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ABSTRACT

The purpose of this paper is to demonstrate that specific spatial and possibly temporal rates of change dominate early infants' looking, that these spatial and temporal events have meaningful and specific empirical correlates in neurophysiology as a function of age, and finally that neurophysiologically constrained models provide testable hypotheses for studies involving infant perceptual development. A model is presented for infant looking duration or pattern preferences depending upon transformation of spatial characteristics of visual stimuli by a developing visual system. It is shown how this model predicts the behavioral data obtained by the author and others and how these behavioral data are reflected in measures of infant brain responses. The inadequacies of a strictly spatial model which force one to incorporate temporal characteristics of stimulation are discussed. (Author/KM)

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Symposium on: Perceptual cognitive processes in the infant

BRAIN AND BEHAVIOR PROCESSING OF CONTRAST INFORMATION BY HUMAN INFANTS: SPATIAL AND TEMPORAL CHANGES

Bernard Z. Karmel, University of Connecticut

My purpose today is three-fold; (1) to demonstrate that specific spatial and possibly temporal rates of change dominate early infants' looking, (2) that these spatial and temporal events have meaningful and specific empirical correlates in neurophysiology as a function of age, (3) and finally, that neurophysiologically constrained models provide testable hypotheses for studies involving infant perceptual development.

I hope to do this by presenting, (1) a model for infant looking duration or pattern preferences depending upon transformation of spatial characteristics of visual stimuli by a developing visual system, (2) showing how this model predicts mine and other's behavioral data, (3) indicating how these behavioral data are reflected in measures of infant brain responses and, finally, (4) briefly comment on the inadequacies of a strictly spatial model which force one to incorporate temporal characteristics of stimulation.

For the past few years, I and my colleagues have been operating under the assumption that early pattern preferences in infants are based primarily on neurophysiological "expectancies" inferred from functional analyses of center-surround receptive field properties characteristic of single neuron responses to visually patterned inputs.

Textured fields when "viewed" by such a neuron would effectively produce spike rate Activity changes that could be characterized by an inverted U-shaped spike rate change function (Activation). (See Figure 1a)

Figure 1 About Here

This function would contain at least two minima (i.e., no rate change) and at least one maximum (i.e., maximum rate change). One minimum would occur when a pattern contained very small elements, since dark and light elements would project both dark and light spots onto both center and surround simultaneously causing cancellation of inhibitory and facilitory effects. A second minimum would occur when very large texture elements were present. Here, eye fixations would effectively project equivalent lumina on both the center and the surround of a given receptive field again causing cancellation. At least one maximum activity rate change would occur somewhere between these extremes, possibly depending on anatomical region and retinal connections, and would correspond at least to some real retinal element size of visual texture element projected.

If an equal number of neurons with such receptive field characteristics existed in all anatomical regions for all inputed texture element sizes and shapes, an integration of Activation across neurons after fixation would produce no differential values. However, empirically, receptive field sizes do not cover large portions of the retina, but are restricted to small circumscribed regions (usually binocular and predominantly foveal) of the retina (Hubel and Wiesel, 1962) and are somewhat larger and more "diffuse" in character in underdeveloped Ss (Wiesel and Hubel, 1965), and in subcortical structures (Hubel and Wiesel, 1962; Schiller and Koerner, 1971). Thus, the aggregate Activation (i.e., the summated spiking rate changes across a specific neuron population at any point in time) would not be equal for all configurations of patterned stimuli at any single point in development or for any specific anatomical locus. However, some Activation level would exist at all times during development. Therefore, given this rather simple analysis, and regardless of what else these neurons affect, we suggest that this specific momentary level of Activation is linearly related to looking preference functions. Further we postulate that shifts in such preference functions are directly related to development of these functional visual cells or to relative dominance during development of certain specifically located cells over others.

Although our model deals with visual stimuli, we are attempting to generalize it to other modalities empirically, but will address ourselves only to the visual here.

One major consistent finding regarding looking preferences and shift in preferences with age has been that there are "optimal levels of complexity" and that infants tend to look at "more complex" patterns as they age. However, our data argue that these functions and corresponding age shifts in the main can be depicted as a shift in looking to patterns containing greater and greater edge density as approximated by use of a pattern descriptor based on the square root of the total amount of contour contained in a pattern regardless of their relative "complexity" ratings by adults. The square root transformation implies that edge-area relationships within the pattern are critical. Figure 2 shows the stimuli we have generally used while Figure 3 summarizes findings for certain studies in which larger stimulus fields having various types of patterns basically varying in arrangement and element size (spatial frequency) have been used.

Figures 2 and 3 About Here

Here we have plotted our own data (Karmel, 1969a) that of Hershenson (1964), Brennan, Ames and Moore (1966), and Greenberg and O'Donnell (1972). Adjusting for differences in pattern sizes and distances between studies and standardizing on retinal angle of elements of a hypothetical 1 ft.-square pattern at 20 inches (for no other reason than these values were initially used by us), the square root of contour descriptor, with progressively shifting inverted U-shaped functions with age, can be shown to describe ordinal relationship empirically observed between stimuli.

Certain reported quantitative discrepancies from these curves occur to uni-directional stimuli such as Horizontal vs Vertical stripes and radially varying stimuli with curves such as bulls-eyes, but these are argued to be special cases of the more general model depending upon non-linear distributions of actual eye scans across stimuli (Kessen, Salapatek, Haith, 1972), or upon non-linear distributions of cells inherent in a developing visual system such as a foveal distribution of cells along with developing cortical magnification of foveal as opposed to peripheral retinal projections (see Maisel and Karmel, in preparation, for elaborations of possible effects of development of retinal eccentricity on preferences).

Our model can account for such shifts depicted in Figure 3 if cortical cell receptive fields characteristics were somewhat larger in immature but still functioning areas or if larger but more mature subcortical receptive field functions dominated for the behavior over the smaller, but less mature cortical fields in younger Ss. These, indeed, are known characteristics of units in the visual system during development in animals. Figure 4 depicts these hypothetical shifting neurophysiological functions to spatial information over development.

Figure 4 About Here

Thus, if the behavioral data can be shown to empirically reflect in the main spatial element density, we conclude that shifting inverted U-shaped functions of spike rate change (i.e., Activation) at the neuronal level might underlie the looking behaviors observed.

In the next part of this talk I will attempt to anchor the model to neurophysiological observables argued to be functions of neuronal spike rate changes from a pool of neurons having visual input in infants.

Since responses from single neurons cannot be directly measured in human infants, measurement of gross visually evoked brain electrical activity (i.e., visually evoked potentials or VEPs) was attempted. Fox and O'Brian (1965) have demonstrated that the probability distribution of a single neuron's spiking activity can be directly predicted from the response envelope of extracellular evoked potentials recorded in the region surrounding the unit. Verzeano, _et al._ (1968) among others, specifically suggest a high correlation of the first derivative of VEP amplitude to the post stimulus probability histogram. Thus, one test of the theoretical position, then, might be generated by observing changes in component amplitudes of slow brain electrical events in infants, as these are evoked by contour information used in behavioral studies. We, thus, assume that these components measure in some complex way the pooled neural Activation effects depicted in Figure 4.

For those unfamiliar with neurophysiological recordings, the occipital pole EEG at a point 10% above the inion on the midline referenced to the back of the ear was recorded most successfully from active and attending infants using a telemetry system (Narco Biotelemetry system) and having mothers bottle-feed during the experiment. That 1-sec portion of the EEG following a brief strobe-flash of light viewed through a patterned stimulus was computer averaged. The evoked response (or EP) represents the average voltage levels, after stimulus onset. The EPs generated in this manner are equivalent to performing a one-way ANOVA with treatments depicted as successive time bins with bin means connected to form a continuous line and bin variance related to the number of trials used for averaging. Typically we use at least 32 consecutive trials for any one stimulus pattern, but only those trials when Ss are judged looking at the pattern.

Five stimuli, consisting of 4 redundant checkerboard patterns and a "blank" equated for luminance were used (check sizes were 20', 40', 1°10', 5°, and 27° respectively. Redundant checkerboards were used since most adult pattern vision EP studies and infant behavioral studies have used these stimuli and possible cross-study comparisons were felt important in initial studies (see Karmel, Hoffmann and F gy, submitted, for details). The major components of the pattern and 'blank' EP are shown in the next slide (Figure 5).

Figure 5 About Here

Usually N_1, P_2, a major negative between P_2 and P_4 and P_4 could be identified. A positive peak prior to N_1 was not reliably discernible in most Ss as is the case reported for adults (Cobb and Dawson, 1958). All Ss (N=33) whose records for all five stimuli could be analyzed for N_1, P_2, a major negative (N) after P_2, and P_4 are reported here. Infants varied from 9-12 weeks of age.

Both the amplitude of P_2 and the peak-to-peak difference between P_2 and the major negative (N) after P_2 were significantly related to the stimulus variable. In some cases P_3 is completely obliterated in our records and N_3 is not discernible or is coincident with N_2. Apparently P_3 and N_3 latency and amplitude may depend on stimulus manipulation, development, and recording site.

Statistical analysis of both P_2 amplitude and P_2-N amplitude differences indicated that inverted U-shaped trends of the component amplitudes accounted for 79% ($r=.89$, $p<.01$) of the significant stimulus factor variance if the stimulus factor is ordered by the identical description (the square root of contour) found to relate fixation preferences to some stimulus variable. It is assumed that the increases in P_2 amplitude at least reflect increased synchronous neuronal activation driven by the contour stimulation and provide support to our model.

Interesting, no significant differences in trend to square root of contour were discernable in the data when <u>S</u>s were divided according to chronological age or estimated gestational age from mothers' reported due dates. But if <u>S</u>s were split on the basis of the average latency of P_2 across stimuli, a significant difference in cubic trend between groups for the stimulus effect is present for the P_2 amplitude and possibly for the P_2-N amplitude difference. These data suggested that relative P_2 latency is longer. Ellingson (1967) has shown that the latency of P_2 decreases with gestational age. If latency of P_2 reflects developmental age, our data would suggest a relatively greater influence of larger element events on component amplitudes the less mature the <u>S</u> neurologically even in this very restricted age range. The lack of relationship to reported due date may be due to the unreliability of this reporting measure along with a severe restriction on age in this study.

Further data with respect to this check effect over wider age ranges are currently being obtained.

Although a limited number of checkerboard stimuli were used, visual inspection of records of a different 3-5 <u>S</u>, indicated, at least, that an inverted U-shaped function existed for P_2-N amplitude differences if both random and checkerboards were used (Karmel, White, Cleaves and Steinsiek, 1970) and that the maxima of the P_2-N difference would occur at larger check sizes the younger the *S* (Harter and Suitt, 1970). However, sufficient group data for statistical analyses under controlled conditions have not been obtained using the flash EP technique just described.

To produce data not restricted to checkerboard stimuli, we employed a technique involving sine wave modulation of light intensity viewed through patterned stimuli instead of the transient flash just discussed. Essentially the stimulus is a continuous waxing and waning of light intensity behind the pattern.

The evoked EEG response to sine light modulation is a Fourier transformation of the fundamental frequency of modulation in adults according to Spekreijse (1966) and others employing linear systems analysis for such phenomena. Indeed, Pollen, *et al.* (1971) have also demonstrated that two-dimensional spatial information (stripes of varying widths) is transformed by striate cortex (SC) neurons into a neuronal frequency code in the form of periodicities in the post stimulus probability histograms of unit firing. (Note our discussion earlier of the direct relationship between the post stimulative probability histogram and the evoked potential envelop.) Spekreijse and others argue that similar periodicities produced by modulated temporal information in the form of modulated light intensity would summate with those periodicities resulting from the pattern information (see Cornsweet, 1970, *Visual Perception*, Chapter 11, for a simplified discussion of modulation). Thus, the output EEG response might consist of compounded frequencies of externally imposed and internally generated periodicities that were interacting over time in the brain. Note the importance here of a transformation of spatial information into a temporal frequency code neurologically, a most common neurological coding mechanism. This effect is represented in the flash EP data as a possibly longer time constant for the full neurological effect of the stimulus to dissipate itself. (See also Ristonovic, 1971, for a similar analysis of adult pattern EP responses).

Using sine modulation of light, each S (N=7) generated EPs to 5 checkerboard then 5 random patterns with a "blank" pattern interposed in each set.

Figure 6 depicts a representative set of EPs from one S. Significant variability was found in a measure reflecting differences between P_2 and P_3 and between P_2 and N_2 (the latter with less precision at this age and this modulation frequency).

Figures 6 and 7 About Here

Figure 7 plots the P_2-P_3 difference to the square root of contour. The inverted U-shaped function accounts for 80%, ($r=.90$, $p>.01$) of the variability. Positive peaks are designated P_2 and P_3 as we feel these are equivalent to P_2 and P_3 obtained in the flash EP records.

Thus, P_3 disappears in some cases for stimuli in the middle of the texture range or is masked by P_2 at faster frequencies of modulation. Preliminary data from 2 Ss 50 days of age indicate that P_3 disappears or coincides with P_2 at 4.5 cps but not at 2.25 cps in younger Ss. This would reflect longer time constants for processing identical environmental information by younger Ss since P_3 does not generally disappear in older Ss at 4.5 cps. These data are reflected in the increased rate for driving found for older Ss in others' studies. (Vitova and Hrbek, 1970)

The use of a temporally varying field whose frequency of constant change interacts with patterns to produce periodicities in the brain, "beating" so to speak, at tuned neurological frequencies as a function of age and stimuli, reinforces the importance of temporal codes for behavior and neurophysiological activity in infants.

The 4.5 cps modulation rate, equivalent to 250 millisec. periods represents a time phase corresponding to rapid eye scanning rates observable in infants. Interestingly, these rates increase with development as do the number of looks during a given stimulus presentation (Cohen, 1972).

In other unreported studies implicating velocity or relative temporal change and where patterns with controlled edge and luminance relationships have been manipulated, behavioral [illegible] for Ss (12-14 wks) (Karmel, Apter, and McCarvill) suggest that distance between surfaces plays some role in preferences over expectations based on retinal angle alone when two distances for patterns were present. Motion parallax information affecting the frequency of texture information encoded and so important for depth avoidance on the visual cliff (Walk, 1965), might be argued to interact with preferences. Indeed, this has been demonstrated in one-two-day-old chicks (Walk and Walters, 1971). These animal Ss have been shown to have similar preference functions as infants (Karmel, 1966, 1969b).

In a modulation VEP study (Karmel, Fegy and Hoffmann) partially completed, where a pattern is controlled for edge but where the edge is displayed on one surface or exactly split between two survaces, both adult and infants show a significant decrement ($\underline{p}>.05$) of P_2-P_3 (in infants) or of the P_2-N_2 responses (in both adults and infants) in the two-surface condition as compared to the single-surface condition. Apparently this effect is a binocular one and might possibly represent decrement due to differential frequency codes summating out of phase for depth but in phase for the single surface. These latter data and interpretation should be treated with caution since more critical conditions need to be run in this experiment.

These temporal effects along with the generally known influence of velocity information on spatial effects suggest the current working model based on empirically testable spatial-temporal interchangeability for looking behavior in infants. (See Figure 8).

Figure 8 About Here

Time prevents me from speculating (at length) on possible neurophysiologically important effects, but the fact, that check sizes producing greatest looking attention or largest deviations from baseline brain response relate to approximate foveal sizes (1-2°) rather than acuity thresholds (<20' in 90-day-old Ss), might imply that both the maintenance and development of foveation are basic to early visual preferences and functions. Salapatek (1969), Lodge, et al. (1969) and Fantz (1965) also suggest that development of foveation may be a critical factor.

Development of the macular region of the retina and presumable foveal stimulation occurs in apparent coincidence with P_2 latency development. Further, pattern-dependent evoked potentials are primarily produced by foveal stimulation in adults. In addition, Superior Colliculus (SCs) cells, which are specifically involved in eye movements and visual orientation in space are known to have specific influences on the later components of VEPs. Interestingly, these cells serve to facilitate foveation and have functional characteristics usually independent of form and orientation but are very much size-dependent as is the case for behavioral preferences. Both SCs cells and Lateral Geniculate Body cells generally contain larger receptive field sizes and are relatively more mature at birth compared to cortical cells. Subcortical dominance over early visually-dependent functioning and orientation might be one specific consequence.

Thus, a shift in distribution from larger to smaller receptive field sizes, whether due to macular development, cortical development and functioning, or due to the relative efficacy of [illegible] structures to cortical influences providing information for central fixation could be correlated with VEP and behavioral findings in infants and animals. Further specific elaboration of such neurophysiological constraints may be useful in models involving the origins of visual perception and visually dependent preferences in infants.

The general lack of experimental effects characteristic of basic contour processing in diverse species including human infants is suggestive of a spatial information processing system that is inherent in the functioning of intact visual systems and is consistent with Gibson's notions regarding the nature of perceptual organization of visual space (Gibson, 1966). A shift in the relative distribution of cells converging on brain loci from the retina and acting to affect shifts in specific Activation levels of neuron pools would appear to be an efficient and parsimoneous set of physical events by which selection pressures could evolve into species' development of spatial perception, accommodation reflexes or pattern sensitivities. (Indeed, Sackett, 1963, suggested a similar mechanism for early imprinting.) Experience during ontogeny affecting such pools would only act to modulate these Activation parameters, not fundamentally alter the processes by which such Activation is achieved (See Piaget, 1972).

Thank you.

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Figure Captions

Figure 1. Hypothetical spike rate change as a function of contour density.

Figure 2. (See Karmel 1969a, Figure 1, p. 344) Basic stimulus set.

Figure 3. Mean looking time plotted with respect to the square root of the total sum of the lengths of all black-white transitions contained in the pattern. Newborn curves extrapolated from Hershenson (1964); Three and 8-week curves from Brennan, et al. (1966), 6- and 11-week curves from Greenberg and O'Donnell (1972), 13-week curve from Karmel (1969a) and Brennan, et al. (1966), 20-week curve from Karmel (1969a).

Figure 4. Shifts in hypothetical Activation functions with corresponding shifts in average receptive field sizes characteristic of developing visual systems.

Figure 5. Sample VEP following flash onset to patterned and non-patterned stimuli from selected S depicting major identifiable components. Positive deflections at O_2 up. Patterns were 12-in^2 viewed from 20-24 inches.

Figure 6. Modulation VEP from selected infant to range of patterned information. Light onset at lowest portion of sine wave. Approximately one cycle of information. Numerals 1-5 correspond to 1/16-, 1/8-, 1/4-, 1/2-, and 1-inch checks respectively viewed from 9-12 inches. The (C) and (R) refer to redundant and random patterns respectively.

Figure 7. Mean peak-to-peak (P_2-P_3) difference to range of patterned stimuli. Element size listed has been adjusted to facilitate comparison to behavioral data from Karmel, 1969a, Figure 3, p. 351 and Figure 3 above.

Figure 8. Hypothetical interaction of spatial and temporal frequency on orienting to visual stimuli.

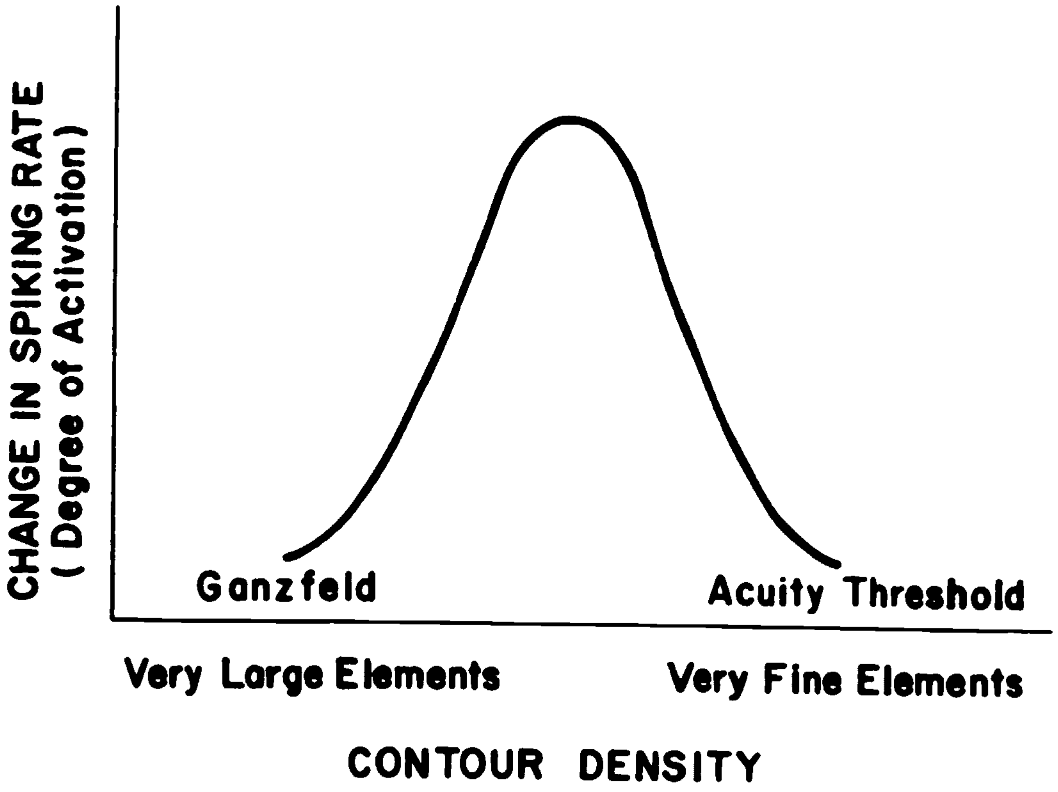

FIGURE 1

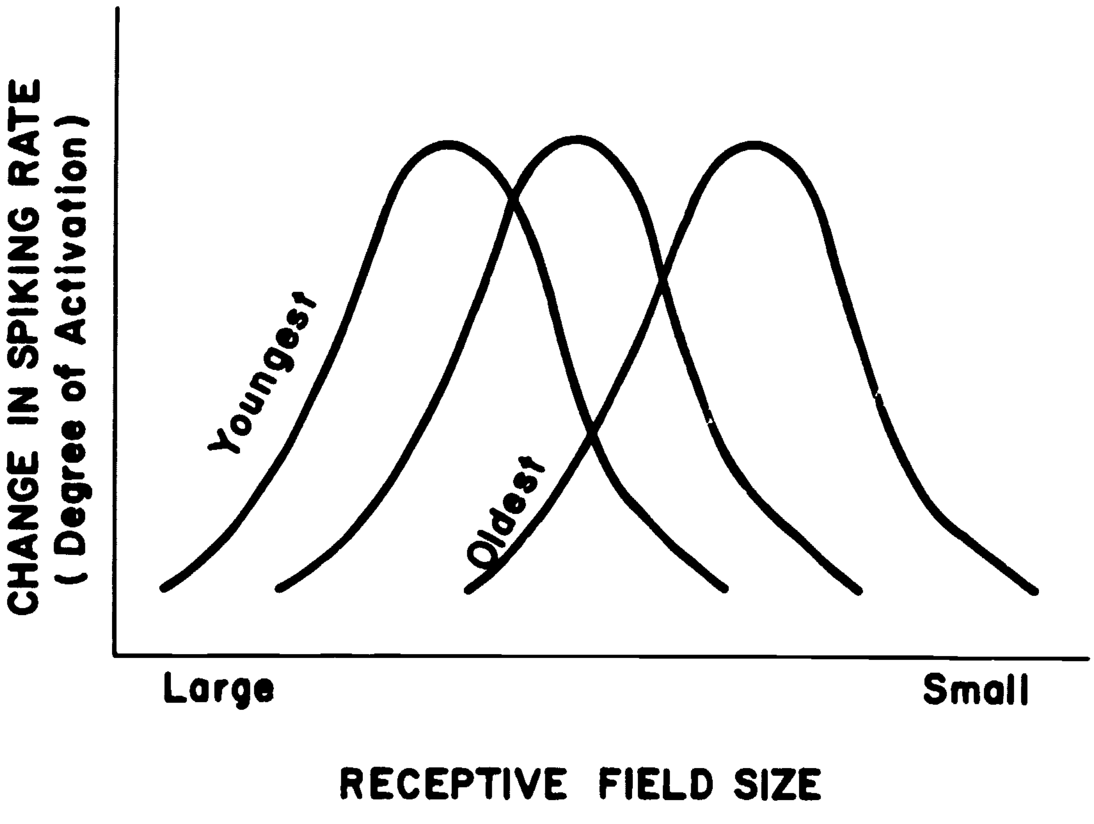

FIGURE 4

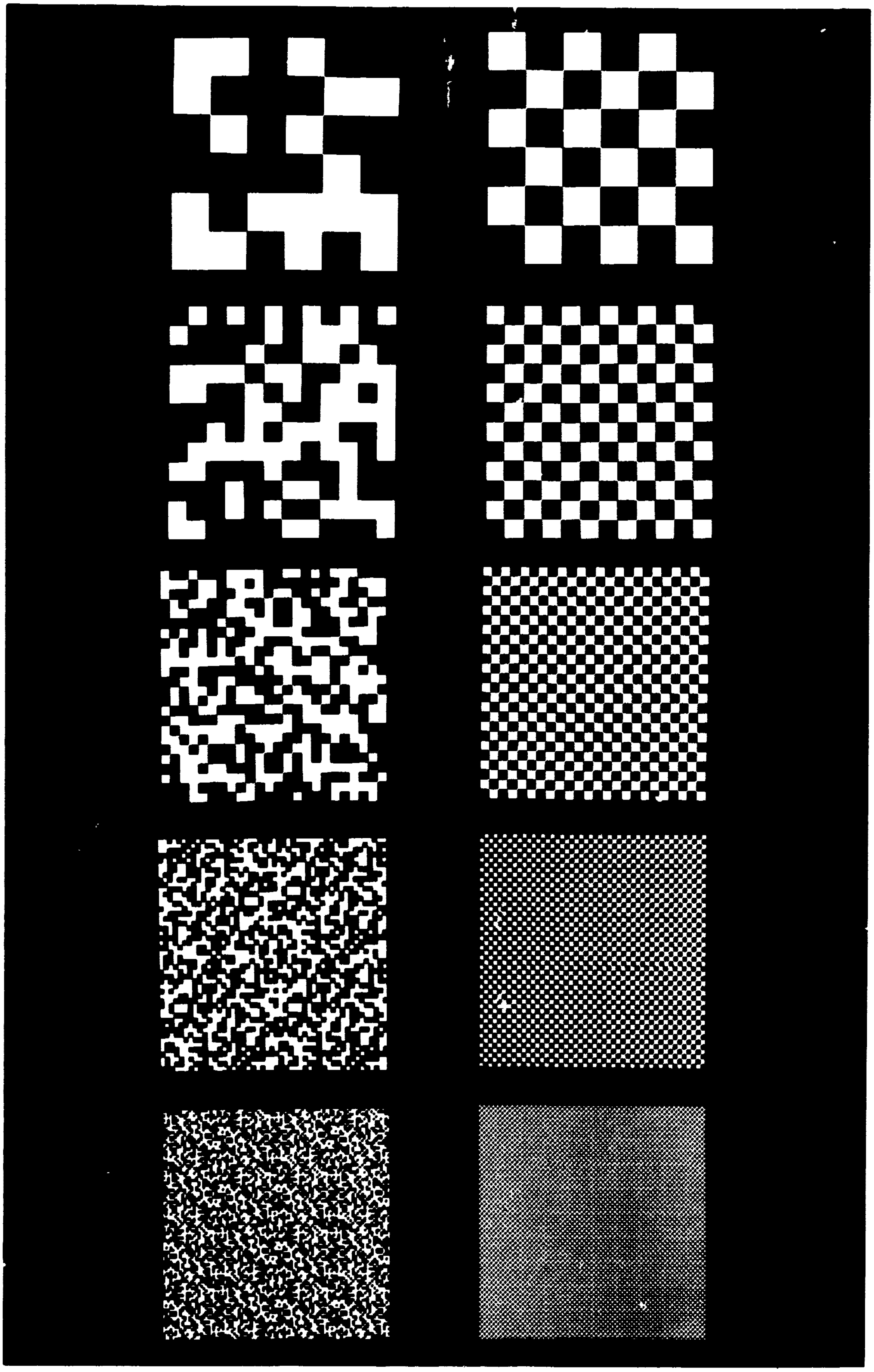

FIGURE 2

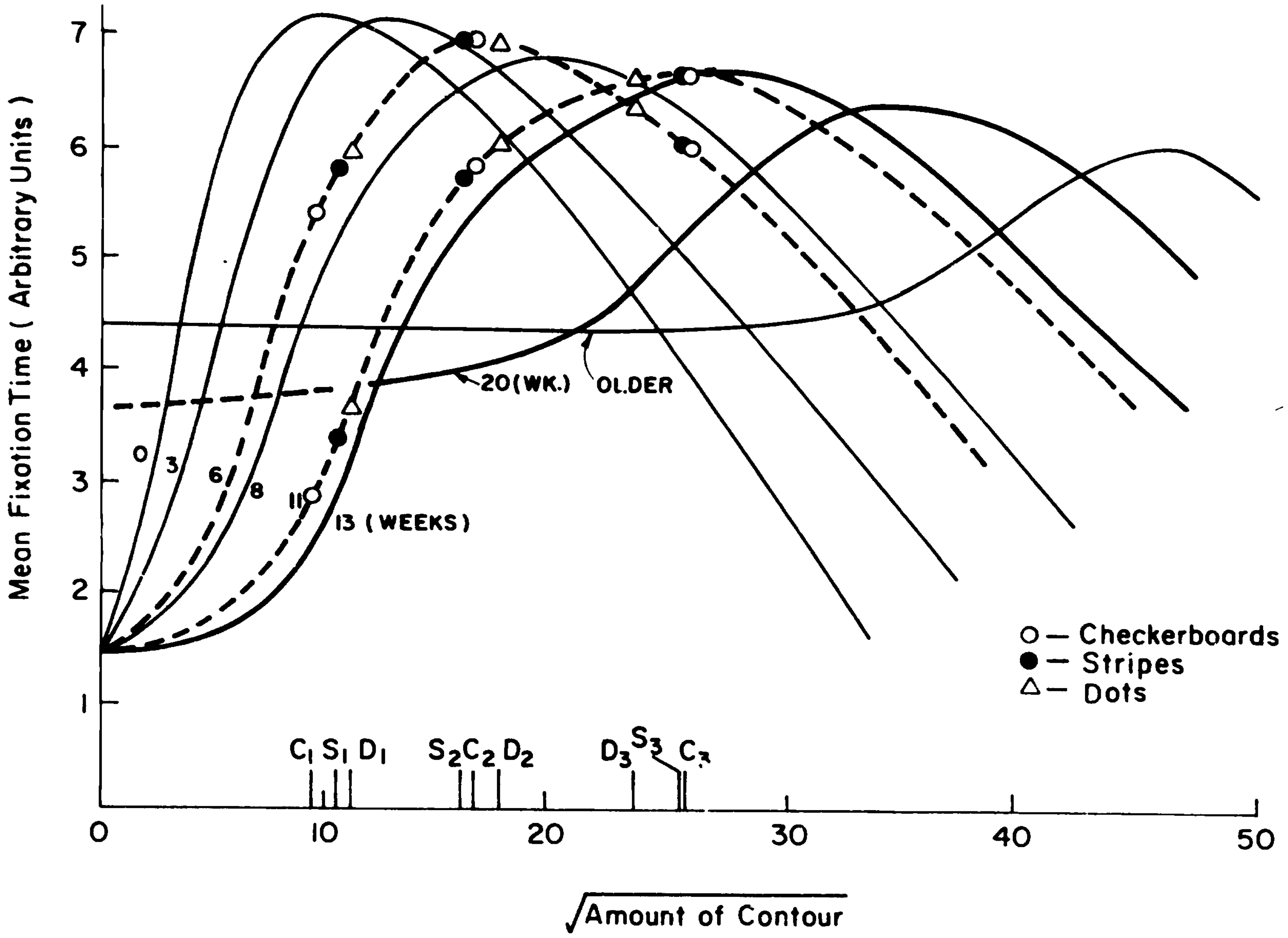
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FIGURE 3

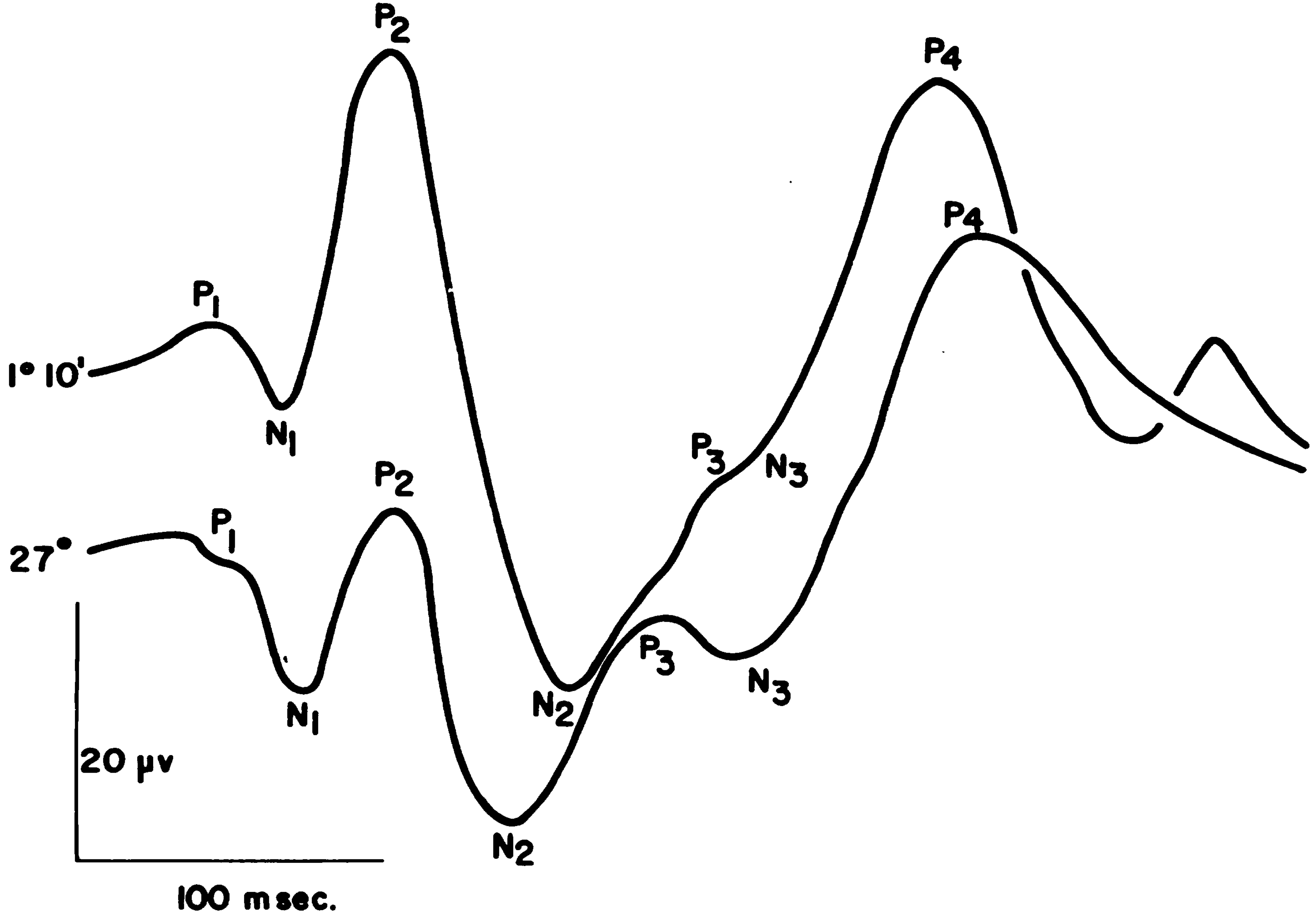
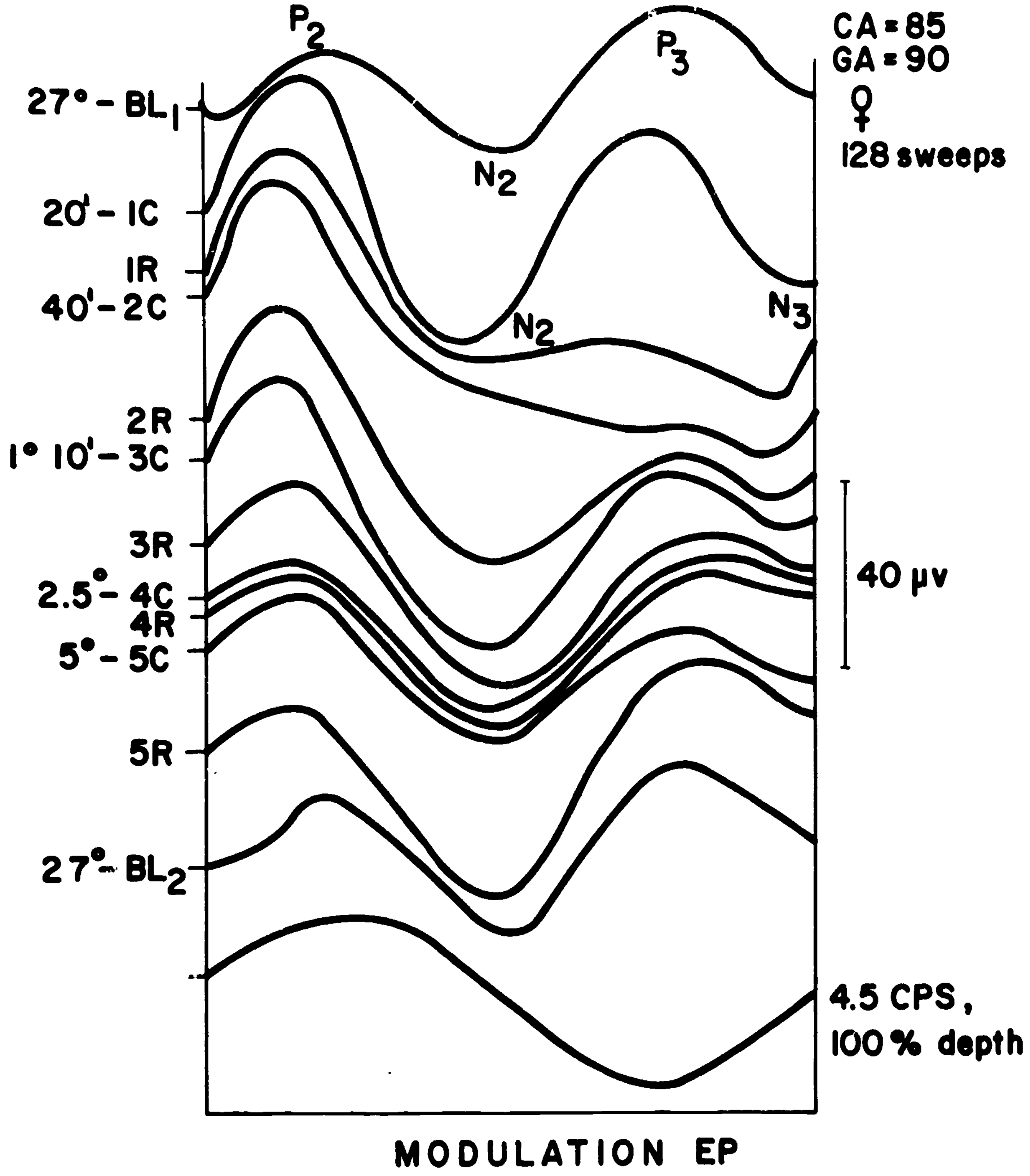


FIGURE 5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100 % depth
MODULATION EP

FIGURE 6

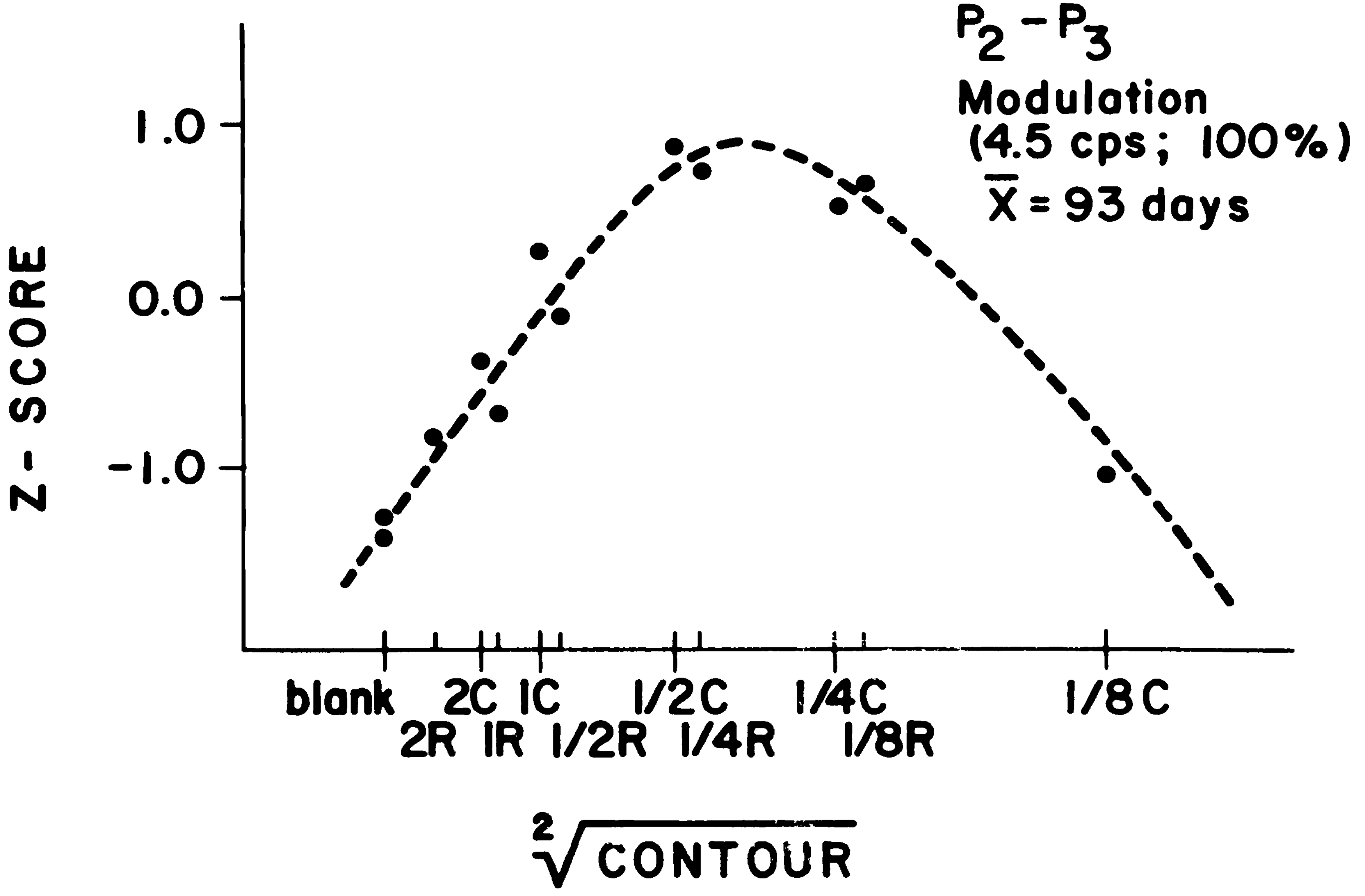
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FIGURE 7

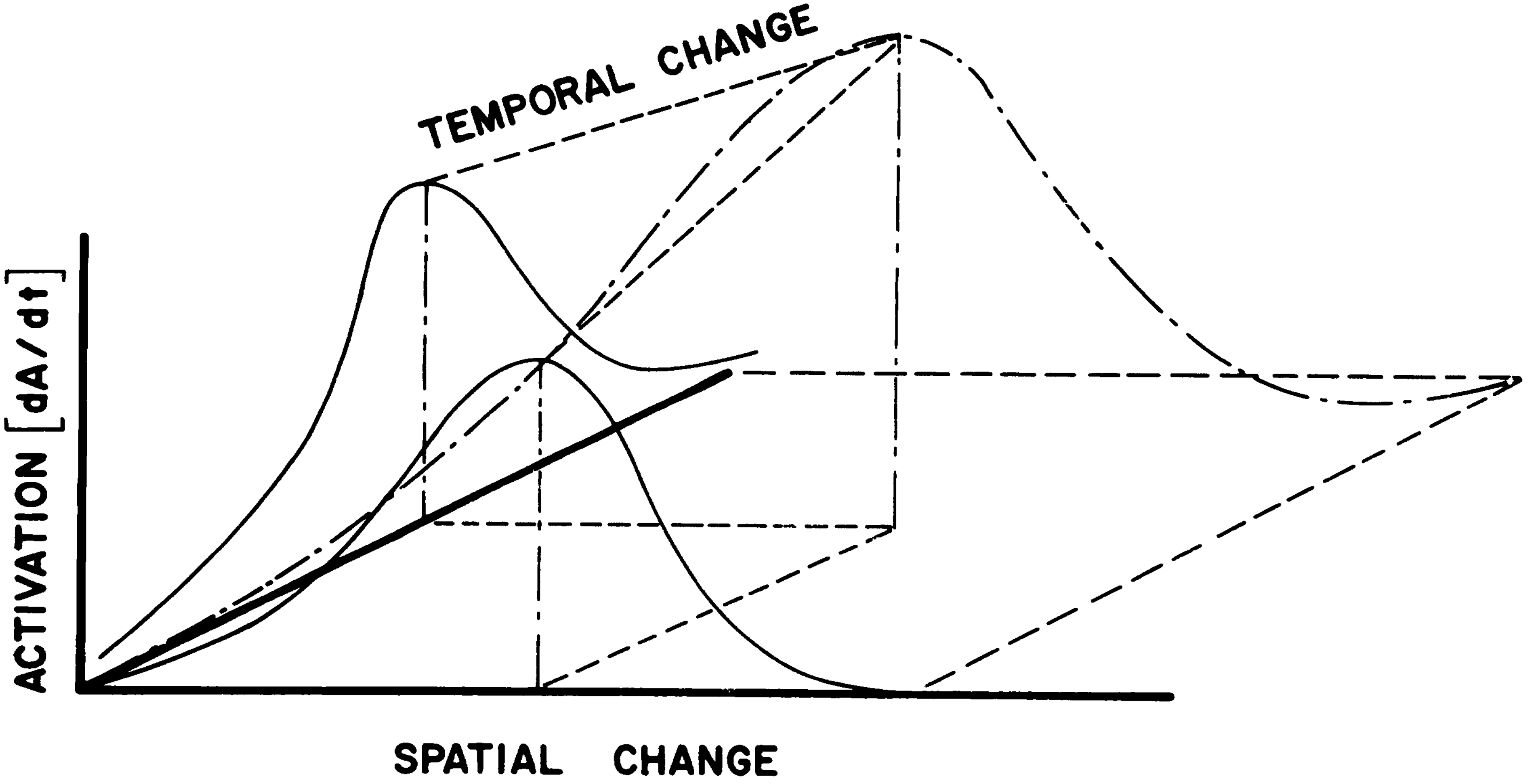

FIGURE 8