pears to be the case. The offspring of C57BL/6J females, mated to C57BL/6J males, had a lower frequency of cleft palate induced by 6-aminonicotinamide when the treated females were maintained on Lab Chow (11.1 percent) than when on Breeder Chow (67.5 percent). In the A/J strain, on the other hand, the frequency of induced cleft palate is not significantly different in the offspring of females maintained on Breeder Chow (55.9 percent) and Lab Chow (64.6 percent).

These findings support the hypothesis that there is a factor, transmitted through the cytoplasm, which makes C57BL/6J mice on a Lab Chow diet more resistant than A/J mice to the cleft palate–producing effect of 6-aminonicotinamide. Since mitochondria are transmitted through the egg cytoplasm, and since 6-aminonicotinamide forms an inactive nicotinamide-adenine dinucleotide analogue that interferes with oxidative phosphorylation in mitochondria (*5*), it is reasonable to postulate that the cytoplasmic factor is associated with a difference in the mitochondria of the two strains (*6*).

This example of the extrachromosomal transmission of a metabolic characteristic adds another to the few cases of maternal inheritance reported in mammals (*7*). It also adds a new complexity to the question of gene-environment interactions in general and drug-induced malformations in particular.

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19 December 1967

Metacontrast and Evoked Potentials: A Reappraisal

Abstract. *Stimulation of the parafoveal retina may give rise to visual evoked responses generated in large part by stray light impinging upon the fovea. This effect appears to account for the absence of changes in the visual evoked response to parafoveal stimulation during metacontrast suppression. When the central retina is directly stimulated, the spatiotemporal interactions associated with brightness suppression during metacontrast may be readily demonstrated in a late component of the visual evoked response.*

Schiller and Chorover (*1*) failed to detect changes in the human visual evoked response (VER) associated with the reduction of brightness induced by metacontrast. They concluded that the VER, although varying with alterations in stimulus intensity, does not necessarily reflect changes in subjective brightness. However, it is possible that the negative finding was due to the specific conditions of the previous study and that it does not imply a general insensitivity of the VER to brightness changes in metacontrast. Although the effectiveness of photic stimuli for eliciting VER's falls off rapidly with distance from the fovea (*2*), even stimuli projected onto the blind spot may produce evoked responses. These are apparently due to stray light, for they are eliminated by an illuminated background field (*3*). A likely reason for the failure of the VER's recorded in the previous study to reflect metacontrast suppression was the use of parafoveal stimuli presented on a dark background.

To evaluate the possibility that stray light striking the fovea might have contaminated the evoked responses recorded to parafoveal stimulation, we repeated the metacontrast experiments under the following four conditions. The disk and ring stimuli were projected onto the fovea and at a point 5° from fixation, in each case against both a dark background as in the previous study and against an illuminated surround about one-fifth as bright as the stimuli themselves (*4*). In addition to the 5° stimulus configuration employed by Schiller and Chorover, we used a disk and ring slightly less than half that size (2.35° in total subtense), providing a stimulus closer to foveal dimensions, yet producing a sizable VER at low stimulus intensities. Due to the limitations of our apparatus, we used a luminance (5.8 millilamberts) considerably less than that used in the previous study. This served to strengthen our results, since the absolute amount of stray light was reduced.

The VER's to presentation of a 5° disk are shown in Fig. 1. The adapting field, which attenuates the effects of intraocular stray light (*5*), virtually eliminated the VER to the parafoveal stimulus, whereas it neither reduced the amplitude nor increased the latency of the foveal VER's. With the smaller stimuli, VER's to parafoveal stimulation were either small or absent, even without the illuminated surround. These results strongly suggest that VER's produced by the larger parafoveal stimuli were contaminated by stray light impinging upon the relatively potent fovea.

We found that subjective metacontrast suppression was readily observed under all four conditions, generally with delays between presentations of the disk and ring (disk-ring delay) of 30 to 90 msec. The VER's, however, showed patterns of behavior different from the perceptual effects. No change in the VER's to the parafoveal stimuli as a function of disk-ring delay was seen, confirming the observations of Schiller and Chorover. In contrast, there was a distinct alteration in the VER's to foveal stimulation during metacontrast suppression (Fig. 2). This consisted of a reduction in size of a VER compo-

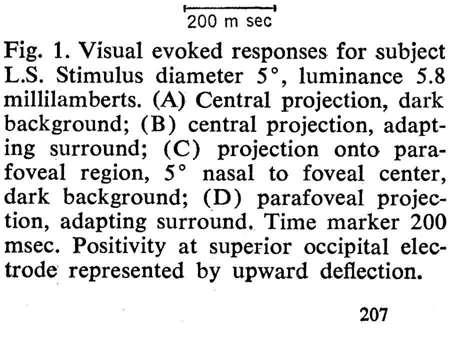

Fig. 1. Visual evoked responses for subject L.S. Stimulus diameter 5°, luminance 5.8 millilamberts. (A) Central projection, dark background; (B) central projection, adapting surround; (C) projection onto parafoveal region, 5° nasal to foveal center, dark background; (D) parafoveal projection, adapting surround. Time marker 200 msec. Positivity at superior occipital electrode represented by upward deflection.

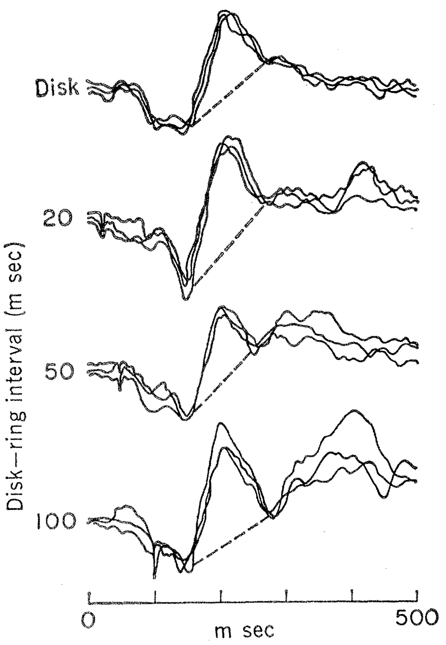

Fig. 2. Visual evoked responses from subject H.V. to 1.5° foveally projected disk (reference stimulus), and disk-ring combination at three different interstimulus intervals (ISI). Interrupted lines indicate the area of the response component measured to obtain the data illustrated in Fig. 3. At 20 msec, ISI apparent brightness of disk is greater than comparison disk; at 50 msec, suppression is maximum; recovery of brightness has occurred at 100 msec ISI.

nent with a maximum at about 200 msec after the first stimulus. The area of this component and the subjective disk brightness, estimated by a method of interocular brightness matching (*6*), are plotted in Fig. 3 as a function of the disk-ring interval. The concordance of these data is excellent except with the 80- and 90-msec delays for subject L.S.

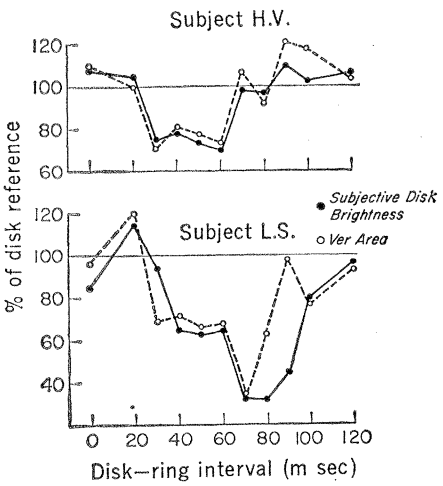

Fig. 3. Plots of VER area and subjective brightness for subjects H.V. and L.S. Values are expressed as a percentage of the disk VER area and of the comparison disk brightness.

A precise quantitative analysis of the relation between brightness judgments and the VER presents complexities which cannot adequately be discussed here. These concern a proper metric for relating changes in subjective brightness of the disk-ring configurations to the alterations in the VER waveform (*7*).

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4. The photic stimuli of 10-msec duration were presented in Maxwellian view to the right eye of each of two subjects (the authors). For the dark background condition a small red fixation cross was provided; for the light-adapted condition, the rectangular adapting field, about 11° by 11°, contained a diamond-shaped fixation pattern formed by four black dots within which the stimuli were projected. Intervals between stimuli, measured from the presentation of the disk to the presentation of the annulus, of 0, 20, 30, 40, 50, 60, 70, 80, 90, 100, and 120 msec were employed. Usually, the disk was presented alone between two successive presentations of the compound stimulus (disk and annulus). A period of 1.5 seconds intervened between the presentation of each stimulus configuration. Visual evoked responses were recorded from silver-silver chloride, bipolar, scalp electrodes with the lower electrode placed on or slightly above the inion and the other approximately 4 cm above and 3 cm to the left of it. The electroencephalogram was amplified by a system set for a bandpass of 0.2 to 50 hz and summated by a modified Mnemotron computer of average transients. Either 100 or 200 samples were summed for each VER recording. The data in Fig. 3 represent the mean area for three separate VER determinations at each disk-ring interval.
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6. We evaluated disk brightness by presenting a comparison disk to the left eye of the subject, alternating at 1.5-second intervals with the disk-ring sequence presented to the right eye. The duration of the comparison disk was varied in ascending and descending steps of 0.5 msec until a satisfactory brightness match of comparison disk to the disk in the compound stimulus was obtained for at least three successive presentations of the test and comparison stimuli. Since the durations employed were less than the critical duration for temporal summation, the stimulus duration was directly proportional to brightness. The brightness data for each disk-ring interval represent the median comparison disk duration for five trials at each separation. This duration is expressed in Fig. 3 as a percentage of the comparison disk duration required to match the brightness of the disk alone presented to the right eye.
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8. This study was supported by PHS grants 1-K3-NB-31,816, MH-06723, and NB-03356. We thank Miss Cleopatria Ross for technical assistance.

5 December 1967; revised 24 January 1968

Dolphins and Multifrequency, Multiangular Images

Most discussions of dolphins inspecting the environment (*1*) stress their presumed ability to range on objects by echo, as by sonar; I submit that they "see" objects acoustically about as well as we do visually. My reasoning follows; I have no proof.

Dolphins emit a series of whistles, slide tones, and sharp sounds (clicks) having basic frequencies that cover a considerable range (200 to 150,000 hz). Each may have more than one transmitter and receiver. In any case, dolphins are generally moving, so that, no matter what object they are concerned with, they observe it from different angles. Thus they obtain multifrequency, multiangular information about the object.

From multiangular information (angular width of lobes in the pattern of scattered intensity) the lateral separation of centers on the object that scatter sound can be determined, and from multifrequency data the radial depth between centers can be determined. For simple geometry the lateral separation L in half-wavelengths $\lambda/2$ between a pair of scatterers is

$$L = (r/\Delta x)(\lambda/2) \qquad (1)$$

and the radial separation R is

$$R = (f/\Delta f)(\lambda/2) \qquad (2)$$

where r is the range to the object; Δx is the lateral distance, at right angles to the "line of sight," between interference fringes at one frequency, due to the pair (that is, the lateral distance required to produce phase shift of 2π in the intensity of the received signal; the variation from maximum to minimum depends on the product of the strengths or cross sections of the scatters); f is the frequency; and Δf is the change in frequency, at one location, needed for phase change of 2π in the intensity of the received signal.

Determination of L and R is equivalent to determination of the true separation $(L^2 + R^2)^{0.5}$ at an angle $\tan^{-1}(R/L)$. With more complicated three-dimensional geometry, additional trigonometric projection terms enter the equations. (Distances are measured in half-wavelengths rather than whole wavelengths because of the two-way path from the dolphin to the object and return. In Eq. 2 one may replace $f\lambda$ by the speed of sound in water, but