Cooperative Neural Processes Involved in Stereoscopic Acuity

G. Westheimer

Department of Physiology-Anatomy, University of California, Berkeley, CA 94720, USA

Summary. Results of psychophysical experiments are reported showing that synchrony, appropriate relative placement, and absence of standing disparity are important conditions to be met by members of a target configuration if they are to participate in the cooperative neural processes leading to the best disparity discrimination. Consecutive binocular presentation of the members of a stereo target decreases stereoacuity by a factor of about 10, and a step disparity displacement of a single line target needs to be larger still to be detected as a depth stimulus. A standing disparity of even one minute of arc at least doubles the disparity discrimination threshold. It is postulated that a differencing mechanism operates on the depth signal of individual features; the temporal and spatial optima of target presentation for stereoscopic acuity outline the character of the concerned operations.

Key words: Stereoacuity – Disparity detection – Neural difference discrimination – Binocular vision

Although it has long been known that the threshold for depth discrimination is only a few seconds of arc, we still lack insight into how this is accomplished. Neither grain size of the retinal receptor mosaic nor steadiness of retinal image seems to set the limit for depth judgments; indeed, stereoscopic acuity does not suffer when targets move laterally or in depth by 5 or more min of arc during a 200-ms exposure (Westheimer and McKee, 1978).

Conceptual formulations of stereoscopic depth localization must cover these facts. Of the various conjectures to account for the independence of stereoscopic acuity of relative image motion in the two eyes, one has already been examined. When viewing a stereoscopic target, feature separations in the right and left monocular views must differ. If such feature separations are processed uniocularly, comparison of the right and left retinal images is in principle possible even when the images are in relative motion. This viewpoint is, however, no longer tenable since it has been demonstrated experimentally that stereoscopic depth thresholds can involve differences in image separation on the right and left retinas that are many times smaller than minimal detectable lateral separation differences (Westheimer and McKee, 1979).

The evidence thus points to a sequence of processing in which a feature is identified by associating similar image components in approximately corresponding retinal locations. Depth would then be assigned on the strength of the disparities of each of the associated right and left eyes' features. If this formulation is correct, the binocular viewing of a single vertical line by itself engenders a depth value; but in the light of the known limits of eye vergence stability, it is unlikely that the absolute depth signal resulting from such an observation of an individual target can have the precision demanded for stereoacuity.

Consequently, further properties of disparity processing are here investigated in the hope of uncovering cooperative relationships between the assigned depth values of individual targets that would confer robustness to convergence instability on the difference signal.

The purpose of the study is to examine the cooperative mechanism between several stereoscopic targets, in particular as influenced by their separation in space and time. As a preliminary it is helpful to design a minimum stimulus configuration that can serve as a basic reference situation. In connection with the present study, the simplest is a single vertical line which, when given a step displacement, can act as a self-reference. The step displacement threshold for such a single target can then also be obtained in the presence of other targets and in this way one can ascertain what cooperative mechanisms between individual targets play a role in stereoscopic depth resolution. The step and pulse disparity stimulation has been used effectively to investigate other aspects of binocular eye movements and stereoscopy (Regan and Beverly, 1973; Foley and Tyler, 1976).

There has always been a conceptual gap between man's resolution capabilities (measured psychophysically) and the currently popular single-cell analysis of the sensory nervous system. A temporal step stimulus would seem to serve as an effective bridge here. For example, the instantaneous brightening of a stimulus would be a good probe for the brightness coding capability of a single neuron in the visual pathway; similarly, the instantaneous disparity displacement would be a good probe for the depth coding capability.

A Note About Terminology

The angle subtended by the interocular distance at the target in object space is called binocular parallax. The difference between the binocular parallax of two targets is called binocular disparity, or disparity in short. When one target is regarded as a standard (for example, when the subject's binocular fixation is maintained on it) the other target can have crossed (convergent) or uncrossed (divergent) disparity, depending on whether its binocular parallax is greater or smaller, respectively, than that of the standard. The subjective correlate of the objectively measured disparity shall be called depth, the appropriate response criterion for a target presented with convergent disparity being "nearer", and with divergent disparity, "farther". Because of the uncertainty of fixation, there is difficulty in the operational definition of retinal disparity, i.e., the difference between strictly corresponding retinal loci on which the two uniocular images of a single target fall, but this uncertainty does not extend to the concept of disparity difference between a pair of binocularly seen lines. Because the concern here is with disparities of a minute of arc and less, present methods of artificial image stabilization would not materially improve the certainty of retinal image localization in the two eyes in a normal subject.

Methods

The experiments consisted of psychophysical determinations of the threshold of depth discrimination in three experienced observers with good stereoscopic vision, optimally corrected for refractive errors, with natural pupils in a moderately dark room. Stimuli were white vertical lines (luminance about 10 mL) against a dark background, created under computer control on a pair of 602 Tektronix oscilloscopes with P4 phosphor. By suitable polaroid filters before the two scopes, seen superimposed by a beamsplitter, and before the eyes, each scope carried the stimulus for one eye. Observation distance was 2.5 m, the lines had an effective width of less than $1/2$ min of arc, and they could be positioned to an accuracy of 2 s of arc. The refreshment rate of the scope was usually once every 5 ms.

To aid fixation and vergence stability, a pattern consisting of four dots or brackets outlining a square $1/2$ degree in side length was visible in the interval between stimuli. A stimulus appeared every few seconds in its middle and the subject had to respond by making a binary decision through setting a switch. In all instances, seven stimuli made up a set, differing from each other in equal steps in the disparity values – one, two or three steps of crossed and uncrossed disparity, and zero disparity. Each stimulus presentation contained a member of this set selected at random; the subject's response elicited an error signal if a stimulus with convergent disparity was called "behind" or a divergent disparity "front." By fitting a psychometric curve to a set of about 300 responses with the method of probits a threshold value was obtained: the disparity value at which the subject's responses were 75% correct. A standard error of this mean was also regularly calculated. Each threshold value given in this study was based on at least 300 responses and often many more.

Results

Step Disparity Displacement Detection

The subject's task at the outset was to judge the direction of displacement when a single vertical line target, 15 min of arc long, was suddenly stepped forward or backward at the exact halfway point during a 1,000-ms exposure. The line was initially in the fixation plane and the seven possible step stimuli comprised: three equally spaced forward displacements, no displacement, and three equally spaced backward displacements. No effective comparison stimulus was available within several degrees of visual angle.

The step disparity displacement threshold of three subjects is given in Table 1. The threshold denotes that step displacement of a single target for which the subject can correctly identify the direction of displacements on 75% of occasions. The thresholds are larger by a factor of at least 10 than the subjects' best stereo thresholds.

The stimulus in this experiment differs in two categories from those in ordinary stereoacuity judgments: (a) there is only one target, which must act as a self-reference; (b) there is a consecutive rather than simultaneous comparison in the depth domain. The enriching of the stimulus situation from the minimal condition of consecutive comparison of the disparity of a single target to the standard stereo paradigm of simultaneous comparison of a binocularly seen target pair is here carried out via an intermediate stage, viz., the consecutive comparison of the two members of a target pair.

Consecutive Presentation of the Two Members of a Stereoacuity Target

Here a vertical line, 15 min of arc high, was presented for 500 ms in the fixation plane. This was followed immediately by the presentation for 500 ms of a second

Table 1. Step disparity displacement threshold for a single vertical line, 15 min of arc long, without immediate comparison stimuli (s of arc)

Subject	Condition		
	Displaced only in disparity	Displaced in disparity and also laterally by 10 min of arc	Displaced only in disparity after a 200 ms delay
G.W.	74.5 ± 12.6	47.7 ± 5.5	60.9 ± 10.8
H.T.	87.9 ± 12.8		68.2 ± 7.7
S.P.M.	56.3 ± 6.7	40.5 ± 5.0	28.6 ± 3.1

Line is shown for 500 ms, and then shown for 500 ms:
Column 1 with a change in disparity but no change in lateral position
Column 2 with a change in disparity and a fixed lateral displacement of 10 min of arc
Column 3 with a change in disparity, but no change in lateral position after a delay of 200 ms

line at a position 10 min of arc to the left of the first line. The second line, in addition, differed from the first in that a step change of disparity had been introduced – one, two or three modules convergent or divergent disparity or no change in disparity, at random. The subject's task was to signal whether the second line appeared in front of or behind the plane of the first line. It is to be noted that here, as throughout this study, there was *no interocular delay*. Exposure of each stimulus always occurred synchronously in each eye: the stereoscopic depth threshold was being determined when the two line stimuli making up the target pair were exposed sequentially rather than synchronously.

Thresholds are shown in the second column of Table 1. It is seen that the threshold is lower now that the step in disparity was between the members of a pair of lines which were laterally separated, than it was when the disparity step was imparted to a single line. This finding might imply that a step change in disparity without change of retinal location is a poor stimulus for depth discrimination. That this is an incomplete description is shown by the next experiment.

Step Disparity Detection in the Presence of Comparison Targets

The original experiment, i.e., threshold of step disparity detection of a single vertical line suddenly given a convergent or divergent (or no) disparity change halfway through a 1,000-ms exposure, was now repeated with one difference: a comparison stimulus was provided that shared all properties of length and exposure with the test stimulus, but that remained in the fixation plane throughout the 1,000 ms, so that during the last 500 ms of the presentation a disparity existed between the test line and the comparison.

Three different configurations of comparison were provided: one in which the comparison was directly above the test line; one in which a pair of comparison lines was above and 10 min of arc lateral to the test lines; and one in
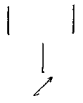
Fig. 1. Above line: Step disparity threshold (s of arc) for a single foveally seen vertical line, 15 min of arc long, in the presence of four different comparison targets. The test line and the comparison lines were exposed for 1,000 ms; the test line, which was initially in the same fronto-parallel plane as the comparison stimuli, was given a step disparity changed at exactly the halfway moment of the exposure. Test line is indicated by arrow. Comparison conditions are, from top to bottom: **a** Single line 15 min of arc long, with 4-min gap, vertically above test line. **b** A pair of 15 min of arc long vertical lines, with a 4-min vertical gap, placed 10 min laterally on each side. **c** A pair of 15 min of arc long vertical lines, placed 10 min laterally on each side. **d** A pair of chevrons, placed 10 min laterally on each side. Below line: **e** Disparity detection thresholds, s of arc, for a 500-ms exposure of a simple three line configuration, 10 min of arc line separation, lines 15 min of arc long, in which the disparity of the middle line has to be detected. This is the second half of the total presentation of configuration (**c**) above, but exposed by itself

which a pair of comparison lines was just 10 min of arc lateral. Results are shown in Fig. 1. Detection here also involved a disparity step of a single line stimulus, but the threshold is now closer to the optimum for stereoacuity. Clearly disparity stepping of a single line per se is not the origin of the poor performance in Experiment 1. Also of interest is the effect in two of the three subjects of differences in location of the comparison target. This seems to be a genuine difference in neural connectivity, because for subject GW this difference persisted in spite of many weeks of practice.

A further survey of features capable of acting as comparison targets, i.e., configurations capable of being associated in the cooperative interaction demonstrated here, awaits another occasion. As a preliminary finding, Fig. 1d shows that a pair of chevrons, i.e., lines that are appropriately placed but do not share orientation with the test line, will do.
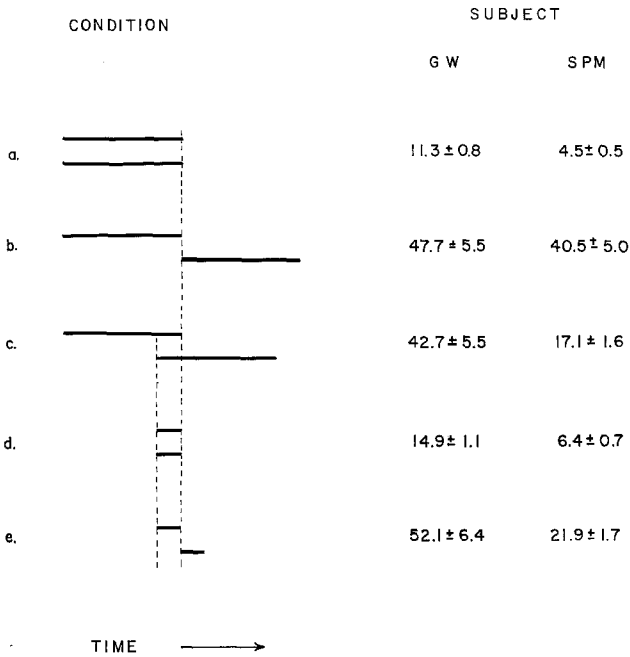
Fig. 2. Threshold for disparity detection (s of arc) of two binocularly seen vertical lines, each 15 min of arc long, laterally separated by 10 min of arc. Onset and exposure duration of the lines are varied in the manner indicated. Two modules of time were used: a long one, which was 500 ms, and a short one which was 50 ms for subject SPM and 100 ms for subject GW. From top down: **a** Simultaneous presentation of both lines for the duration of the long time module. **b** Sequential presentation of each of the two lines for the duration of the long time module. **c** Presentation of each of the two lines for the duration of the long time module, but onset of one line preceded offset of the other by the duration of the short time module. **d** Simultaneous presentation of both lines for the duration of a short time module (this condition is contained in condition **c**). **e** Sequential presentation of each of the two lines for duration of the short time module

Temporal Comparison

In the experiments so far described, a step disparity stimulus was the probe for testing contiguity effects. In the following experiments, spatial contiguity remained constant, while temporal onset asynchrony was made the variable.

The basic configuration was a pair of vertical lines 15 min of arc high and 10 min of arc apart, seen by each eye. One line was shown with one of a set of seven disparities relative to the other, and the subject's task was the detection of the direction of the disparity. In all experiments described in this section, whenever a part of the target was exposed, it was done so synchronously to the two eyes. Variation here was in exposure asynchrony of the left member of the target pair with respect to the right.

The basic results are seen in the upper two conditions of Fig. 2. When the right and left members of the target pair were exposed synchronously for 500 ms, stereo threshold was 11.3 arc s for GW and 4.5 for SPM (Condition a).

When the left side of the pattern was delayed 500 ms with respect to the right so that there never was the possibility of contemporaneous viewing of the two members of the target pair (Condition b), the threshold rose precipitously to 47.7 arc s for GW and 40.5 for SPM. Then, the asynchrony was made slightly shorter (by 100 ms for GW and 50 ms for SPM), allowing a brief simultaneous view of both parts of the target, albeit flanked temporally in opposite direction in each. This improved the threshold somewhat (Condition c). Further, this brief simultaneous presentation of the target pair (100 ms for GW, 50 ms for SPM) was given by itself, i.e., freed from the temporal flanking that it had to form Condition (c). The threshold was much better now (Condition d). Finally, onset asynchrony of even these brief stimuli led to a serious decrement of performance (Condition e).

The conclusion drawn from these experiments is that good stereoacuity has as a prerequisite the *simultaneous* unencumbered view of at least a pair of targets.

Disparity Tuning

Now that it has been demonstrated that good disparity detection involves the simultaneous presentation of at least a pair of optimally placed targets, we may enquire over what range of standing disparities this holds true. In the findings described so far, the ensemble of test-line disparities, within which the subject had to identify those members engendering a 'near' and a 'far' sensation, was centered around zero disparity. In other words, the set of seven configurations contained three with uncrossed disparities, one lying wholly in the fronto-parallel plane and three with crossed disparities. In the following experiment, there were three parallel vertical lines laterally separated by 10 min of arc. The outer two lines always remained in the fixation plane, but the middle line was shown with disparity and the enquiry was directed to finding the just detectable disparity difference. To facilitate the judgment, the psychophysical procedure was modified by making a comparison pattern available immediately preceding the test pattern. For example, to test the disparity difference discrimination at 1 min of arc crossed disparity, the subject was first shown for 500 ms a three line test pattern whose center line had one minute of arc crossed disparity. After a 200 ms pause, this was followed by the presentation, also for 500 ms, of the three line configuration but this time with the center line at one of seven equally spaced crossed disparities in the range of 0.6–1.4 min of arc. The subject had to indicate whether, in the second presentation, the center line appeared nearer or farther than in the first presentation. In this way, the sensitivity for differences in disparity was measured for both crossed and uncrossed disparities. As can be seen in Fig. 3, there is a steep rise in threshold as soon as any standing disparity is introduced. For there to be a detectable depth difference, at least twice as much disparity change is needed when there is a 1' disparity than when there is none.

That this decrement is associated not with the showing of the test stimulus in disparity, but with the difference in disparity between the members of the
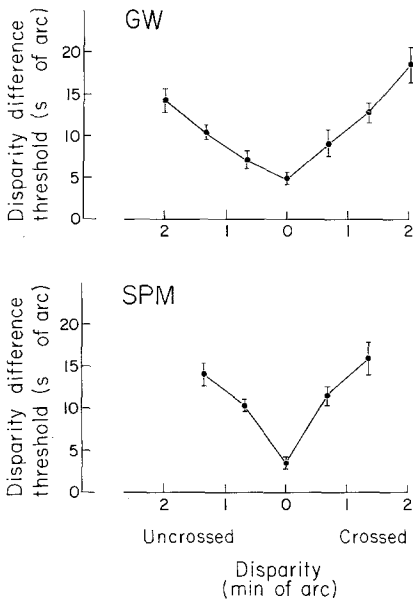
Fig. 3. Sensitivity for detection of a disparity difference as a function of disparity in a three-line stereoacuity target. The lines were 15 min of arc long, laterally separated by 14 min of arc, seen binocularly with normal pupils. Initially, for 500 ms, the outer two lines were in fixation plane and the middle line was seen with the disparity shown on abscissa. After 200 ms pause, this was followed for 500 ms by the test situation in which the middle line was shown with a smaller or larger disparity, the outer two lines remaining in the fixation plane. Subject's task was to judge whether in the test situation the middle line appeared farther or nearer than in the initially seen comparison situation

Table 2. Disparity difference thresholds in s of arc

	Subject GW			Subject GW		
	40″ uncrossed	In fixation plane	40″ crossed	40″ uncrossed	In fixation plane	40″ crossed
Exp. A	15.2±1.5	6.9±0.8	14.8±1.4	16.0±1.5	4.4±0.4	43.0±3.3
Exp. B	6.9±0.7	6.2±0.3	6.9±0.7	7.1±0.7	6.0±0.6	5.3±0.5

Three-line configuration, lines 15 min of arc long, 14 min of arc apart. Exposure duration – 200 ms throughout
Experiment A. Outer two lines exposed in fixation plane, middle line shown with disparity as indicated. Thresholds show the necessary change in disparity between the middle line and the outer lines for the middle line to have a detectable change in depth
Experiment B. Outer two lines were exposed in the disparity plane indicated. Thresholds show what differences in disparity between the outer lines and the middle line are necessary in order that all three lines just fail to appear to be at the same depth

configuration, is demonstrated in the following experiment (Table 2). Here, all exposures were 200 ms, to obviate the possibility of changes of eye vergence during a given exposure. The data shown in the first row are based on the identical experimental procedure as those in Fig. 3 (except for the exposure duration being reduced to 200 ms) and show concordant results. In the second row are shown disparity difference thresholds in a simple stereoacuity paradigm (is the middle line nearer or farther than the outer two lines?) when the outer test lines were shown with the indicated disparity with respect to the fixation plane. There was no decrement in performance when the subject had to judge

whether all three lines are aligned, even when they were shown with a small disparity. The decrement in the earlier experiment (Fig. 3 and upper row of Table 2) was, therefore, due not to poorer ability to make depth judgments for a target when it is seen in disparity, but rather to poorer ability to make depth difference judgments between the middle and outer lines of the target configuration when they have a disparity difference exceeding even half a minute of arc. We can, therefore, add to the previous list of conditions for best stereoacuity (viz., synchrony and optimal relative placement of at least two binocularly seen targets) the further condition that the standing disparity between the members of the configuration should be minimal.

Discussion

The relatively poor response to a step disparity stimulus of an isolated target is somewhat surprising. In this study it is taken to be a pointer that the best stereoacuity results from cooperative interaction of at least two separate stimuli; it is important, therefore, to examine the possibility that special circumstances conspire to make step disparity detection of a single stimulus singularly ineffective. Two such circumstances will be considered.

Sequential presentation of the stimulus pair in a step necessarily involves the possibility of an intervening convergence change. Convergence stability to a few seconds of arc cannot ever be assured, even with good techniques of image stabilization. A random variation in eye vergence between the sensory registrations of the stimulus before and after the step would entail a reduction in stereothreshold as measured here. It cannot be ruled out by the experiments reported here that there is such a component, but there is some evidence that this by no means accounts for the whole difference between ordinary stereo thresholds and single-line step-stereo thresholds. For example, sequential presentation of a stimulus with 50 ms components, during which a convergence change is much less likely than with 500 ms components, still leads to a major reduction in sensitivity (Condition e, subject SPM, Fig. 2).

A further experiment was designed to distinguish between convergence instability and another possible factor producing an increase in step stereo threshold of a single target. Here a 200-ms pause was introduced between the first and the second halves (each lasting 500 ms) of the disparity step stimulus. To the extent that convergence changes take place, this ought to reduce sensitivity even further. In fact, all three subjects showed an improvement in sensitivity (Table 1, column 3). This was particularly marked in subject SPM, who had about the same threshold in the 500-ms – 200-ms pause – 500-ms step condition as in a 50-ms – 0-ms pause – 50-ms step condition.

These results, while not excluding convergence instability as a factor in the poor performance of the step disparity detection of a single target, point to the prominence of another factor: the preempting of sensitivity to a depth response by an immediately preceding one in the same location. We have three pieces of evidence for this. First, there is the finding reported just now, viz., the pause that improves, which seems analogous to similar findings in vernier acuity

(Westheimer and Hauske, 1975). The second finding can be seen by comparing columns 1 and 2 of Table 1. When the disparity step is given along with a lateral displacement step, the stereo threshold is improved. This implies that while sequential (as distinct from simultaneous) presentation of stereo targets never produces a good threshold, sequential presentation in the same retinal location, i.e., step disparity stimulus, has even worse sensitivity than sequential presentation in different positions in the visual field.

Finally, there is the experiment shown in Fig. 1. Step disparity stimulation of a single target was measured in the presence of steady flanking targets in the fixation plane, i.e., in the plane of the center line before it was stepped in the crossed or uncrossed disparity direction. At the bottom of the figure (Condition e) there is shown also the stereo threshold for a simple three-line target presented for 500 ms without a step; i.e., all three lines being exposed synchronously with the center line having near-threshold crossed or uncrossed disparity. The threshold is better than in any other condition. In particular, one can compare the threshold in Condition (e) of Fig. 1 with that in Condition (c). The latter has included in it the entire presentation of Condition (e) but is preceded by a 500-ms presentation of the three-line target in a flat configuration. Clearly, the stepping of the middle line into a disparity configuration is not as easily detected as its presence in disparity during a single presentation. While the stereo threshold in Condition (c) is worse than in Condition (e), its value, about 8 s of arc, nevertheless represents very respectable performance in a stereo task.

These experiments allow an important conclusion. The precision of the depth signal of a single unaccompanied target is of the order of 1 min of arc or perhaps slightly less. This means that, if a single foveal target were briefly presented in a Ganzfeld with such a disparity relative to a zero disparity somehow previously established, the subject would correctly signal the direction of the disparity – front or back – on 75 % of occasions.

The performance is dramatically improved by making available a comparison target. And for the targets then to act cooperatively they need to have temporal synchrony (Fig. 2), appropriate spatial relationship (Fig. 1), and they should all lie near the same frontal plane (Fig. 3 and Table 2).

It is tempting to relate these depth threshold values to those obtained by neurophysiological studies (Barlow et al., 1967; Burns and Pritchard, 1968; Pettigrew et al., 1968; Hubel and Wiesel, 1970; Poggio and Fischer, 1977; Heydt et al., 1978). Disparity specificity can be found in single cells in the visual cortex of experimental animals, i.e., the firing of units can be modulated by varying stimulus disparity. Though the criterion of a necessary condition is hereby satisfied (disparity affects firing rate), that of sufficiency (*only* disparity affects the firing) is clearly not, so it would be inaccurate to look to such units to act alone in associating depth with a stimulus. The disparity "tuning" for the units is, moreover, too coarse to expect them to reach the needed precision of 1 min of arc, even with sharpening by lateral inhibition in the disparity domain (Nelson, 1975). It seems unavoidable to postulate the existence of a differencing operation, from which a depth value may arise that is elaborated separately or independently from any of the other visual qualities associated with a feature.

The point made in this paper goes somewhat further, however. Because strong simultaneity and adjacency demands of a pair of binocularly seen features have to be met to achieve optimal stereoacuity, we need to postulate that even after the depth value has been assigned to each individual feature (by whatever process) there is a further refinement of information leading to the exceedingly good capability called stereoacuity. This would be achieved by subjecting the depth values of adjacent features to another differencing operation, whose optimal performance depends on good synchrony, favorable spatial placement of the stimuli, and minimal standing disparity.

It should be pointed out that the postulated mechanisms differ from the operation of lateral inhibition in the disparity domain which has been previously suggested. Lateral inhibition might highlight the response of one member of the ensemble at the expense of neighboring ones, but this would not by itself lead to precision finer than the spacing of ensemble members. Rather we are here thinking of a mechanism like that of a differential amplifier, whose output is a difference signal which has been decoupled from absolute values of the two inputs. Such a differencing mechanism has the advantage of allowing accurate depth judgment from relatively coarse disparity tuning of the neural signals that reach it. Moreover, the differencing mechanism can be available to a whole range of inputs, and thus would not have to be duplicated for every single spatial information line coming into the cortex. The results of the present study, temporal and spatial contiguity, point to the operation of such a differencing mechanism also at the next higher level, i.e., on the depth signals of two or more individual features. This conjures up the view of a modular neural arrangement which is brought into play whenever differential judgments are needed, without necessarily obtruding itself on the global ordering of sensations. One thinks of the application of a vernier caliper to whatever place of a scale needs a particularly fine measurement.

Since this particular mechanism will be necessarily shared by a range of incoming signal lines, its preempting would manifest itself in interference phenomena which have already been reported (Butler and Westheimer, 1978).

If one wishes to follow the tradition in sensory physiology and psychology of regarding the just discriminable step to be approximately proportional to the stimulus, the data of Fig. 3 may be regarded as a confirmation of the existence of a depth difference signal. When the signal is zero (the members of the configuration all lie in the fixation plane) the just discriminable step is a minimum; as the signal increases in magnitude (there is a progressive increase in the standing disparity between members of the configuration) the just discriminable step also rises.

Figure 4 illustrates schematically what is thought to be involved. The discussion is confined to the horizontal plane through the centers of the two eyes' entrance pupils. The right and left eyes' lines of sight for various objects A, B . . . make angles ϱ_A, ϱ_B . . . and λ_A, λ_B . . . with their respective primary lines of sight. We can postulate a mapping of ϱ and λ onto coordinated ordered sets ϱ' and λ', the primes indicating that we are now within a domain that is removed but derived from that of ϱ and λ. It may help the reader to think of an ordered sequence of cortical units with an input from the right and left eyes, respectively.
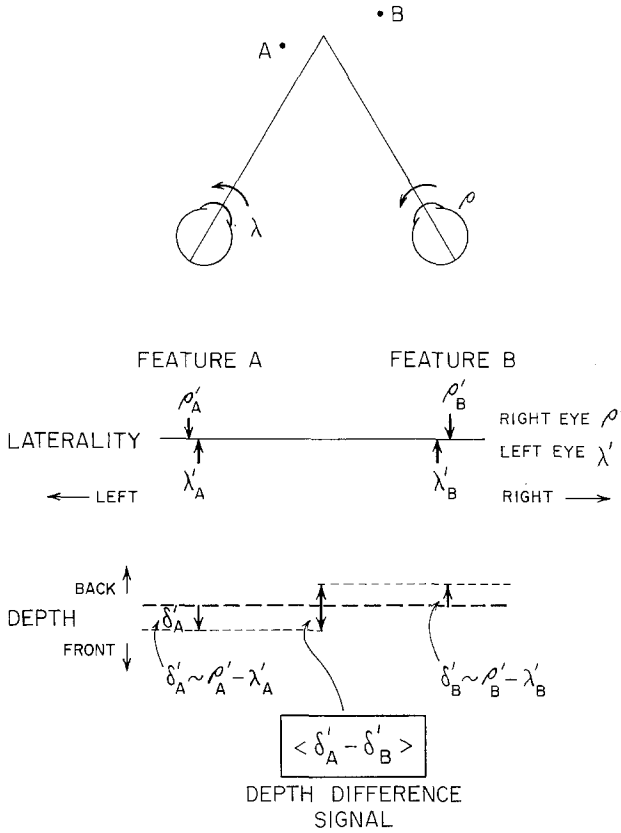
Fig. 4. Schema for cooperative mechanism that provides high sensitivity for discrimination of depth differences and is not dependent on ocular stability. Two targets A, B are imaged on horizontal meridians of both retinas, making angles ϱ_A, λ_A and ϱ_B, λ_B with primary lines of sight of eyes. The images have central neural elaborations, ϱ'_A, λ'_A and ϱ'_B, λ'_B, and an associated representation δ'_A, δ'_B in depth domain. Sensitivity for detection of a step change in δ'_A is substantially les than for detection of difference $\delta'_A–\delta'_B$ for two simultaneously seen optimally placed targets. This implies the existence of a differencing operation for the generation of the signal $\delta'_A–\delta'_B$ without immediate reference to the absolute values of δ'_A and δ'_B

The transformation between ϱ and ϱ' and λ and λ' need not concern us here. It has interesting properties (sharpening, location of centroid of light distribution, etc.) but the main point is that under the experiments considered here there is a unique and orderly representation of targets A and B in the ϱ' and λ' domain. The associated domain of depth values can, without loss of generality, be mapped in an orthogonal direction. Just now, the particular operation by which δ'_A is derived from ϱ'_A and λ'_A is left open, so long as a given δ' can have the quality 'near' or 'far' and can be ordered in magnitude. The observed phenomenon is that for a just discriminable step difference in δ'_A, the generating δ_A ($= \varrho_A–\lambda_A$) has to be about 1 min of arc, whereas for a just discriminable $(\delta'_A–\delta'_B)$ the generating $(\delta_A–\delta_B)$ need to be only a few seconds of arc. And for

this discrimination of $(\delta'_A - \delta'_B)$ to be optimal, A and B need to be generating synchronous and favorably placed excitations. The view being formulated here is that, though δ'_A and δ'_B may be independently elaborated, a mechanism exists for the operation $\langle \delta'_A - \delta'_B \rangle$. It has considerable sensitivity, i.e., $\delta_A - \delta_B$ is quite small for a j.n.d. $(\delta'_A - \delta'_B)$. Such a mechanism has the obvious advantage of allowing ϱ' and λ' to be developed through and in the presence of a variety of naturally occurring disturbances, including movement. To make depth difference detection substantially transcend certain limits set by peripheral stages, such as finite size of elements of the retinal mosaic, summation of retinal signals, and ocular instability, the process of extracting an instantaneous difference signal would seem to be ideal.

References

Barlow, H.B., Blakemore, C., Pettigrew, J.D.: The neural mechanism of binocular depth discrimination. J. Physiol. (Lond.) **193**, 327–342 (1967)

Burns, B.D., Pritchard, R.M.: Cortical conditions for fused binocular vision. J. Physiol. (Lond.) **197**, 149–171 (1968)

Butler, T.W., Westheimer, G.: Interference with stereoscopic acuity: spatial, temporal and disparity tuning. Vision Res. **18**, 1387–1392 (1978)

Foley, J.M., Tyler, C.W.: Effect of stimulus duration on stereo and vernier displacement thresholds. Percept. Psychophys. **20**, 125–128 (1976)

Heydt, R. von der, Adorjani, C., Hänny, P., Baumgartner, G.: Disparity sensitivity and receptive field incongruity of units in the cat striate cortex. Exp. Brain Res. **31**, 523–545 (1978)

Hubel, D.H., Wiesel, T.N.: Cells sensitive to binocular depth in area 18 of the macaque monkey cortex. Nature **225**, 41–42 (1970)

Nelson, J.I.: Globality and stereoscopic fusion in binocular vision. J. Theor. Biol. **49**, 1–88 (1975)

Pettigrew, J.D., Nikara, T., Bishop, P.O.: Binocular interaction on single units in cat striate cortex. Exp. Brain Res. **6**, 391–410 (1968)

Poggio, G.F., Fischer, B.: Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. J. Neurophysiol. **40**, 1392–1405 (1977)

Regan, D., Beverly, K.I.: Some dynamic features of depth perception. Vision Res. **13**, 2369–2379 (1973)

Westheimer, G., Hauske, G.: Temporal and spatial interference with vernier acuity. Vision Res. **15**, 1137–1141 (1975)

Westheimer, G., McKee, S.P.: Stereoscopic acuity for moving retinal images. J. Opt. Soc. Am. **68**, 450–455 (1978)

Westheimer, G., McKee, S.P.: What prior uniocular processing is necessary for stereopsis? Invest. Ophtalmol. **18**, 614–621 (1979)