eating and sleeping would provide a cyclical reinforcing action somewhat analogous to that of the 3-day morphine cycles. Seven choice tests were given during the experiment; five were given at approximately 2-week intervals during the reinforcing stage (68 days of alcohol drinking). Then, alcohol was removed and all rats returned to plain tap water for 2 weeks, after which they were given a final choice test.

Three rats (two resistant and one susceptible) died during the treatment. One more rat in each group died during the 2-week abstinence period. One death was due to a tumor. The remaining deaths appear to have been due to the age of the animals and the physiological stress of the treatment. The drinking records of these rats were like those of other rats in their respective groups. There are no indications that the overall results would have been different had they lived.

The susceptible rats drank significantly more alcohol on about half the training trials (35 out of 68). Most significant differences occurred early; the first 14 trials were all significantly different, but the last 14 trials were all statistically nonsignificant. In contrast, the rats did not differ significantly in ADB on the first five choice tests. The difference in their ADB scores (-0.092 versus -0.475) on the sixth choice test, which terminated training, was barely significant (P < .05). The susceptible rats drank more alcohol (means: 19.0 versus 11.9 ml).

But the relapse scores were quite different. After a 2-week interval of no alcohol, the susceptible rats drank twice as much alcohol as the resistant rats (means: 24.0 versus 12.0 ml). The mean final ADB score of the susceptible rats was -0.024 versus -0.473 for the resistant rats (P < .005).

These strains, bred for a differential relapse to morphine drinking, show a similar differential relapse to alcohol drinking. This is the effect of an addicting drug; quinine, equated in initial aversiveness and given in a similar drinking regimen, causes little or no change in the behavior of either strain. We have not yet isolated the factors responsible for this difference in addiction liability, but one factor seems to be passed on from generation to generation.

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- 6 June 1967

# Stereopsis Based on Vernier Acuity Cues Alone

Abstract, Random-line stereograms were generated in which the only monocular cues were minute breaks occurring at random in thin vertical (or horizontal) line grids. The breaks were binocularly correlated. The stereograms yielded global stereopsis (of a square standing out in front of a surface) even with monocular breaks of as little as 16 seconds of arc, which is below the threshold for resolving two lines. This technique led to the clarification of relations between local and global stereopsis.

Our visual system is remarkable in that it enables us to detect tiny breaks in lines even when the breaks are much smaller than the separation between the cones in our foveas. The limit of this super-resolution is called vernier acuity when the lines break in a plane and is called stereoscopic acuity when the break occurs in depth. Ordinary visual acuity is the limit of resolution for two dots (or seeing the spaces between lines in a grid, or detecting a gap in a ring). Optimal visual acuity for line gratings is reported to be 28 seconds of arc (1) (actually acuity is defined as the logarithm of the reciprocal of this value), and optimal vernier and stereoscopic thresholds are about 2 seconds of arc, depending on the type of test targets used (2). These values are obtained under optimal laboratory conditions and with selected subjects; in practice, values are much worse [for instance, stereoscopic threshold was measured in one terrain situation to be 24 seconds of arc, which for that situation corresponded to a distance of 580 m (3)].

The limits of visual acuity seem to be completely accounted for by the coarseness of the retinal mosaic, that is, by the distance between the cones. However, since vernier and stereoscopic acuity are much better than the intercone separation, they must be obtained by central nervous system processing. Additional evidence supporting this view is the fact that the longer a line (up to a limit), the smaller the break that can be detected (4). The present study provides information as to whether this superresolution process precedes or follows binocular combination.

The technique of random-dot stereograms devised by one of us (5) enables the researcher to determine whether certain perceptual cues are processed at the retinal or the cortical level. In earlier studies regular square arrays of  $100 \times 100$  cells were used, with individual cells painted black or white randomly. The left and right eyes' images were such arrays, identical except for a center square which was shifted horizontally in one image by an integral number of cells as if it were a solid sheet. When these images are viewed monocularly, they give the impression of a uniformly random texture without any gap or boundary. When viewed stereoscopically the center square is seen in depth in front of the unshifted surround.

The present studies used, in place of square black and white cells, short line segments. These line segments will be referred to as picture elements. Arrays of the elements were drawn by a computer-controlled display device. The smallest unit that can be portrayed is a single dot or a vector (line segment) having one-dot width. The picture elements of Fig. 1 are composed of vertical line segments one dot wide



Fig. 1. Random-line stereogram of thin vertical line segments with two-dot local disparity. In the binocular view a center square appears in front of a surround (ten-dot global disparity).

and ten dots long, placed within an area  $10 \times 10$  dots in size. Two types of such picture elements were selected at random with equal probability. The picture elements of type A have the vertical line segment in the five-dot position, while those of type B have it displaced horizontally into the sevendot position. Thus the only difference between the two kinds of picture elements is a two-dot horizontal disparity. Figure 2 illustrates by an array of  $5 \times 4$  picture elements the way Fig. 1 has been generated. A center square of  $2 \times 2$  picture elements (shown by the dotted lines) is horizontally shifted by one picture element to the left in the right array and the uncovered  $2 \times 1$ area of the surround is randomly covered by the two types of picture elements. Otherwise the left and right images are identical. Figure 2 clearly shows the two types of picture elements made up of line segments which differ only in a two-dot horizontal disparity.

Actually, the left and right images of Fig. 1 are similar to Fig. 2 except that they are composed of a  $100 \times 100$  array of picture elements  $(1000 \times 1000)$ dots). The center square is  $40 \times 40$  picture elements. In one image, the center square is displaced one picture element to the left of its location in the other image (ten dots). When the images (as printed herein) are viewed from a comfortable viewing distance of 30 cm, they extend about 10 deg; thus the one-picture-element disparity of the center square is 6 minutes of arc and the two-dot disparity between the local line segments (the extent of the breaks in the lines) is 72 seconds of arc. The monocular patterns look like vertical

gratings of lines one dot wide, ten dots (6 minutes of arc) apart, with random 72-seconds-of-arc breaks. Figure 3 is similar to Fig. 1 in all respects except that the line segments are horizontal and the two-dot disparities between the two types of picture elements are in the vertical direction.

Both Figs. 1 and 3, when stereoscopically viewed from 30 cm, give rise to stereopsis: the center square is seen in front of the surround. When Fig. 3 is stereoscopically viewed so that the fused image extends 2.2 deg (which corresponds to 140 cm viewing distance for this figure) the only monocular cues that are perceptible are the breaks in the lines; these breaks amount to only 16 seconds of arc. Since the separation between the adjacent horizontal line segments was 10, 12, or 8 dots, each separation being more than 1 minute of arc, the images appeared monocularly as fine horizontal line grids with tiny irregular breaks in them. The lines and the spacings between the lines in the grids were clearly seen. We tested four subjects under these conditions and all of them could see the center square in depth (the corners appearing to be rounded off). The criterion used was the appearance of the center square as a dense texture. With much further reduction in size of the images,



Fig. 2. Illustration of the method by which the stereogram of Fig. 1 was generated.

the center square was still seen in depth as a transparent (lace-like) surface, but it was difficult to agree on a common criterion to be used by the subjects.

It is likely that the reader will be able to obtain similar results, since we did not try to create optimal viewing conditions and did not preselect our subjects. Thus, it seems more realistic to compare our 16-seconds-of-arc finding with the usual 1-minute-of-arc threshold for visual acuity, rather than with the 28-seconds-of-arc threshold found under optimal conditions.

The results clearly show that global stereopsis can be obtained well below the visual acuity threshold. The term "global stereopsis" refers to the binocular pattern-matching process which finds corresponding large areas (composed of local picture elements having the same disparity values, such as the center square or its surround) in the left and right fields. Although 16 seconds of arc is a larger break than the optimal vernier acuity threshold, it is known that for optimum vernier acuity the line segments have to be fairly long on both sides of a break. In our stimuli about half of the breaks have, on one side, a line segment only ten dots long, which would be too short (only five times the break size) to obtain maximum vernier acuity.

Vernier and stereoscopic acuities are inseparable for classical test targets in which a single vertical wire breaks in depth. At stereoscopic threshold, binocular disparity is the sum of the breaks in the left and right retinal projections and is in the vernier acuity range. On the other hand, in Fig. 3 the monocular vernier acuity cues are separated from binocular disparity. The latter can be orders of magnitude larger than the monocular breaks. Furthermore, in the classical investigations of stereoscopic acuity the line segments had to be vertical with horizontal breaks, while in Fig. 3 the line segments are horizontal with vertical breaks. Our findings indicate that the process which determines vernier acuity is utilized in the patternmatching operation on which global stereopsis depends. The way the global stereoscopic process evaluates the many local stereoscopic processes will be discussed now.

It is particularly interesting that Fig. 1 does yield stereopsis. In that array, 50 percent of the picture elements are identical in the left and right images owing to chance alone (A-A and B-B); these elements could have been per-



Fig. 3. Random-line stereogram similar to Fig. 1 except composed of horizontal line segments. Figure 3 yields stronger stereopsis than Fig. 1 under laboratory conditions.

ceived in a depth plane with zero disparity. Moreover, 25 percent of the picture elements (A-B) could have easily been fused with two-dot (16 seconds of arc) disparity as a lace-like transparent plane slightly in front of the zero-disparity plane, while 25 percent (B-A) could have been fused with a minus-two-dot disparity (behind the transparent zero disparity plane). This possible organization would have been an easy solution to the problem of fusing the two images. The fact that a more global organization is actually perceived (center square above the background) indicates that the central nervous system searches for a particular solution even if it is more unlikely. In this case, the ten-dot disparity of the center square is 5 times more than the two-dot disparity between the A-B and B-A picture elements. We have found that stereopsis can be obtained even for 20-dot global disparity (fully 10 times the local disparity). Thus the fusional process apparently favors a solid (densely packed) organization with a large disparity in preference to a transparent (lace-like) organization, even if the latter has much smaller disparity. It seems likely that this weighting process between various organizations occurs higher than the local binocular fusion of similar picture elements.

When the same experiments are tried with horizontal line segments, shown in Fig. 3, one would predict a different outcome, because of the anisotropy of stereopsis. When two vertical line segments are horizontally displaced by a small amount, as in Fig. 1, local stereopsis occurs with great ease; however, for horizontal line segments with a vertical displacement of even a few dots, local stereopsis would require that the

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fusional mechanism shift the entire line segment (ten dots long in Fig. 3). Therefore, local fusion of horizontal line segments should be more difficult and the global organization (that is, the center square) should be more likely. Because of the difficulty of reproducing patterns with this detail, the actual viewing of the stereograms illustrated here may deviate from the reported findings.

Stereoscopic viewing of Fig. 3 bore out this expectation. In spite of having the same local and global disparities as Fig. 1, Fig. 3 yields stronger global stereopsis. Even with 60-dot disparity the center square was perceived in depth, while the limit for the vertical case was 20-dot disparity.

The perceptual difference between global stereopsis with horizontal and with vertical line segments has another implication. The anisotropy of stereopsis (that is, vertical disparity does not yield stereopsis, while horizontal disparity does) has to be contrasted with the isotropy of binocular fusion. Panum's fusional area is about the same for horizontal and vertical disparities, and disparities under 6 minutes of arc should be easily fused in any direction. The finding that horizontal line segments yield stronger global stereopsis than vertical ones suggests that global stereopsis does not depend on local fusion, but rather on local stereopsis.

In these and similar experiments the local elements resemble the simple receptive field shapes found by Hubel and Wiesel (6), while the global percept is obtained by searching for the binocular organization. The study of how local features yield local stereopsis and how local stereopsis affects global stereopsis may be a bridge linking neurophysiological findings with perceptual psychology.

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18 May 1967

## Archosaurian Reptiles: A New Hypothesis on Their Origins

Abstract. The characteristics of the first archosaurs, the proterosuchian thecodonts, show that neither of the supposed common ancestors of archosaurs and lepidosaurs could actually be an ancestor of archosaurs. Instead, the evidence seems to indicate that the archosaurian ancestors are probably in the ophiacodontvaranopsid group of the pelycosaurian synapsids. In particular, the Varanopsidae are strongly indicative of proterosuchian relationships, as they have evolved some characters which are elsewhere found only in archosaurs. Archosaurs and lepidosaurs apparently have different origins; the former come from the pelycosaurs, and the latter come from the captorhinomorph cotylosaurs through the Millerettiformes.

Dinosaurs, crocodiles, pterodactyls, and thecodonts are members of the reptilian subclass Archosauria—the ruling reptiles—a group of vertebrates (including the ancestors of birds) highly diversified and greatly expanded during Mesozoic times. From the lower Triassic to the Recent, the history of the archosaurs is fairly well represented in the fossil record. Though many points are still controversial, there is much evidence to support the hypothesis that all the post-Triassic archosaurian orders (Sauris-