuli are presented at intervals of a few seconds without reinforcement to subjects with a very slow rate of extinction. Since the E-wave presumably represents depolarisation of the apical dendritic plexus, the possibility of "recruitment" in such a mechanism would be interesting to study in more detail. The subjects who have shown signs of this effect are highly suggestible and easily

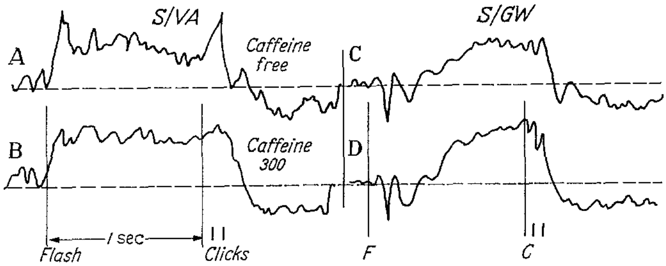

Fig.3A—D. Effect of Caffeine deprivation and administration in two normal subjects, S/VA and S/GW. A Caffeine-free responses to conditional flashes followed by imperative clicks; the E-wave drops before the imperative response which shows a clear negative component; B After taking Caffeine the E-wave is maintained until the positive decline of the imperative response; C A similar but less pronounced effect in the other subject

hypnotised (Black and Walter 1964); the capacity to maintain a high and even cumulative level of expectancy may be typical of this disposition, and may depend on some idiosyncrasy of the electro-chemical relations in the superficial cortical levels.

The effects of neurotropic drugs have not been studied systematically but most of the patients investigated have at some time been under the influence of the various compounds used for treating mental disturbance. As would be expected, sedatives and ataractic drugs tend to accelerate habituation, the failure of which seems to be the neurophysiologic correlate of anxiety. The E-wave is very sensitive to distraction, whether exogenous or endogenous, so that both excitement and depression are associated with depression and irregularity of the E-wave development. In normal subjects, conditions including medication which increase the capacity for concentration and attention tend to augment and stabilise the E-wave. Two normal subjects were studied after 36 hours' abstention from caffeine in tea and coffee. Both were accustomed to a normal intake, equivalent to a clinical maintenance dose. In both, the E-wave was significantly attenuated during abstention, and was restored when a full clinical dose of caffeine sodium citrate was ingested. Both subjects had pronounced symptoms of withdrawal, also rapidly relieved by restoration of the caffeine level. Similar effects have been observed with amphetamine, but marked idiosyncratic differences have been seen in normal subjects. One subject was observed for several hours during the action of 100 μg of LSD 25. The E-wave following visual stimuli (single light flashes) was enormously augmented and spread to nearly all regions. During this phase normal alpha rhythms were first accelerated and then entirely suppressed and at the same time the subject reported vivid illusions of grandeur and revelation following each visual stimulus.

The function of the E-wave has already been described as "priming" the frontal cortex; in a sense it is also inhibitory since it seems to regulate the time-relations of a motor discharge. However, the term "inhibition" should be used tentatively here; an alarm-clock may be considered as an inhibitory device since it prevents the sleeper from awakening too soon, but this is not a very useful sense of the word. The E-wave seems to act very much in this way, at least in an operant conditioning situation, since the muscular response becomes progressively more accurate and economical as the E-wave develops. This effect can be seen particularly clearly in experiments in which the operant response is arranged to be effective only if it is made after the onset of the imperative stimulus. In such a situation, without a conditional stimulus the reaction time is rarely shorter than 200 msec and the EMG of the operant muscles shows a rather massive and prolonged contraction, often with increased tonic activity between trials. When the conditional stimulus is introduced, say one second before the imperative stimulus, an E-wave appears after a dozen or so trials and the reaction time diminishes steadily; it may fall to 80 msec or even less. At first it was thought that this was a simple time-reflex; the subject might have learned to respond at exactly one second after the conditional stimulus. This explanation is incorrect, however, for two reasons. First, the reaction times are not distributed normally around the target interval—there are rarely any premature responses once the E-wave has developed. Second, when the imperative stimuli are withdrawn as in extinction trials or the conditional stimuli are given alone occasionally as in equivocation, no muscular responses appear at the expected instant when the imperative stimuli would have been expected. This means that the muscular activity must be dependent on the imperative stimulus but is considerably accelerated by some process initiated by the conditional stimulus and terminated by the imperative one. Furthermore, the pattern of the operant EMG becomes briefer and more synchronised; the muscular control is more precise and economical.

Psychological studies of reaction-times have demonstrated that the abbreviation of latency following a warning signal is greatest when the interval between warning and imperative signals is between 0.5 and 1.5 seconds. A similar effect is seen on the E-wave when the interval between paired physiological stimuli is varied (Fig. 4). The primary components of the conditional response in non-specific regions last about 250 m sec. and consist essentially of a sharp surface negative wave superimposed on a longer surface positive deflection. When the interval before

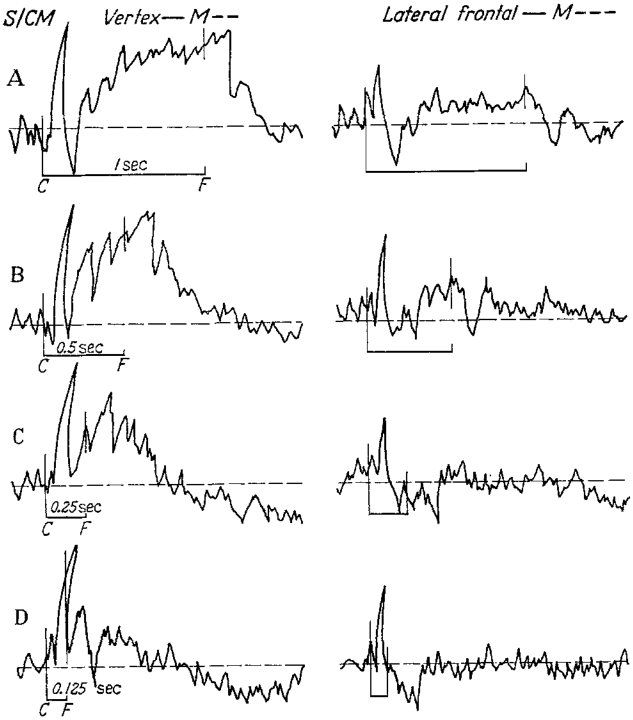

Fig. 4. The effect of inter-stimulus interval on the E-wave in vertex and lateral frontal region. A Clicks followed by imperative flashes one second later; the E-wave shows a typical development. The lateral frontal derivation is similar to the vertex on a smaller scale; B With 0.5 sec interval the E-wave can still reach full potential and shows in both derivations; C At 0.25 sec the E-wave cannot develop fully and the lateral derivation shows no secondary negative component; D At 0.125 sec the auditory and visual responses are merged so that the final positive component of the auditory response is cancelled by the first negative wave of the visual response. This shows that there is no inter-modality occlusion. The subject's reaction time was shortest and most constant at intervals between 0.5 and 1.5 sec

the imperative stimulus is one second or more the E-wave develops from the end of positive conditional component, but at shorter intervals the E-wave starts from the falling phase of the negative wave and in effect replaces the positive component. This is probably an instrumental synthesis, since the lateral frontal regions still show the positive component when the inter-signal interval is shorter than 0.5 sec. At short intervals (less than 0.2 sec) the subjective impression changes; the subject cannot always decide whether the conditional or imperative stimulus came first and responds to the association as a whole. The reaction times are distributed normally, with several anticipations. At these intervals there is apparently insufficient time for the E-wave to develop fully after the primary response process. This effect accords well with the psychological data and provides objective evidence of an optimal time-relation between warning and imperative signals for greatest efficiency and economy. Here again the individual variations are considerable and estimates of the optimal range of stimulus interval for development of the E-wave might be useful in the selection of candidates for training in precision control tasks which require rapid decision and attention to multiple cues.

A matter of great interest which has not yet been fully investigated is the degree of specificity of this effect. Can an E-wave which has developed from the association of a particular pair of signals and response also influence the response characters of an entirely different action, or are its accelerating and synchronising functions limited to the specific system with which it is associated? According to the Pavlovian hypothesis which this phenomenon seems to support, the early "generalised" stages of conditioning should be associated with rather widespread facilitation, but as the conditioned response becomes "concentrated" the effect should become more and more specific to the particular association. In operant conditioning (that is when a voluntary movement is made according to instruction) the E-wave seems to remain rather generalised for long periods covering many hundred trials, but in "classical" conditioning, for example of the corneal reflex, the E-wave reaches a maximum amplitude after perhaps 20 trials and tends to decline thereafter. There is a possibility therefore that when a specific voluntary action is involved, however trivial, a large area of cortex is engaged in the E-wave and responses to other stimuli might be expected to be accelerated and synchronised. This would be equivalent to "general alerting", the state in which a person is capable of an optimal performance, for example in driving a car or playing a game, when sustained anticipation, precision and economy of effort in several modalities are essential.

As already mentioned, the E-wave is very sensitive to social influences and may be evoked as readily by a word as by a purely physiological stimulus. In many experiments the preparatory movements of the experimenter were found to initiate an E-wave, and great care must be taken to avoid or mask any event which may precede the presentation of the relevant stimuli. The cessation or modulation of a stimulus is as effective as its initiation; unlike responses evoked in primary receiving areas, the E-wave is not proportional to the intensity or energy of a stimulus (Fig. 5). In this experiment a normal adult subject who was well-informed about the whole problem and was accustomed to the association of paired auditory and visual stimuli, was presented with a continuous tone of moderate intensity in a pair of earphones. He was told that the tone would be interrupted occasionally and that when this happened there would be a flash of light one second later as a signal for him to press a button. He found the continuous gentle sound very soporific but its interruption evoked a small non-specific response and after a few associations with the visual stimulus and operant response an E-wave appeared exactly as if the conditional event had been a stimulus in the physiological sense, and his reaction time also was abbreviated to the same degree. Experiments of this sort are providing interesting information on the relation between stimuli, signals, perception and experience.

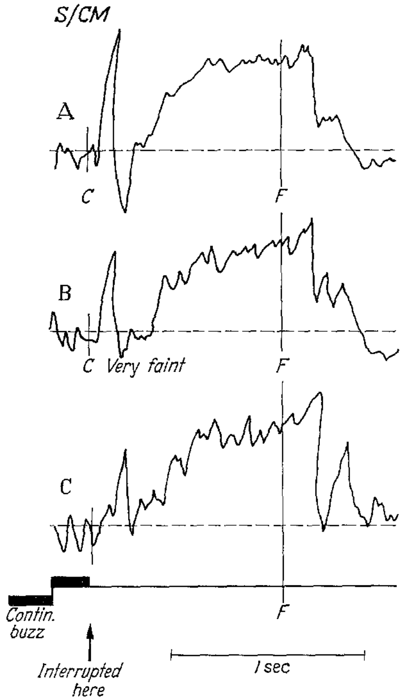

Fig. 5A—C. Independence of E-wave on stimulus intensity. A Responses to loud conditional clicks followed by imperative flashes; B Responses to very faint clicks in the same situation; the primary responses are diminished but the E-wave is identical; C Responses to conditional interruption of a continuous auditory stimulus; there is a long latency off-response and again the E-wave is the same as that evoked by a positive stimulus

In a sense the E-wave reflects the amount of information in a signal irrespective of its physical energy, but of course the "information" here is subjective, that is it depends on the attitude and motivation of the subject, as well as on the objective significance of the associated stimuli.

The application of these studies to clinical problems is still in the early experimental stage, but there is already ample evidence of correspondence between disturbances of mental state and the development of the E-wave. In normal adults the E-wave is the most constant and predictable electro-cortical feature—far more regular than the frequency, distribution and responsiveness of the intrinsic rhythms which may be entirely absent in quite normal people. The full development of the E-wave is a character of full maturity, however. In a group of twenty children aged 15 only 12 showed clear sustained E-waves and out of 6 university students aged 20, two had rather small and irregular

E-waves which were particularly susceptible to social influences. It would seem that the conventional age of 21 as the entry to the "years of discretion" is a happy and presumably not fortuitous choice. Below this age young people are unlikely to be capable of discreet associations and decisions, and are particularly sensitive to social influences of all sorts, whether "good" or "bad".

Patients suffering from chronic neuroses show a wide range of anomalies in the E-wave. Those whose ailment is primarily anxiety or fear develop E-waves slowly to moderate stimuli, and often show very slow or little habituation as well, but they are usually particularly sensitive to equivocal presentations. Whereas normal subjects maintain an E-wave down to an objective probability of association of about 0.7 (that is say 14 out of 20 conditional stimuli reinforced), anxious or phobic patients tend to lose their E-waves completely when only 2 or 3 conditional stimuli are unreinforced, and the effect of brief equivocation may persist for very long periods even with full reinforcement. On the other hand, some delinquents, particularly those with so-called psychopathic personalities who seek excitement for its own sake at the expense of society, are alerted by equivocation in the sense that the primary non-specific evoked responses are augmented, but they show little or no sign of an E-wave linking the two sets of stimuli even with unequivocal association. Correspondingly they appear to be unable to learn from experience and are therefore recidivist criminals, undeterred by punishment or the prospect of retribution.

Patients with compulsive-obsessional disorders display many irregularities, particularly in relation to the effect of the operant response. In one or two in this category the performance of the operant response has actually suppressed the expectancy wave and restored the negative component of the imperative response, suggesting that the mental disturbance may involve undue attention to unconditional or imperative stimuli for their own sake, with failure to exploit the value of conditional warnings.

From this outline of some of the relations of the E-wave it can be seen that a new field of psycho-physiological investigation is now acessible. One of the first and most obvious lines to follow is that mentioned above, the correlation of E-wave variations with traditional psychological and psychiatric tests and classifications. Neurophysiology has contributed very little so far to the extension of mental science; empirical use of such effects as the galvanic skin reflex, changes of pulse rate and alpha-rhythm blocking have added little to our understanding, because the physiological effects themselves are rather obscure in their mechanisms and are related only indirectly to the structure of personality and the mental processes of learning. The cortical changes which underly the E-wave, on the other hand, seem to be very closely connected with the machinery of adaptive behaviour. This machinery is certainly more complex than would be indicated by a simple electro-negative wave and indeed the description given of the E-wave is itself an over-simplification because of the relatively crude techniques with which it has been studied so far. For example, the termination of the E-wave is as interesting and significant as its onset. In the simplest conditioning situations the fall of potential is typically abrupt and limited to the zero base-line. In more complex situations, where the imperative signal is essentially semantic, in the form of a problem pattern or provocative illustration which the subject feels bound to inspect in detail, the E-wave often terminates in a marked and prolonged swing to the positive side of the base-line, sometimes with several secondary negative waves superimposed on it. This appearance has been seen most consistently when the signals are a series of briefly exposed novel and varied patterns which challenge the subject's powers of recognition and decision. Here again the amplitude and complexity of the cerebral responses are related to the novelty and intricacy of the signals and not to their energy or physiological intensity; in fact the signals in such experiments usually contain less energy than the background field.

The details of the techniques used for these experiments have not been described since this is really a subject in itself. Inevitably they are more exacting and elaborate than the traditional EEG or psychological procedures, partly because each discipline introduces constraints on the other. The experiments described here were made with direct immediate computation of averages in two channels with elaborate controls of other variables. The system has been progressively simplified however, to permit application to less co-operative subjects and the introduction of adequate data storage equipment and facilities for telemetering will liberate both subject and experimenter from much of the tiresome restrictions on freedom of movement and analysis time. Not least of the advantages of data storage is the possibility of retrospective computation, including "opisthochronic" studies, such as those described by Kornhuber and Deecke (1964), to identify cerebral changes preceding an unforseeable event or action.

Whatever the difficulties of experimentation the systematic study of these effects should at last permit physiologists to do justice to the human brain as the supreme organ of selection and decision.

Summary

1. Stimuli in any modality evoke responses over wide regions of frontal non-specific human cortex.

2. When identical stimuli are monotonously repeated these responses diminish irregularly and finally disappear.

3. When stimuli are presented frequently in association, the responses to the first or conditional stimuli are amplified while those to the second or indicative stimuli are attenuated.

4. When a subject is instructed to perform a relevant operant action to the second "imperative" stimulus the primary response to the conditional stimulus is followed by a prolonged negative wave which submerges the negative component of the imperative response.

5. The negative wave linking the conditional and imperative responses is described as an Expectancy Wave (E-wave) because it reflects very accurately the attitude of the subject to the stimulus association and his intention to act on it.

6. Comparison of intra-cranial and scalp records suggests that the E-wave arises from depolarisation of a small proportion of the apical dendrites in the frontal and premotor cortex.

7. Development of the E-wave is accompanied by economical abbreviation of the motor reaction time to the imperative stimuli by synchronisation and restriction of the efferent motor volleys.

8. When the imperative stimuli are withdrawn (extinction) without warning the E-wave subsides slowly over about 50 trials in normal adults. However, when a previous verbal warning is given the E-wave disappears at once.

9. When the significance of the association between conditional and imperative stimuli is diluted by presenting a proportion of unreinforced conditional stimuli (equivocation) the E-wave is diminished accordingly and in normal adults vanishes when the probability of association falls to about 0.5.

10. Stimuli involving no energy transfer to the subject but with a high information content evoke E-waves as long as the subject considers the signals interesting and important, whether they are isolated, imperative or conditional.

11. The E-wave seems to indicate the subjective significance assigned by a particular person to the signal association or "Gestalt" used for the experiment. The significance thus determined includes the need for recognition or decision, and involves social as well as physiological influences.

Zusammenfassung

1. Sinnesreize aller Modalitäten erzeugen über weiten Bereichen der frontalen Hirnrinde elektrische Antworten, die im integrierten EEG oder durch direkte Hirnableitung registriert werden.

2. Wenn gleiche Reizmodalitäten wiederholt werden, vermindern sich die Reizantworten in unregelmäßiger Abfolge, um schließlich zu verschwinden.

3. Wenn zwei Reize häufig nacheinander gegeben werden, so werden die elektrischen Antworten nach dem ersten konditionierenden Reiz vergrößert, nach dem zweiten indikativen Reiz vermindert.

4. Wenn die Versuchsperson die Aufgabe erhält, auf den zweiten „imperativen" Reiz zu reagieren, so folgt der ersten Reizantwort auf den bedingenden Reiz eine verlängerte negative Welle, die mit der negativen Komponente der imperativen Antwort verschmilzt.

5. Die negative Welle, die bedingende und imperative Antworten verbindet, wird als *Erwartungswelle* (Expectancy Wave, E-wave) bezeichnet, weil sie genau einer Erwartungshaltung der Versuchsperson auf die Reizkombination und seiner Aktionsbereitschaft entspricht.

6. Vergleiche von intrakraniellen und Kopfhaut-EEG-Registrierungen lassen vermuten, daß die E-Welle durch Depolarisation eines kleinen Teiles apikaler Dendriten der frontalen und prämotorischen Hirnrinde entsteht.

7. Die Entwicklung der E-Welle ist verbunden mit einer zweckmäßigen Verkürzung der motorischen Reaktionszeit auf den imperativen Reiz durch Synchronisierung und Begrenzung der efferenten motorischen Entladungen.

8. Weglassen der imperativen Reize (Extinktion) ohne Warnung läßt die E-Welle allmählich nach etwa 50 Reizen beim gesunden Erwachsenen erlöschen. Wenn das Ausbleiben des imperativen Reizes sprachlich angekündigt wird, verschwindet die E-Welle sofort.

9. Wenn die Bedeutung der Verbindung von bedingendem und imperativem Reiz durch isolierte Bedingungsreize vermindert wird (Äquivokation), so vermindert sich die E-Welle dementsprechend und verschwindet beim normalen Gesunden, wenn die Wahrscheinlichkeit einer Reizverbindung unter 0,5 fällt.

10. Reize mit hohem Informationsgehalt ohne Energieübertragung lösen E-Wellen so lange aus, wie die Versuchsperson die Signale als interessant und wichtig auffaßt, gleichgültig, ob sie isoliert, imperativ oder bedingend gegeben werden.

11. Die E-Welle ist offenbar Zeichen der subjektiven Bedeutung, die eine Person der Signalverbindung oder einer Gestalt beim Experiment zuschreibt. Die Bedeutung enthält damit die Notwendigkeit vorangehender Erkennung und Entscheidung und korreliert mit sozialen und physiologischen Einflüssen.

References

Black, S., and W. Grey-Walter: Human brain responses to variations in the subjective and objective probability of association between stimuli. Brit. med. J. (in press) (1964).

Caspers, H.: Changes of cortical d.c. potentials in the sleep wakefulness cycle. In: The Nature of Sleep. London: Churchill 1961.

COOPER, R., A. L. WINTER, H. J. CROW, and W. GREY-WALTER: Comparison of subcortical, cortical and scalp activity using chronically indwelling electrodes in man. Electroenceph. clin. Neurophysiol (in press) (1964).

KORNHUBER, H. H., and L. DEECKE: Hirnpotentialänderungen beim Menschen vor und nach Willkürbewegungen, dargestellt mit Magnetbandspeicherung und Rückwärtsanalyse. Pflügers Arch. ges. Physiol. **281**, 52 (1964).

ROWLAND, V., and M. GOLDSTONE: Appetitvely conditioned and drive-related bioelectric baseline shift in cat cortex. Electroenceph. clin. Neurophysiol. **15**, 474 (1963).

RUSINOV, V. S.: General and localized alterations in the electroencephalogram during the formation of conditioned reflexes in man. Electroenceph. clin. Neurophysiol. Supp. No. **13** (Moscow Coll.), 309 (1960).

SHVETS, T. B.: Slow electrical processes in the cerebral cortex of the rabbit. Conf. Electrophysiology of Higher Nervous Activity (Russian abstracts) Moscow, 138 (1958).

WALTER, W. GREY: The convergence and interaction of visual, auditory, and tactile responses in human nonspecific cortex. Ann. N. Y. Acad. Sci. **112**, 320 (1964).

WALTER, W. GREY, R. COOPER, V. J. ALDRIDGE, W. C. MCCALLUM, and A. L. WINTER: Contingent negative variation: An electric sign of sensorimotor association and expectancy. Nature (Lond.) **203**, 380 (1964).

WALTER, W. GREY, and H. J. CROW: Depth recording from the human brain. Electroenceph. clin. Neurophysiol. **16**, 68 (1964).

Dr. W. GREY WALTER,
Burden Neurological Institute, Stoke Lane, Stapleton Bristol/Great Britain