

odor stimuli by switching from the accessory olfactory pathway that can detect odors dissolved in a liquid medium to the main olfactory pathway that detects airborne odors.

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16. The day of copulation counted as day 0 of gestation. On the morning of E22, the pregnant rat was removed from the home cage, placed in a restrainer, and administered [^{14}C]2DG (50 to 60 Ci/mmol) in physiological saline (300 μCi) through the tail vein.
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18. Two fetuses had poor histological sections and therefore unclear autoradiographs. Thus, technical limitations made it difficult to assess whether 2DG uptake occurred in the accessory olfactory bulb. However, at the level of the present analysis, the remaining 18 fetuses consistently exhibited 2DG uptake in the accessory olfactory bulb (Fig. 2).
19. There appeared to be no consistent factors (sex was not determined in this study) that accounted for this result.
20. The procedure for 2DG image analysis is similar to that described by C. Gooch, W. Rasband, and L. Sokoloff [*Am. Neurol.* **7**, 359 (1980)]. The autoradiographs of fetuses were analyzed at Image Processing System, of Drexel University and the University of Pennsylvania.
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24. One-day-old rat received an intracardiac perfusion of 2 ml of 0.9 percent NaCl and 10 ml of Bouin's solution at room temperature. Routine procedures were followed for obtaining paraffin-embedded, cresyl violet-stained 10- μm sections of the olfactory bulb.
25. This research was supported in part by NINCDS grants F32-NS06978 to P.E.P. and NS 16993 to G.M.S. and W.B.S.

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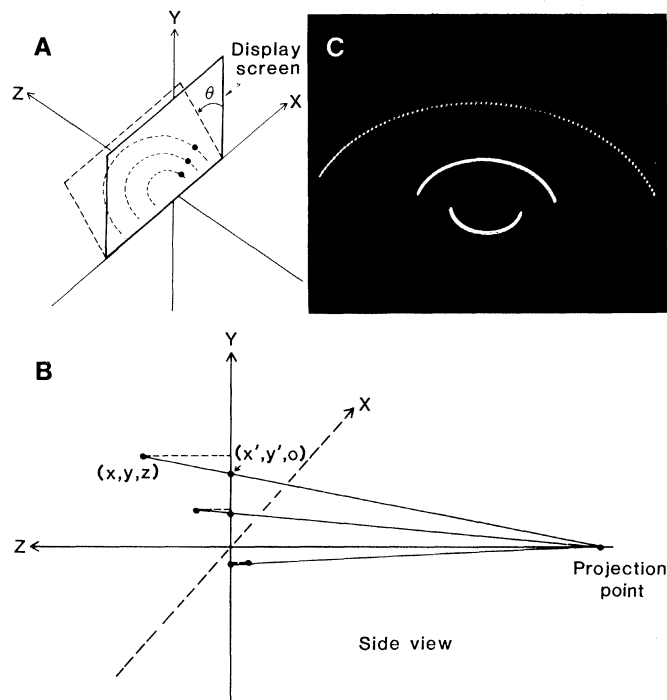
Accurate Visual Measurement of Three-Dimensional Moving Patterns

Abstract. Human observers discriminated relative three-dimensional distances in simple patterns of motion parallax with an acuity similar to vernier acuity under comparable conditions. Accurate visual measures of three-dimensional distance can be derived from the structural invariance of patterns undergoing perspective transformations.

A principal function of vision is to measure the environment. Virtually all visual tasks involving either visual-motor coordination or recognition of objects require geometric information. Everyday observations of human athletes and other rapidly moving animals suggest that such visual measurements are usual-

ly very accurate. Controlled laboratory evaluations of vernier "hyperacuity" (1), of stereoscopic acuity (2), and of the rapid recognition of three-dimensional (3-D) structure in moving patterns (3) also indicate that vision provides precise geometric information under some conditions.

Fig. 1. Stimulus patterns. (A) Schematic illustration of CRT displays of three collinear dots rotating as if in a plane tilted in 3-D space. (B) Schematic side view of the perspective projection, drawn to scale for the first experiment. The distance of the perspective projection point from the center of rotation was 2.5 times the distance between the two endpoints. (C) Time-lapse photograph of one of the CRT displays, showing the complete paths of three equally spaced points rotating through 160° in the 45°-tilt condition. In the first experiment the rotation was through an angle of 160°. The visual subtense of the distance between the two endpoints was 1.02° in the 0° tilt condition of the first experiment; with 30°, 45°, and 60° of tilt the projected distance between the endpoints in the perspective displays was reduced to a minimum of 0.89°, 0.70°, and 0.48° visual arc, respectively, at the middle of the path. The displays were viewed monocularly in the dark from a distance of 94 cm. The temporal duration of each rotation in the first experiment was 0.94 seconds, and each trial consisted of four successive rotations. In subsequent experiments, performance was essentially unimpaired with the use of a single rotation through an angle of 120° over a temporal duration of 0.47 seconds. Observers responded to each display as centered or displaced, and auditory feedback was given for each correct response.



Neither experimental evidence nor theoretical understanding of the origins of geometric structure in vision are well developed, however. The hypothesis that positions and distances are specified by reference to a retinally defined 2-D coordinate space is inconsistent with experimental evidence on the perceived structure of both 2-D (4) and 3-D (5, 6) stimulus patterns. One alternative hypothesis suggested by several authors (6, 7) is that measures of geometric structure might be derived from invariant relationships intrinsic to spatio-temporal stimulus patterns.

The purpose of the present experiments was to evaluate the acuity with which visual measures of 3-D distance could be obtained from simple patterns of motion parallax. We have found that the 3-D structure of such patterns can be discriminated with a surprising accuracy—comparable to the so-called hyperacuity for collinearity.

The stimulus patterns consisted of three collinear points of light presented on a computer-controlled cathode-ray tube (CRT) screen. The points moved across the screen as if they were the projected images of points that were rigidly connected and rotating in a plane tilted in 3-D space. By varying the tilt of the plane of rotation away from the fronto-parallel projective plane, the relative distances between the points in the 2-D display could be varied while the relative interpoint distances in 3-D space were held constant. Because of the perspective projection, the images of points that were equally separated in 3-D space were generally not equally separated on the 2-D display screen (Fig. 1).

The observer's task was to decide (respond "yes" or "no") whether the middle of the three points was exactly centered in 3-D space between the other two points. On half of the trials the middle point was centered, and on the other half it was displaced a small 3-D distance toward either one of the two endpoints, maintaining the 3-D rigidity and collinearity of the three points. Acuity was measured by the psychophysical function relating detection accuracy to displacement distance (8).

The objective of the principal experiment was to determine whether observers could accurately discriminate 3-D distances in 2-D perspective displays of rigid motion and, if so, to determine the acuity for such metric relations. Three experimental conditions—with various amounts of tilt of the plane of rotation away from the fronto-parallel projective plane—were compared to determine

whether performance was based on perception of 2-D or 3-D distances. In one condition the plane of rotation was in the fronto-parallel (xy) projective plane, involving no 3-D depth. In a second condition the plane of rotation was tilted 45° around the horizontal (x) axis away from the xy projective plane. In the third condition the tilt of the plane of rotation was randomly varied between trials—30°, 45°, or 60° from the xy projective plane. If discriminations were based on the varying interpoint distances on the 2-D display screen rather than on the invariant 3-D distances, discrimination should be most accurate in the 0° tilt condition and least accurate in the variable 30°-45°-

60° condition. If, instead, discriminations were based directly on the 3-D rather than the 2-D relationships, performance should be equal for the three conditions, because 3-D distances among the points remained constant over conditions. As an additional check on the 3-D structure of the visual information, we also compared the discrimination accuracy for parallel and perspective projections. (With parallel projection, points centered in 3-D space were also centered in the 2-D display, so that there was no conflict between the 2-D and 3-D structures.)

Three well-practiced observers each served for six sessions, each session

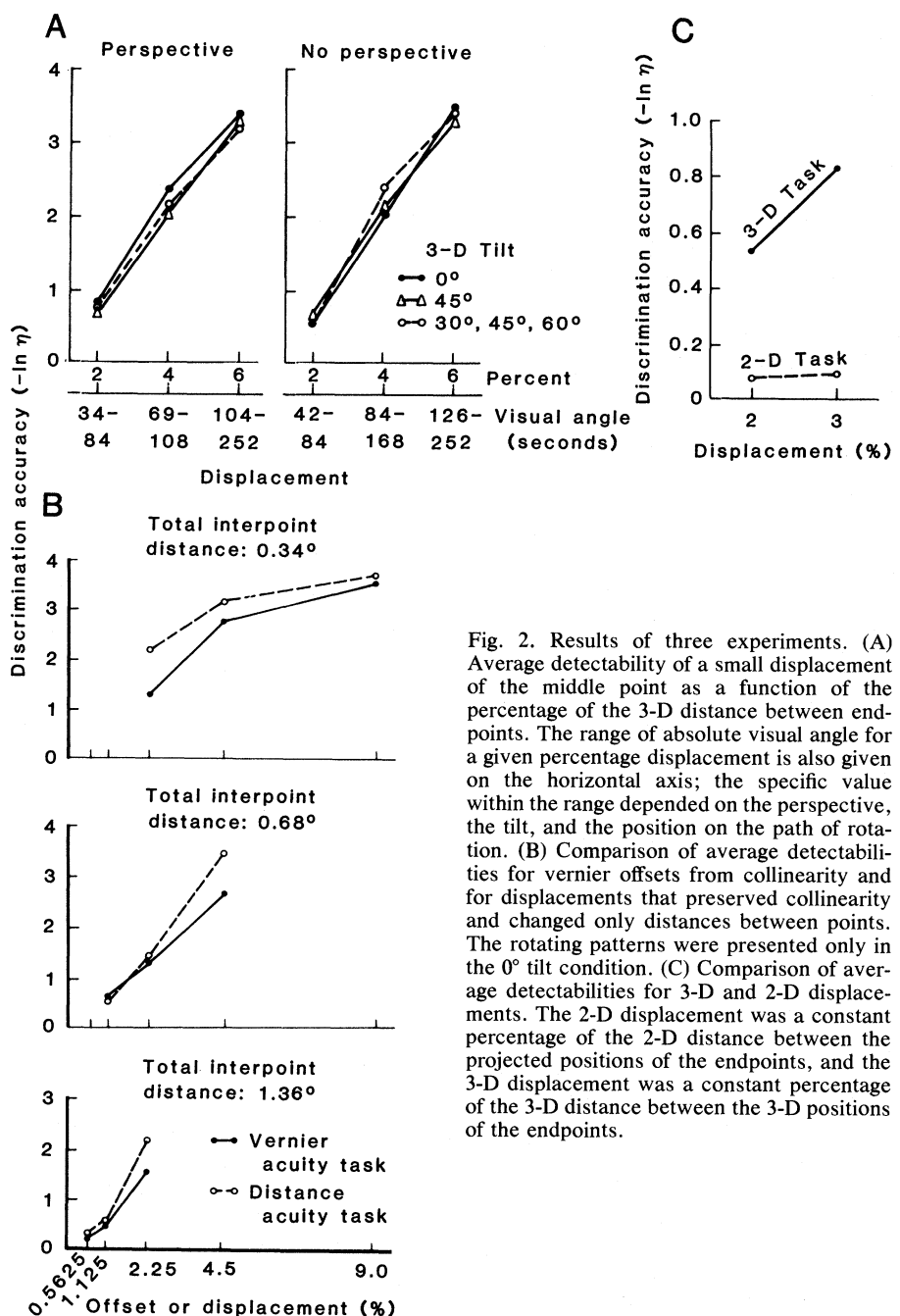


Fig. 2. Results of three experiments. (A) Average detectability of a small displacement of the middle point as a function of the percentage of the 3-D distance between endpoints. The range of absolute visual angle for a given percentage displacement is also given on the horizontal axis; the specific value within the range depended on the perspective, the tilt, and the position on the path of rotation. (B) Comparison of average detectabilities for vernier offsets from collinearity and for displacements that preserved collinearity and changed only distances between points. The rotating patterns were presented only in the 0° tilt condition. (C) Comparison of average detectabilities for 3-D and 2-D displacements. The 2-D displacement was a constant percentage of the 2-D distance between the projected positions of the endpoints, and the 3-D displacement was a constant percentage of the 3-D distance between the 3-D positions of the endpoints.

consisting of nine blocks of 48 trials. The nine blocks were devoted to each of the nine combinations of the three different tilt conditions and three different amounts of displacement of the middle point (2, 4, or 6 percent of the 3-D distance between the two endpoints). Three sessions were devoted to displays with perspective projections and three to displays with parallel projections.

Detection accuracy was a linear function of the magnitude of the 3-D displacement of the middle point and was unaffected by variation in the 3-D tilt or by perspective projection (Fig. 2A). (Performance was virtually identical for all three observers, so only the average data are plotted in this and subsequent graphs.) A single linear function accounted for 98.3 percent of the variance in accuracy among the 18 conditions. Therefore, the geometric information for this discrimination must have been some aspect of the 3-D structure that remained invariant under projective transformations.

The best measure of the magnitude of displacement in this task is the percentage of the distance between the two endpoints rather than the absolute angular distance at the retina. This derives partly from the geometrical fact that this percentage remains invariant under motion in 3-D space and partly from empirical evidence, not reported here, that detection of a given percentage displacement remains invariant under scalar changes in distances among the three points.

In experiment 2 we compared the performance of this distance acuity task with that of more familiar vernier acuity tasks. Whereas the distance acuity task involved collinear displacements that altered only the distances among the points, the vernier acuity task involved orthogonal offsets that altered the collinearity of the points. These patterns were presented only in the 2-D projective plane.

Accuracy was slightly higher in the vernier acuity task in eight of the nine conditions, although the overall difference was not statistically significant by analysis of variance. Both tasks were similarly affected by the distance between the endpoints, depending on the relative percentage rather than the absolute retinal distance of the displacement. Additional experiments have shown, however, that acuity in both of these 2-D tasks is lower than with displays of three stationary points, presumably owing to the rotary motion of the present displays.

In a final experimental test of the 3-D structure of the visual information we

asked observers to detect displacements from the 2-D center (rather than the 3-D center) of patterns whose endpoints were rigidly rotated in 3-D space and displayed by perspective projection onto the xy display screen. Three observers served for two sessions, one of which was devoted to detection of centers in 2-D space and the other to the detection of centers in 3-D space. The 3-D tilt—0°, 30°, 45°, or 60°—was randomly varied between trials. One block of 96 trials in each session was devoted to the detection of one of two different amounts of displacement—2 or 3 percent. Observers were not significantly better than chance at detecting the 2-D centers of these patterns (Fig. 2C). The reason for the difficulty of the 2-D task was that the displays still appeared as 3-D, but the middle point appeared neither centered nor rigidly connected to the endpoints.

We have also found that motion is necessary for the perception of 3-D distance in these displays. When observers were presented with stationary patterns like that in Fig. 1C, they detected the 3-D centers little better than chance, though few errors occurred when the same set of points was sequentially displayed as three points rotating in 3-D space.

The general finding is that precise visual measures of 3-D structure can be derived from the invariant structure of optical patterns undergoing perspective transformations.

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8. The measure of accuracy, from Luce's choice theory [R. D. Luce, in *Handbook of Mathematical Psychology*, R. D. Luce, R. R. Bush, E. Galanter, Eds. (Wiley, New York, 1963)], was defined by the equation,

$$-\ln \eta = (1/2) \ln \left\{ \frac{[N(y|C) + 0.5][N(n|D) + 0.5]}{[N(n|C) + 0.5][N(y|D) + 0.5]} \right\}$$
 where y and n represent the responses "yes" and "no," C and D represent the two stimulus alternatives, centered and displaced, and $N(\cdot)$ represents the number of trials on which the designated response was made to the designated stimulus. This measure was used because it corrects for biases in the tendency to respond "yes" or "no" and because it has the mathematical properties of a measure of distance. This measure is similar to the signal detection measure, d' .
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Social Wasps: Discrimination Between Kin and Nonkin Brood

Abstract. *In experiments in which nest boxes were switched, colony foundresses of the social wasp Polistes fuscatus accepted sisters' combs with little brood destruction but destroyed younger brood in the combs of less closely related females and sometimes deserted these combs. Discrimination between related and unrelated brood does not appear to depend on prior brood contact or environmentally acquired cues.*

It is well known that adult social insects discriminate between nestmates and other conspecifics, probably using odors (1, 2). Despite the importance of adult-brood interactions in the evolution and maintenance of insect sociality, little is known about the frequency or mechanism of adult-brood discrimination (2). In particular, the ability of adults to discriminate among brood on the basis of adult-brood relatedness is unexplored, although heritable recognition cues have

recently been strongly implicated in adult-adult kin discrimination in several social insect species (2, 3). We now report that colony-founding queens of a social wasp, *Polistes fuscatus*, discriminate between brood-filled combs (nests) of their sisters and those of less closely related females, possibly through the use of inherited cues.

In a study conducted at the Macbride Field Campus of the University of Iowa, we used free-living *P. fuscatus* colonies