logical solutions. An effective increase in reliability is obtained with a small hole perforated membrane reference electrode.

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Evoked Potentials reflecting Interocular and Monocular Suppression

IT is well known that averaged visually evoked potentials (EPs) from the human occipital scalp show correlations with a number of subjective features of perception; but recent attempts to find EP correlates of the phenomenon of image suppression, as in interocular rivalry, seem to have yielded conflicting results[1–4]. In most of these experiments contrasting stimuli to the two eyes were allowed to set up spontaneously fluctuating rivalry, and the subject was required to press a key to indicate which stimulus was dominant at any time. There are, however, situations in which the perceptual dominance of one stimulus over another is stable. In the two experiments reported here, perceptual suppression of one stimulus by another in such stable situations has been found to be clearly accompanied by correlated changes in the averaged EPs.

The stimulus conditions used were dictated by an interest in a quite different phenomenon, and the discovery of EP correlates of image suppression was accidental. When a randomly patterned stimulus ("visual noise") is followed by a blank flash optically superimposed on the same area of the visual field, curious perceptual anomalies, and corresponding anomalies in the EP, occur at repetition rates of the order of 10–15/sec, which are not seen if the patterned and blank fields are presented to different eyes[5]. At lower rates of the order of 2/sec, these anomalies disappear; but two kinds of suppression phenomena are still observed.

(1) When the blank field, B, is flash-presented simultaneously to the same eye or eyes as the noise-patterned field, N, it suppresses perception of the patterned field, which becomes gradually visible as the number of milliseconds between B and N is increased. The critical interval depends on relative brightness, and in the present case was between 10 and 20 msec. This suppression of one stimulus by another presented to the same eye is termed "perceptual blanking".

(2) When N is presented to one eye and B to the other, perception of B is normally suppressed over a wide range of time intervals between B and N, and there are no perceptual effects of changing the timing or brightness of B over several tens of msec and several log units, respectively. This phenomenon is referred to as "interocular suppression".

In the present experiments, the EPs in response to single pairs of noise-patterned and blank stimuli presented approximately twice/sec, were recorded (by conventional averaging methods) with varying time intervals of the order of 0–50 msec between noise and blank, and with the two stimuli presented to either the same or different eyes. The two stimuli (N and B) were back-projected on separate screens and optically superimposed by means of a half silvered plane mirror, after optical polarization in orthogonal planes. Two pairs of polaroid spectacles were provided (fixed to the main framework, not worn) with polarizing orientations chosen to enable the two stimuli to be presented either (*a*) each to separate eyes or (*b*) both to the same eye or eyes at roughly half intensity.

Repetition intervals of about 0·5 sec were found long enough to prevent significant overlap between successive EPs, and the responses were averaged over runs of 60 to 105 presentations lasting from 0·5–1 min. Every run was repeated and the two results were superimposed on the cathode ray tube screen before photographing, to give an indication of their statistical significance. Two orthogonal bipolar recording placements were used, just to the left of the occipital midline, the lowest electrode being 1 cm left of the inion (Fig. 1).

Typical evoked responses to presentation of noise-patterned, N, and blank, B, flashes alone, at intervals of 573 msec, were recorded in the same subject on a separate occasion and are shown for reference in Fig. 1. N and B in this case were matched for subjective brightness (0·1 log ft. Lambert). Each trace is a superposition of the results of two successive runs of 105 responses each, indicating the run to run consistency obtainable. The upper of each pair of traces represents the average evoked potential, L, parallel to the midline; the lower represents the potential, T, transverse to it. It will be seen that although the longitudinal components are similar, the transverse components are strikingly different for patterned and blank stimulation; and the lowest pair, recorded 10 min later than the first but in the same conditions, indicates that this difference is also consistent. Its principal feature lies in the contrast between the rapid downward deflexion in response to "noise", and the slower upward deflexion at the same latency in response to "blank". These records were taken with binocular view and without polaroid, to give maximum signal to noise ratio. They have been found to be repeatable at any time in the same subject. Although bipolar, they reveal a similar contrast to that observed by Rietveld *et al.*[6] between the monopolar responses to checker-patterned and blank fields.

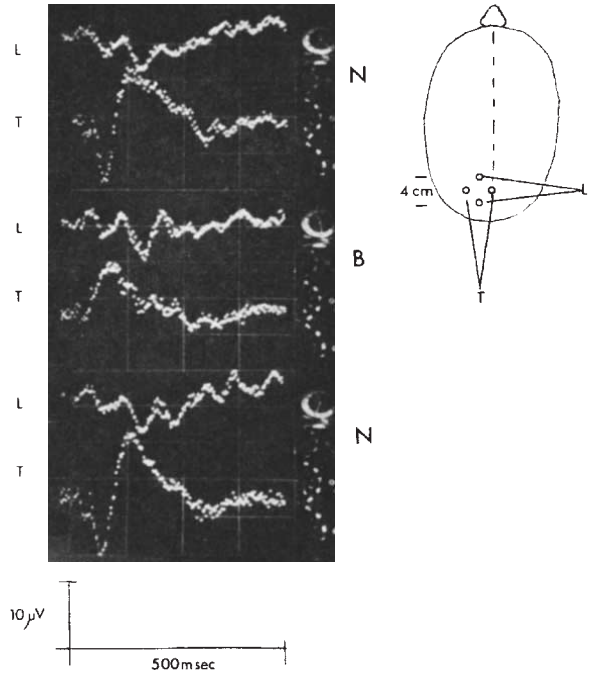

Fig. 1. Typical averaged responses to 105 exposures of noise-patterned, N, and blank, B, stimuli. Bipolar potentials recorded, L, parallel, T, transverse to midline. Each trace shows the results of two successive runs superimposed to indicate run-to-run consistency. Repeatability of N responses after an interval of 10 min may be checked by comparing upper and lower N records.

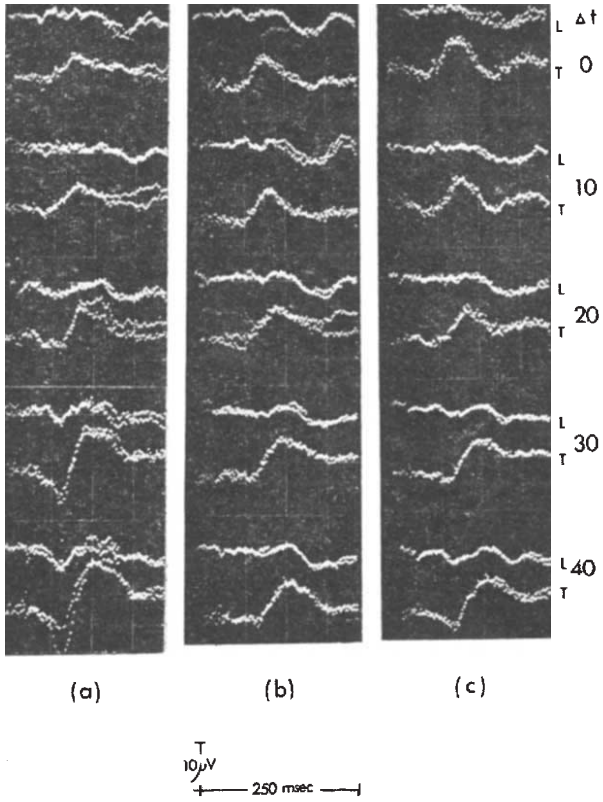

Fig. 2. *a*, Effects of increasing time interval, Δt, between N and B during normal binocular viewing. Note change of time-scale from Fig. 1. Each trace shows two successive results superposed. *b* and *c*, The same for left-eye and right-eye viewing, respectively.

Figs. 2*a–c* show the effect on the evoked potentials of increasing the time interval, Δt, between noise-patterned and blank flashes during normal binocular and monocular viewing. A repetition interval of 473 msec was used, and the blank flashes were adjusted to be subjectively 0·7 log units brighter than the noise. At low values of Δt, the transverse EP in all three cases shows the typical upward response to B (compare Fig. 1 B noting the difference in time scale), and the subject reports masking of the noise pattern. As Δt increases above 20 msec, the noise pattern becomes progressively more visible subjectively, and the EP correspondingly shows the initial downward deflexion (compare Fig. 1 N) evoked by N. With monocular viewing (Figs. 2*b* and *c*) the downward deflexions are much less pronounced, but the general trend (especially with right-eye viewing) is similar.

When the noise-patterned field is flashed to one eye and the blank to the other, suppression caused by interocular rivalry is observed, with the opposite effect; the blank field is rendered invisible by the noise-patterned field. The corresponding changes in the transverse EP are illustrated in Fig. 3. The longitudinal component, as before, showed no significant changes and has been omitted for clarity.

The first two rows show typical responses to N and B, respectively in left, L, or right, R, eyes, with $\Delta t = 0$, 30, 90 msec. The third row shows clearly how simultaneous presentation of N and B to opposite eyes gives the downward deflexion characteristic of N, with suppression of the upward "B" deflexion. With binocular viewing of N and B together, the responses in the fourth row of Fig. 3 were obtained, as in Fig. 2.

The contrast between third and fourth rows shows that a noise flash in one eye renders the transverse EP insensitive to the timing as well as the brightness of a blank flash in the other. With normal binocular viewing of N and B, blanking of the downward "N" component can be seen at $\Delta t = 0$, when the N stimulus is perceptually "blanked" by B, but not at $\Delta t = 30$ and 90 msec, when both stimuli are seen. The upward "B" component is present throughout. With dichoptic viewing of the same stimuli (third row), the downward "N" response is present at all values of Δt, the form of the EP shows no trace of the "B" response, and there is no significant change with Δt. This tallies with subjective experience, which is also quite insensitive to the brightness or timing of B in one eye (over this range) provided that N is presented only to the other eye.

These results seem to give definite evidence of EP changes correlated with two kinds of subjective suppression of one stimulus by another. Their detailed implications will be discussed elsewhere, but they suggest that whatever switching mechanisms are involved in the perceptual blanking and the interocular suppression

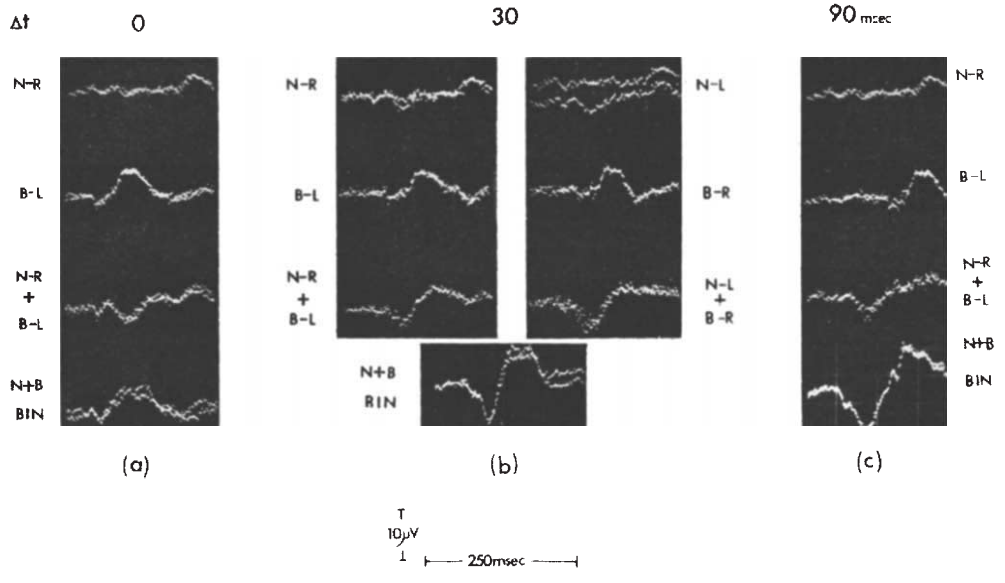

Fig. 3. Comparison of monocular (first two rows), dichoptic (third row) and binocular (fourth row) conditions: *a*, with $\Delta t = 0$; *b*, with $\Delta t = 30$ msec; *c*, with $\Delta t = 90$ msec. Note clear suppression of upward "B" response with dichoptic but not with binocular viewing. L = Left eye. R = right eye, N = noise, B = blank. Each picture shows two successive results superposed.

observed, they lie peripheral to the origin of the pattern-specific component of the EP. It is interesting to note that combination of the EPs to blank and noise is approximately linear when both stimuli are applied to the same retina, with a relative time interval of 30 msec or above. As this was also the condition in which both stimuli were subjectively visible, it suggests that the cerebral EP generating mechanisms activated by blank and patterned stimuli are largely independent. This would be expected if patterned stimulation excites in man a cortical population which is specifically contour-sensitive, analogous to those found in cat and monkey[7]. It might also explain some of the negative findings by other investigators using patternless fields.

These results may have some bearing on the recent finding by Lehmann and Fender[8] that the average EP to a blank flash was reduced according to the amount of structure presented (steadily, not flashed) to the other eye. They report that "spontaneous fading" occurred, but rely on earlier negative findings to discount its effect on the EP. If, however, what they observed occasionally with a steady pattern was the kind of interocular suppression that happens predictably with a flashed pattern, nothing more might be needed to explain a reduction in the average EP.

The reported lack of correlation between EPs and the fading of stabilized retinal images[9] would not discount this possibility, unless such fading were known to depend on the same mechanism as interocular suppression. The perceptual differences between the two phenomena make this unlikely.

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Antagonism of Presynaptic Inhibition in the Cuneate Nucleus by Picrotoxin

An afferent volley in a cutaneous forelimb nerve produces on the surface of the cuneate nucleus a characteristic electrical response. This consists of a brief initial spike potential indicating the arrival of the primary afferent volley, followed by a negative wave (N wave) lasting about 4–5 msec and a prolonged positivity (P wave) reaching a maximum in 20–30 msec and lasting for about 200 msec[1]. Similarly, N and P waves result from electrical stimulation of the contralateral sensorimotor cortex[2]. The N wave produced by the afferent stimulus is thought to be caused by synaptically induced depolarization of the cuneate cells by the ascending volley in the dorsal column[3]. Systematic investigation of the P waves produced by cutaneous volleys and by cortical stimulation led Andersen *et al.*[3] to suggest that both are caused by prolonged depolarization of cuneate tract fibres close to their synaptic terminals in the cuneate nucleus. This suggestion was further supported by excitability testing of these presynaptic fibres at their terminals and along their length, and by intracellular recording from these fibres[4]. With the technique of extracellular single cell recording, Jabbur and Towe[5–8] had shown earlier that the sensorimotor cortex (primarily the contralateral) produced excitatory and inhibitory influences on cuneate and gracile neurones. With the additional technique of antidromic activation of dorsal column neurones after medial lemniscal stimulation[9,10], two types of neurones have been identified. These are direct projection neurones, or dorsal column-thalamic relay neurones, which are depressed by antecedent descending volleys from the sensorimotor cortex, and interneurones, through which the cortex exerts presynaptic (and sometimes post-synaptic[11]) inhibition on the afferent inflow passing through the dorsal column nuclei. There is histological evidence for the presence of these corticofugal projections[12].

Presynaptic inhibition has been reported to be reduced by the convulsive drug picrotoxin in doses which do not appreciably interfere with postsynaptic inhibition[13]. Strychnine, on the other hand, can block postsynaptic inhibition without altering presynaptic inhibition[13]. If the P wave produced in the cuneate nucleus by peripheral and by cortical stimulation is a reflexion of afferent terminal presynaptic depolarization, as proposed originally[3], then it would be expected to be sensitive to picrotoxin. Similarly, cortical inhibition of the response of cuneothalamic neurones to peripheral stimulation would be reduced by picrotoxin, if this inhibition were mediated, at least in part, presynaptically.

Cats were anaesthetized with α-chloralose (60 mg/kg) or pentobarbital sodium (36 mg/kg) and immobilized with a muscle relaxant (gallamine triethiodide or decamethonium bromide). The cuneate nucleus was exposed for recording gross potentials with a silver ball surface electrode placed about 3 mm below the obex where the largest N and P waves are usually recorded[3]. The contralateral sensorimotor cortex was also exposed and a pool of warm paraffin oil was made around it. Bipolar platinum electrodes were used to stimulate the forearm area of the pericruciate region. Stimulating needle electrodes were inserted into the ipsilateral forepaw. Above-threshold stimuli of 0·1 msec duration were applied peripherally, whereas a single pulse lasting 0·04–0·08 msec, or a train of four such pulses at a frequency of 312/sec, was applied to the cortex. A master unit drove both stimulating channels at 1 c.p.s. Typical responses to peripheral stimulation and to cortical stimulation are depicted in Fig. 1 $A1$ and $B1$, respectively.

The effects of 0·2–1·0 mg/kg of picrotoxin, administered intravenously, appeared within 4–5 min. Gradual reduction in the size of the P wave was observed, and in 10–20 min the higher doses resulted in almost complete disappearance of the P wave with little or no reduction in the size of the N wave. At the peak of action, the previously positive wave gave way to prolonged negative discharges. Both peripherally and cortically evoked P waves were depressed. Reduction in the size of the P wave could also be produced by local instillation of a few drops of 0·1 per cent picrotoxin on the surface of the cuneate nucleus (Fig. 1). All these changes could be effectively reversed by intravenous administration of small doses of pentobarbital sodium (10–15 mg/kg). Intravenous injection of 0·1 mg/kg of strychnine sulphate failed to depress the P wave; instead it frequently increased it in size. Preliminary experiments with single unit extracellular recording from cuneothalamic neurones indicate that inhibition by conditioning contralateral cortical stimulation can also be reduced by picrotoxin, whether administered intravenously or applied locally.

These results support the hypothesis that the P wave recorded in the cuneate nucleus, whether produced by