Effect of stimulus size and retinal locus of stimulation on visually evoked cortical responses and reaction in man*

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A study was made of the effects of variations in the size of a circular light flash presented to each of three retinal areas on the averaged evoked cortical response and reaction time. Flashes varying in size from 0.14 to 20.63 deg of visual angle were centered about the fovea and at distances of 20 and 40 deg from the fovea. Evoked response latency and reaction time varied inversely with stimulus size and directly with distance from the fovea. The initial deflection of the evoked response increased with stimulus size for all retinal locations. Later deflections either decreased, showed no change, or first increased, then decreased with increasing stimulus size, depending on retinal locus of stimulation. The results were explained in terms of areal summation and a model of evoked cortical activity which postulates an alpha-like neural process momentarily controlled by an "extrinsic pacemaker."

While considerable attention has been given to the relationship between visually evoked cortical responses (VERs) and the physical characteristics of the stimulus (Cobb & Morocutti, 1967; Bergamini & Bergamasco, 1967; Perry & Childers, 1969), the effects of stimulus size on the VER has received little study. Some data have been reported by Armington (1968), Clynes & Kohn (1967), and Rietveld (1963), but a thorough parametric study seems to be lacking. Therefore, this experiment investigated the effects that wide variations in the size of homogeneous circular light flashes falling on each of three widely separated retinal areas have on the VER and also on reaction time (RT).

No a priori predictions were made, but, since certain aspects of VER data reported below are interpretable in terms of an evoked potential model previously described by Eason et al (1967) and others, a brief description of the model and predictions based on it are presented here to provide a conceptual framework for interpreting certain results.

The model holds that VERs recorded from the scalp, which, in their simplest form, are sinusoidal in appearance, reflect an alpha-like process having the same neural substrate as the spontaneous alpha rhythm and which are temporarily under the influence of an external "trigger" or "extrinsic pacemaker." The "trigger" consists of an envelope of stimulus-evoked afferent impulses arriving at the primary visual cortex, association cortex, or both. Once triggered, the reverberatory activity of

an ensemble of cortical cells lasts for 300-400 msec (i.e., three or four 8-12 Hz waves generally are recordable at the scalp) before the ensemble is brought back under the influence of the brain's "intrinsic pacemaker."

A very brief, but potent, envelope of incoming impulses with a sharp leading edge is assumed optimal for setting off an alpha-like discharge in a given ensemble (Lindsley, 1969). Longer duration envelopes may set off discharges sequentially in other ensembles, thus generating several concomitantly occurring sets of reverberatory events which lag one another in time. A scalp recording of the underlying composite cortical activity would tend to reflect accurately the reverberatory activity of a single ensemble, but the out-of-phase activity of several ensembles would summate algebraically to produce an attenuation of the later components of the scalp-recorded event. Based on the premise that spatial information is, in part, temporally coded, we might expect stimulus flashes covering large retinal areas to evoke envelopes of sensory impulses of relatively long duration which, from the above reasoning, would result in the progressive attenuation of the later components of the scalp-recorded VERs as the size of the stimulus is increased. As we shall see, the data tend to support such a post hoc "prediction."

SUBJECTS

Two males and one female served as Ss. Two Ss wore corrective glasses; vision was normal for the other.

DESIGN

Three retinal positions and seven stimulus sizes generated 21 experimental conditions. Each

condition was replicated six times for two of the Ss and three times for the other.

Stimulus size was varied across sessions and retinal location within sessions, order of presentation being counterbalanced for each variable.

VISUAL STIMULUS

The visual stimuli consisted of homogeneous circles of light, ranging from 8.6 min to 20.6 deg of visual angle. In area, the smallest stimulus was 1 sq mm; the largest was slightly above 16,000.

Flashes of 10 microsec duration were generated with a Grass PS-2 photostimulator. A given sized stimulus was presented by passing the light flashes through an aperture of appropriate diameter onto the back surface of a translucent diffusion screen viewed by S from the front side. The screen had a background intensity of 2 mV, the stimulus being approximately one log unit brighter than the background. From the center of the screen, the background field extended 80 deg into the periphery in all directions, thereby assuring a nearly constant level of retinal adaptation far beyond the particular retinal area being stimulated. Stimulation of the "blind spot" with a 1-deg patch of light yielded no VER, thus ruling out the possibility of VER contamination due to light scatter.

Flashes were presented irregularly at an average rate of one every 3 sec. S viewed the flashes at a distance of 40 cm. By maintaining the appropriate point of fixation, the center of each stimulus patch appeared either at the fovea or at retinal locations lying 20 or 40 deg along a horizontal plane to the right of the fovea. Continuous "white noise" masked extraneous sounds during data collection.

RECORDING PROCEDURE

VERs were obtained monopolarly. The "active" electrode was placed 1 in. above theinion and 1 in. to the right of the midline; the "inactive" electrode was attached to the right earlobe. The responses were amplified with a Grass Model 7 polygraph equipped with a 7P3 preamplifier, were averaged with a Computer of Average Transients (CAT), and were recorded with a Moseley X-Y plotter. Averaged responses for a given condition were based on 100 flashes.

RT

RT was measured to the nearest millisecond with a Hewlett-Packard electronic counter which was triggered at the instant a stimulus was presented to S and stopped upon S's releasing his finger from a microswitch.

RESULTS

The effects of size and locus of retinal stimulation on the VER are shown in Fig. 1 for one S. Similar

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Fig. 1. Averaged evoked potentials of one S to homogeneous circular flashes of light as a function of size and retinal locus of stimulation. Superimposed tracings represent replications.

responses and effects were obtained from the other Ss. Sinusoidal deflections are observable in nearly all of the tracings. The first positive deflection (P1) is succeeded by alternating waves of opposite polarity (N1, P2, N2, P3, etc.), the total number varying with both size and locus of stimulation. Only the first three deflections (identified in the lower left tracing of Fig. 1) are observable in the VERs elicited by foveally centered stimulation (left column of tracings).

Visual inspection of the rows and columns of Fig. 1 reveals that the latencies of P1 and N1, as well as of subsequent deflections, are inversely related to size and directly related to the distance of the locus of stimulation from the fovea. Amplitude changes across columns (retinal location) and rows (size) also are evident, but the degree and direction of change depends on the specific deflection being observed. For example, P1 shows a dramatic increase with size for all three retinal loci, being virtually nonexistent for the smallest stimulus. In contrast to P1, later deflections (e.g., P2) show an initial tendency to increase with stimulus size, but, thereafter, their amplitudes are attenuated with increasing size. This

increasing-decreasing tendency is particularly evident during peripheral stimulation (middle and right columns of Fig. 1). For very large stimuli, the peripherally evoked responses have a flat appearance after the first 200 msec, which resembles the VERs evoked by foveally centered stimuli of all sizes (compare bottom two rows of middle and right columns to all rows of left column).

The effects of size and locus of stimulation on the VER were studied quantitatively by determining the latency of N1, the average amplitude of N1 and P2, and by subjecting the measures to statistical analysis for each S. N1 and P2 were chosen because they occurred consistently and were measurable under all conditions. Since later deflections (N2, P3, etc.) tended to change in a manner similar to the changes in N1-P2 with respect to size and locus (see Fig. 1), it may be assumed that the changes noted for N1-P2 also hold in general for the later components. Quantitative results for the amplitude of N1-P2, latency of N1, and RT are graphically presented in Fig. 2.

Regarding the amplitude of N1-P2 (top row of graphs), retinal locus had a significant effect, largest responses being evoked by foveal stimulation and smallest by the 40-deg locus of stimulation. A significant interaction

Fig. 2. Changes in amplitude of N1-P1, latency of N1, and reaction time as a function of size and retinal locus of stimulation.

between size and locus was obtained for Ss 2 and 3. During foveal stimulation (solid lines), N1-P2 decreased in amplitude as stimulus size was increased from the smallest to the next larger value; during peripheral stimulation, the amplitude increased (compare first two points of each function). With further increases in stimulus size, the amplitude of N1-P2 either tended to level off or to decline, depending on the S and retinal locus.

With respect to the latency of N1, significant changes occurred as a function of both retinal locus and stimulus size for all Ss. The interaction effects of these variables also were significant. These effects may be observed in the middle row of graphs of Fig. 2, as well as in the VER tracings of Fig. 1. Latency was shortest for foveal stimulation and longest for 40-deg stimulation. It decreased curvilinearly with increasing stimulus size, the greatest changes occurring among the three smallest stimuli. The interaction between locus and size is reflected in the convergence of the latency functions, in going from the smallest to the largest stimuli.

Considering RT (bottom row of graphs of Fig. 2), the same types of effects were obtained as for latency, but in a more exaggerated manner. A variance analysis revealed that the effects of locus, size, and their interactions were highly significant.

DISCUSSION

From the above results, we conclude that size and retinal locus of stimulation affect scalp-recorded VERs and RT in the following manner: (1) The amplitude of the initial (positive) deflection of the VER varies directly and its latency inversely with size. (2) Effect of size on the amplitude of deflections occurring between 100 and 200 msec (N1-P2) after the flash depends on locus of stimulation. As size increases, amplitude remains nearly constant for foveally centered stimulation, but, for peripheral stimulation, there is an initial increase followed by a progressive decrease. (3) Effect of size on the amplitude of deflections occurring after 200 msec (N2, P3, etc.) also depends on locus of stimulation. During foveally centered stimulation, the VER is essentially flat after 200 msec, regardless of stimulus size. During peripheral stimulation, these late deflections, like the earlier N1-P2 deflections, reach a maximal amplitude, then decline with increasing size, becoming virtually nonexistent for stimuli subtending 10 deg of visual angle or more. (4) With relatively small stimuli

subtending visual angles of 2 deg or less, the VERs evoked by foveally centered stimuli are 30-60 msec shorter than those evoked by stimuli presented far in the periphery. With increasing stimulus size, the latencies of peripherally evoked responses become as short or shorter than foveally evoked responses. (5) The effects of size and locus on RT tend to parallel the latency changes of the VERs, differing only in that the interaction effects are more dramatic for RT. Similar parallels between latency and RT were obtained by Eason et al (1967).

The increase in amplitude and decrease in latency of P1 with increasing size also was observed by Clynes & Kohn (1967). We interpret the amplitude change as reflecting an increase in the massiveness of the leading edge of the envelope of impulses arriving at the cortex. The decrease in latency of P1 (and later components), as well as the shorter RTs, reflect the envelope's earlier arrival.

The greater effect of stimulus size on both latency of VER and RT during peripheral than during foveal stimulation is assumed to reflect the greater convergence of receptor elements on bipolar cells.

The attenuation of late VER components during peripheral stimulation with increasing stimulus size may be explained in terms of the VER model described earlier. The scalp-recorded composite response of late components of all underlying ensembles of out-of-phase alpha-like activity is assumed to summate to a smaller amplitude than would the recordings of a single ensemble. Since foveally evoked responses contain no late components even for small stimuli, we must conclude, from the model, that minute changes in spatial extent at the fovea are, in part, temporally coded and that the envelope of incoming sensory impulses is always of sufficiently long duration to set off out-of-phase reverberations in several cortical ensembles.

The increasing-decreasing relation between amplitude of the late components of VERs and stimulus size during peripheral stimulation may reflect the combined effects of areal summation and the duration of the incoming envelope of sensory impulses. When a very small stimulus is presented peripherally, we would expect minimal spatial summation and the temporal coding of the highly restricted spatial information to be very short. Thus, a brief low-amplitude envelope of impulses should arrive at

the cortex, which serves as a weak "trigger" and elicits a weak VER (e.g., top row, Columns 2 and 3, Fig. 1). Larger stimuli which are still localized to a fairly small retinal area but which produce some degree of spatial summation may elicit envelopes of impulses of greater magnitude, but with little increase in duration. This type of "trigger" should evoke higher amplitude activity in one or only a few ensembles of cortical cells which are insufficiently out of phase to produce much attenuation of the late components of the scalp-recorded VER (e.g., Rows 2-5 of Fig. 1). Stimuli covering large areas of the retina should elicit sensory envelopes of both high amplitude and long duration, since both areal summation and temporal coding of areal extent are maximal. A "trigger" of this type should evoke large out-of-phase reverberations in several ensembles which algebraically cancel the late components of the scalp-recorded VER (e.g., last two rows of Fig. 1).

It is also possible that attenuation of late components reflects actual diminution of underlying cortical activity, due to long-latency lateral inhibitory activity in retinal receptive fields (Jacobs, 1969).

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