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LATERALIZED CORTICAL POTENTIALS EVOKED IN HUMANS BY DYNAMIC RANDOM-DOT STEREOGRAMS[1]

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Abstract—Dynamic random-dot stereograms of 72 × 71 dots array size forming a horizontal rectangle of 14.5° × 9° were computer-generated on-line at 100 frames/sec with special display hardware. The stimulus, a vertical rectangular area of 4.6 × 5.7° within the array with binocular disparity different from its surround, was perceived in depth when binocularly viewed left (or right) to a center fixation point for 512 msec at periods of 1024 msec. Monocularly, only "snowstorm" could be perceived. Averaged visual evoked responses (VER) were obtained from eight subjects in 2-channel recordings, and from one subject in 37-channel recordings of the VER scalp field distributions.

Presentation of the disparity area to the left hemiretinas evoked an average EEG response up to 280 msec latency over the left posterior hemisphere (ipsilateral to the stimulated hemiretinas); simultaneously, the right hemisphere showed a smaller evoked potential of similar waveform. Stimulation of the right hemiretinas yielded opposite localization, i.e. mirrored results.

The findings indicate the presence of a major generator of the evoked potential in the input-receiving hemisphere up to 280 msec after the stimulus onset. Thus, without stimulus-synchronous activation of retina and LGB units, the responses of pools of cortical binocular disparity detectors (cyclopean retina) are measurable on the human scalp, and stereopsis is not associated with preferential activity of the right hemisphere.

INTRODUCTION

The quest to clarify the significance of cortical evoked potentials is greatly handicapped by the fact that classical stimuli (e.g. spatial and temporal luminance gradients) are processed at different sites in the nervous system by a great variety of neural units. Volleys of unit discharges, which are time-locked with the stimulus, can be recorded from several processing stages in the retina, the lateral geniculate nucleus, and the striate cortex, and beyond, and assumedly contribute to the visually evoked response in unknown ways. Random-dot stereograms (RDS's, Julesz 1960, 1964), and, particularly, dynamic RDS's (Julesz, 1971; Julesz, Breitmeyer and Kropfl, 1976) made it possible to operationally skip all processing stages prior to cortical pools of binocular disparity detectors.

Evoked potential studies of depth perception were performed by Fiorentini and Maffei (1970); however, monocular cues of disparity (movement parallax) could not be avoided in their stimuli. Static RDS's were used in evoked potential studies by Regan and Spekreijse (1970) and Regan and Beverly (1973), but even with these stimuli monocular motion parallax is not completely ruled out. Mol and Caberg (1977) used dynamic RDS's, but employed central fixation within the area of changing depth.

In the present study (for a preliminary report see Lehmann, Julesz and Ginzler, 1976a) we used dynamic RDS's which, monocularly viewed, appear as a continuous snowstorm (dynamic TV noise). When binocularly fused, the dynamic noise segregates in percepts of distinct surfaces in vivid deepth as the binocular disparity of certain correlated areas is periodically changed from zero to a finite value. Perception-linked eye movements were excluded by fixation outside of the target area. The periodic change of a pulsating depth target emerging from and receding into the background served as the synchronizing stimulus event, while the monocular processing stages (retina and lateral geniculate nucleus) received only the stimulation of continuous dynamic noise. We hoped that visually evoked responses (VER) to dynamic RDS's would reveal activity of detectors tuned to binocular disparity in humans.

While dynamic RDS's clearly skip operationally all early processing stages prior to the activation of binocular disparity detectors, the output of these detectors reaches consciousness and, for example, the subject could count the stimuli as they occurred. Thus, it is *a priori* possible that a VER which we record is caused by some higher nervous activity, such as counting. In order to investigate this possibility, we presented the pulsating depth target to hemifields, and examined the distribution of the VER over the scalp, on the assumption that an event occurring in the visual areas would be lateralized if it was presented to one hemifield, while a higher nervous activity would not be lateralized as function of the lateralization of the input.

Finally, the question of hemispheric lateralization for steroeoscopic depth perception could also be answered by this experimental paradigm. There is convincing clinical evidence that adequate con-

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ceptualization of three-dimensional space requires intact functioning of the right hemisphere (Benton. 1969). In addition. a presumably crucial role of the right hemisphere for visual depth perception was also claimed (Holmes, 1919; Benton and Hecaen, 1970; Carmon and Bechtold, 1969; Durnford and Kimura, 1971). However, experiments with dynamic RDS's failed to support this claim, and found no difference for stereopsis in the left and right hemifields (Breitmeyer, Julesz and Kropfl, 1975; Julesz *et al.*, 1976). Furthermore, psychophysical studies on neurological patients by Lehmann and Walchli (1975) also failed to support any right–left anisotropy for stereopsis. As will be seen in the study reported here, the VER recorded on the right as well as on the left hemisphere measured effects of contralateral depth stimulation and appeared about equal. The question and criticism of why the Carmon and Bechtold (1969) and the Durnford and Kimura (1971) studies found right hemisphere advantage of stereopsis is discussed elsewhere (Lehmann and Walchli, 1975, Julesz *et al.*, 1976).

After we were able to measure VER to dynamic RDS's in conventional evoked potential recordings we also used these stimuli for a more detailed topographic study, employing the multichannel-scalp field recording and analysis techniques (Lehmann, 1971, 1977; Lehmann, Meles and Mir, 1977).

In summary, we examined in healthy human subjects the activity of cortical detectors of binocular disparity in scalp VER recordings, using on-line computer-generated dynamic RDS's, and presentation of the stimulus to either the right or left hemi-retinas, an experimental design which permits the distinction between evoked left and right hemisphere activity. In order to achieve this, a small stereo target area was used, and recordings from brain hemisphere electrodes against a midline reference were compared. The experimental set-up had the subject fixate on the stationary frame of the target field, which excludes stimulus-related eye movement artifacts. Indeed, eye movement recordings in this paradigm had shown no movements which were time-locked to the appearance and disappearance of the depth stimulus. It will be shown that without monocular cues for stimulus onset or depth, VER's are obtained, and that lateralized activity in the input-receiving hemisphere persists at least for about 280 msec after stimulus onset. We repeated these experiments on one subject, using multichannel-scalp recordings (Lehmann, 1971, 1977), and found peaks of the evoked potential fields localized over posterior scalp areas ipsilateral to the stimulated hemiretinas.

METHODS

We used two women and six men, healthy and aged between 22 and 31, as subjects. All subjects had been screened for intact depth perception using the target display described below. During the experiment, subject sat comfortably in a light and sound-shielded room with an intercom to the equipment room. A chin and forehead rest was mounted at 85 cm in front of a Hewlett Packard HP 1310A oscilloscope display. A half-silvered mirror plate at half distance, slanted at 45°, permitted simultaneous observation of a second HP 1310A oscilloscope. The scope faces were covered with polarizing foil at excluding polarization angles; the subject wore matched polarizing glasses so that each eye saw only one of the two displays.

Target

On the scope faces, both eyes saw an identical dynamic random-dot matrix of 73 × 72 dots as a rectangle of $14.5^\circ \times 9.1^\circ$ since the separation between horizontal picture elements was selected 56% larger than between vertical elements. This matrix was on-line generated at 100 frames/sec with 25% display density (i.e. the ratio of randomly displayed vs omitted dots) using a PDP 11/40 computer with additional special hybrid hardware constructed by Mr Kropfl (for details, see Julesz *et al.*, 1976). Five steady brightness-enhanced dots in a cross arrangement in the upper 10% of the midline of both displays served as fixation mark. The depth target was a vertical rectangle of 24 × 45 dots ($4.6^\circ \times 5.7^\circ$) which, during depth condition, were binocularly disparate by two picture elements in reference to the surrounding dot frame, thus creating the percept of a hovering rectangle in depth (Julesz, 1971). This rectangle was shown for 512 msec every 1024 msec, either to the left or to the right of the fixation mark, its inner border at 0.8° from the midline, and its upper border six dots below the lowest dot of the fixation cross, in order to stimulate only the upper hemiretinas for minimal variance of the VER waveforms, since upper and lower hemiretina responses differ in latency (Lehmann and Mir, 1976; Lehmann *et al.*, 1977).

Experimental regime

A considerable methodological problem in evoked potential studies is the control of vigilance, and of attention to the stimulus percept, particularly when expected responses are very small, as is the case in our paradigm. We observed in pilot experiments that mental counting or commenting ("yes ... yes ...") of the appearance of the depth target subjectively improved the stability of the percept. Nevertheless, even when using this method, the intermittent depth target usually was not perceived for much more than a minute. Accordingly, we instructed the subjects for the data collection to count the target appearances, but told them that this was a measure to keep their attention on the target and that the number counted was unimportant. We also used data collection times of less than 1 min for each run.

The subject was asked to put his head into the chin–forehead rest, and to observe the fixation mark, changing his gaze between the five dots of the cross. The intermittent depth target was generated, and data collection was started with the eighth target appearance after cessation of muscle artifacts. Each data-averaging run consisted of 50 presentations. Then, the subject was told to rest, and not to observe the display. The depth target was switched from one to the other side of the fixation mark after each run or after every second run. After 2.5 min, the next data collection was initiated. After usually two initial training runs, there were between 10 and 14 data runs for each of the eight subjects with 2-channel recordings, and 22 runs for the single subject recorded with 37 channels.

VER Data

GRASS gold cup electrodes were attached with GRASS paste over the midline at 15% of the inion–nasion distance above the inion, and at the same distance laterally from the midline electrode over the right and left hemisphere. Two "unipolarly" recorded evoked responses from the right and left hemisphere electrodes vs the midline electrode were averaged ($n = 40$) in each run. Average ($n = 40$) responses showed a large variance of the very small evoked response, and therefore median-evoked responses for each of the two conditions were constructed from the average evoked responses obtained in repeated runs (for example, see Fig. 1), using technical zero (short-circuited preampli-

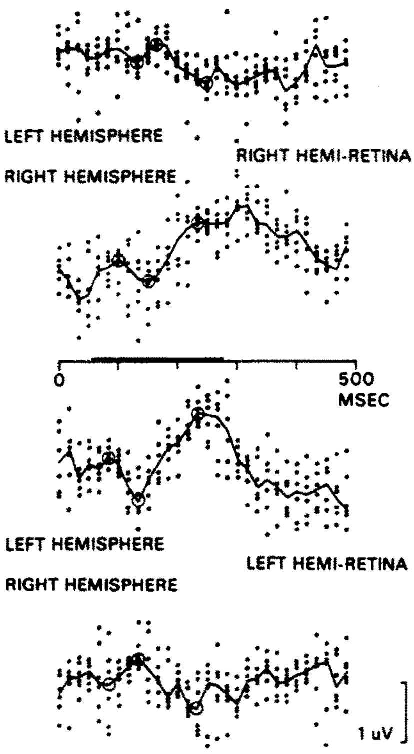

Fig. 1. Median evoked responses, constructed from six average (each $n = 40$) responses evoked by depth target presentation to the right (upper two traces) or left (lower two traces) hemiretinas, and recorded from left and right hemisphere occipital electrodes vs the midline reference. Downward deflection indicates negativity at reference electrode—the usual convention. At each sampling time point, the values of the six average responses are indicated by dots. Maximal and minimal median response values within the analysis period (indicated by heavy bar on time axis) are marked by circles.

fier input) as reference. Thus, four median responses were obtained for each S (two for each stimulus condition), each median response representing 5–7 averages of 40 original evoked responses.

For the multichannel-recording from the single subject, 37 of the electrodes were attached at about equal distances on the scalp, covering an area which extended from the inion to a point at 70% of the inion–nasion distance, and symmetrically around the midline over 70% of the distance between the meati acustici externi. The 37 recordings were amplified, AM multiplexed at 650 samples/sec per recording channel (system construction by J. M. Madey and V. Corti), and recorded on six channels of an instrumentation tape recorder (Lehmann, 1971; Lehmann *et al.*, 1977). The recordings were demultiplexed and further computer-analyzed. The data were averaged over the 40 presentations of each of the 22 runs (11 averages for either stimulus condition), and plotted as field distributions in intervals of 10.25 msec.

RESULTS

(*A*) *General considerations*

The experimental design which provides input to the right or left hemisphere is laid out to decide between the three following outcomes: (1) one major source exists in the input-receiving hemisphere; (2) one major source exists in the right hemisphere as a result of either stimulus condition; or (3) one major source exists in the center (or there is a similar source in either hemisphere) without lateralization for both stimulus conditions.

If there is a single response generator in one hemisphere, our recordings from electrodes over the hemispheres (referred to a midline electrode) are expected to show similar waveforms which are inverted in polarity (because one derivation sees an "uphill" gradient, the other a "downhill" gradient), and bigger responses over the source hemisphere (because the gradient is steeper close to the source). If there is a generator in the center (or similarly behaving generators in both hemispheres), then the VER waveshapes in our recording arrangement are expected to show similar waveforms of identical polarity, and of identical amplitudes. Since the VER data in our experiment have a large variance, one cannot readily examine such global symmetries, but has to revert to considerations of the most important local characteristics. Such a local characteristic is a "wave". The simplest description of a wave—that also has a heuristic value to human pattern extraction—requires three alternating extremes (local maxima/minima/maxima or vice versa). These three alternating extremes, which we shall call from now on "peaks", define a wave. For hypotheses 1 and 2, the waves in our two recordings should be each other's mirror images in shape, and they should differ in amplitude. For hypothesis 3, they should be identical in polarity and amplitude. Finally, for hypothesis 1, the larger wave should be found over the input-receiving hemisphere, and for hypotheses 2 and 3, the results should be identical for both stimulus conditions.

When reviewing our data we were unable to find three alternating peaks that defined similar waves for hypotheses 2 and 3. However, for hypothesis 1, there was a time-period where we could find such VER peaks. This period between 60 and 280 msec latency (time of occurrence after the stimulus) will be used as "analysis epoch".

Our main results can be extracted from Fig. 1, which shows a typical subject's averaged VER's. A cursory inspection already shows that within the "analysis epoch" one can find three alternating peakss (local extremes denoted by small circles in Fig. 1) which describe mirror waves for the left and right hemisphere VER's. This mirroring occurs both for stimulation of the right and left hemiretinas. Furthermore, the upper two curves in Fig. 1 show that right hemiretina stimulation results in bigger amplitudes between the three successive peaks measured over the right hemisphere than between those over the left hemisphere. The lower two curves of Fig. 1 show a corresponding result for left hemiretina stimulation. Here, the amplitudes between the successive peaks are much larger for the left hemisphere VER than for the right hemisphere VER.

The solid lines in Fig. 1 upon which this informal analysis is based are the median VER values, and the dots show the scatter of the data for a given subject. Although there is considerable variance, these tendencies described above clearly show up. For all eight subjects, similar tendencies can be detected by cursory inspection.

Table 1. Latencies in msec (median, mean and standard deviation over eight S's) of peaks of median ($n = 5$ to $n = 7$) VER evoked by depth targets shown to the right or left hemiretinas, and recorded from left and right hemisphere vs midline (Wilcoxon tests)

Hemiretinas	Hemisphere		Peak 1	Peak 2	Peak 3
R	L	mdn	77	154	239
		$\bar{x}$	98	152	229
		SD	(40)	(46)	(44)
		P	NS	NS	NS
R	R	mdn	102	150	248
		$\bar{x}$	99	154	250
		SD	(42)	(33)	(31)
L	R	mdn	85	163	239
		$\bar{x}$	92	157	246
		SD	(51)	(60)	(33)
		P	NS	NS	NS
L	L	mdn	68	145	231
		$\bar{x}$	81	154	225
		SD	(49)	(41)	(40)

A problem for a given subject, with the large intra-subject data variance, as shown in Fig. 1 (top two curves), is that the three successive peaks of the median VER do not appear at exactly the same time for the left and the right hemisphere recordings (for the lower two curves of Fig. 1 they happen to be identical). In the subject population we can test the simultaneity of peak occurrence, and the difference of amplitudes between hemispheres, as follows: We incorporate the main ideas of our informal analysis (i.e. that we define the VER wave by three latencies and voltage differences) in a data assessment for each of the eight subjects; we then carry out statistical analysis of the latencies of the three peaks, and of the voltage differences between the peaks (Tables 1 and 2). Test of the data in Table 1 shows that across the eight subjects the latency differences for a given peak are not significant between hemispheres and between stimulus conditions. Table 2 shows that the tendency for larger voltage differences between successive VER peaks over the input-receiving hemisphere vs the functionally secondary hemisphere is significant across the eight subjects.

(*B*) *Statistics*

Positive and negative peak values during the "analysis epoch" (60–280 msec after the stimulus) were determined in the four median-evoked responses of each subject. During the "analysis epoch" the median VER's from the input receiving hemisphere (right hemisphere when target on right hemiretina, and vice versa) were searched for the positive peak (peak 2), and the preceding negative peak (peak 1) and the following negative peak (peak 3), as shown in Fig. 1; the responses from the functionally secondary hemisphere contralateral to the stimulated hemiretina were searched for the negative peak (peak 2), and the preceding positive peak (peak 1) and the following positive peak (peak 3), as shown in Fig. 1.

The latencies of the peaks show no significant difference in Wilcoxon tests for a given peak between responses from simultaneously recorded hemispheres, and between retinal target localizations across the eight subjects (Table 1). We conclude that there is a polarity inversion of the waves that are obtained from the two hemispheres for a given target localization, indicating a single model generator which would account for the major features of the VER's.

In order to test the difference of successive peak latencies of a given response in the population data, paired Wilcoxon tests cannot be used since the peaks

Table 2. Voltage differences (median, mean and standard deviations over eight S's) measured in right and left hemisphere median average responses between values at peak times (see Table 1) of the response obtained from the input-receiving hemisphere (R/R and L/L), for depth targets shown to the right and left hemiretinas

Stimulated hemiretinas	Recorded hemisphere		Voltage differences between peaks 1 and 2	Voltage differences between peaks 3 and 2
R	L	mdn	−20	−24
		$\bar{x}$	−24	−35
		SD	(25)	(25)
		P	< 0.05	< 0.005
R	R	mdn	56	92
		$\bar{x}$	57	87
		SD	(19)	(16)
L	L	mdn	47	81
		$\bar{x}$	55	77
		SD	(26)	(20)
		P	< 0.01	< 0.005
L	R	mdn	−19	−19
		$\bar{x}$	−6	−26
		SD	(34)	(28)

Wilcoxon *P* values for differences of absolute size.

were determined as "preceding" and "following", which makes contradictory results impossible. As an estimate of the difference of peak time values we used unpaired U-tests; all eight possible tests (between the two successive peaks of each of the four population medians) were significant, with $P = 0.025$, and better.

Let us now determine which hemisphere shows the larger voltage difference between two waveform peaks of different polarity. Voltage differences were measured between all successive peak points (to be called halfwave amplitudes) used in Table 1. In order to give equal weight to all subjects, the measurements for each subject were scaled so that the largest was equal to 100%. These halfwave amplitudes were constantly greater for the responses of the input-receiving hemispheres than for the functionally secondary hemispheres (median values, halfwave 1: 56% vs – 50% and 47% vs – 39%; halfwave 2: 92% vs – 49% and 81% vs – 65%). However, this gradient of the electrical field distribution is meaningful only when the data to be compared are sampled at identical times. We therefore used each subject's peak latency times in the VER from the input-receiving hemisphere to measure voltage differences of the halfwaves recorded from both hemispheres, using the scaling factors obtained earlier for equalization. The results shown in Table 2 for the subject population demonstrate bigger values for the voltage differences (P-values between 0.05 and 0.005) over the input-receiving hemisphere, indicating that an assumed waveform generator is closer to the electrode over the input-receiving hemisphere.

(*C*) *Multichannel data*

The multichannel scalp field distributions obtained from the single subject were searched for the locations of their maximal and minimal field values which describe the main features of the fields. For each field map, the median location of the maximum ($n = 11$) and median location of the minimum ($n = 11$) location were computed for either stimulus condition, and the significance of the location difference between conditions was tested (U-tests). The distribution maps at 225 msec after stimulus appearance showed the most significant differences (P for different locations of maxima and of minima were < 0.005 for both stimulus locations, on the right and on the left hemiretina). Figure 2 illustrates the mean locations and their lateral and saggittal standard deviations of the maximal and minimal field values for the two stimulus conditions at 225 msec latency. (We note that as early as 60 msec after stimulus onset significant lateralization was found for the mapped field distributions obtained in the two conditions.)

The corresponding mean field distributions for the two stimulus conditions (each computed over 11 average field distributions) are illustrated in Fig. 3 as equipotential line plots on a schematized head. They show the parietal-occipital localization of the extremal field values, with a steeper gradient over the posterior areas for the negative field maxima (which correspond to the "positive peak" in Fig. 1) than for the positive field maxima, indicating that an assumed single generator of the distribution would have to be localized in the input-receiving hemisphere. These topographical data illustrate the significant lateralization of the EEG response in the input-receiving hemisphere at 225 msec after the stimulus.

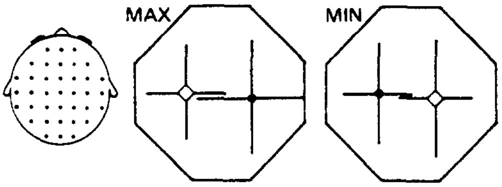

Fig. 2. Mean positions (and their lateral, and anterio-posterior standard deviations) of maximal and minimal scalp field values, recorded in one subject 225 msec after the appearance of the binocularly disparate (depth) target area within the dynamic random-dot stereogram on the right (◇), and on the left (●) hemiretinas. Each entry was computed from data of eleven average ($n = 40$) evoked potential fields; averaging runs with "target right" and "target left" were alternated. The octagons indicate the outline of the array of the 37 recording electrodes on the scalp, as shown in inset. The mean positions were almost identical with median positions. Significance of topographical differences of maximal (and of minimal) values between the two stimulus conditions in U-tests, $P < 0.005$. From same data as Fig. 3.

DISCUSSION

The VER responses which we obtained with the presentation of the depth targets by dynamic RDS's cannot have been triggered by a privileged synchronized impulse volley in the retina or the lateral geniculate body: there is no privileged display dot arrangement that can give monocular cues for the depth target. Only the binocular disparity of some display elements in relation to the others which remain correlated can be considered as input candidate for the brain response. We note in addition that, in our arrangement, depth-related eye movements are excluded as possible sources of artifacts, since the fixation point was outside the depth target area. The hemisphere which received the hemiretinal input showed a large response, and the other hemisphere at the same time

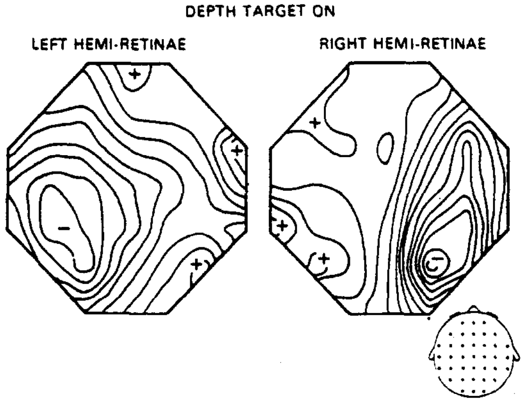

Fig. 3. Equipotential line plots of mean ($n = 11$) average ($n = 40$) evoked potential field distributions, computer-interpolated from data obtained from the 37 electrodes, 225 msec after the binocularly disparate (depth) target appeared on the left (left plot), or on the right (right plot) hemi-retinas. + = positive, – = negative field maxima. Equipotential lines in steps of 0.15 μV. Note steeper gradient over occipital areas around negative maxima than around positive maxima. From same data as Fig. 2.

showed a smaller response of inverted polarity: it did not matter whether the input-receiving hemisphere was the right or the left hemisphere. These results indicate the existence of a major source of evoked activity in the input-receiving hemisphere which persists until about 280 msec after the onset of the depth stimulus. This indicates that for quite some time after depth information input the right or left hemisphere (or both) will process information on visual depth, depending on the retinal localization of the binocularly disparate stimuli, but there seems to be no difference between the processing ability of the hemisphere for stereopsis. This is in agreement with a clinical study which found no hemisphere preference for disturbed visual depth perception (Lehmann and Walchli, 1975), contrary to other reports (Carmon and Bechtold, 1969; Benton and Hecaen, 1970; see also Durnford and Kimura, 1971). Our results are also in agreement with reports by Breitmeyer *et al.*, 1975, and Julesz *et al.*, 1976.

Lateralized hemifield stimulation resulted in partially conflicting reports about correct (e.g. Cobb and Morton, 1970; Lesèvre, 1973; Lehmann, Meles and Mir, 1976b; Jeffreys, 1977) and incorrect (ipsilateral) scalp lateralization (Barret, Blumhardt, Halliday, Halliday and Kriss, 1976; see also Lehmann *et al.*, 1976b) of VER's. It appears that correct lateralization is achieved with stimuli of small angular extent. Lesèvre (1973) showed in addition, that lateralization for checkerboard-evoked VER's persisted up to about 140 msec latency; later waves did not exhibit response lateralizations which depended on stimulus lateralization, contrary to our depth-evoked VER's.

The major characteristics of the lateralized VER to depth stimuli (negative/positive/negative peaks[3] at 96/156/248 msec latency) are in good agreement with the major characteristics of the VER responses obtained with centrally fixated depth stimuli (when the responses are expected over both hemispheres) by Regan and Spekreijse, 1970 (negative/positive peaks at 94/160 msec latency), and Regan and Beverly, 1973 (positive/negative peaks at 120/220 msec latency), although these depth VER's were superimposed on basic VER's which were generated by the monocularly visible stimulus change without depth percept. Mol and Caberg (1977) reported different waveforms (negative at 150 and positive at 400 msec) with centrally fixated RDS's, a condition where expected eye movements complicate the interpretation.

It is significant that our recorded, lateralized responses are a manifestation of selective activity of neural elements that are sensitive to binocularly disparate visual inforrmation. This is supported further by the consideration that a hemispheric lateralization which would follow the lateralization of the sensory input is not conceivable for higher functions such as, for example, counting, or general recognition processes. Our experimental design, where the subject fixates a point outside of the depth target, excluded perception-related eye movements as confounding factor.

While, admittedly, the technique of dynamic random-dot stereograms seems to result in rather small VER's, the fact that these VER's are not contaminated by components of earlier processing stages might make this stimulis class an interesting candidate for further evoked potential studies. It remains to be seen whether one might be able to enhance the useful VER segment with more efficient stimulus parameters (target area, dot density, disparity values).

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[3] Note that the convention of our recording arrangement (reference electrode negative in relation to hemisphere electrode = downward deflection of the VER) makes a negative value of the field over the hemisphere into a "positive peak" of our conventionally recorded VER.

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