preferred the twigs that were lower in monoterpene concentration (*4*).

The extent to which α-pinene influences the choice of food by tassel-eared squirrels was investigated in another series of tests in which subjects were allowed to choose between plain mash (made from ground sunflower seeds and laboratory food) and mash laced with varying amounts of α-pinene (*9*). Repeated-measures analysis of variance indicated that the α-pinene content affected food consumption [$F(2,\ 14) = 3.72$; $P = .025$, one-tailed test]; as the amount of α-pinene increased from 0.1 to 0.3 to 0.5 ml per 100 g of mash, the proportion of food consumed decreased from 0.45 to 0.41 to 0.24, respectively. The drop in consumption at 0.5 ml per 100 g was significant (Scheffé test; $P < .05$, one-tailed test) and showed that higher concentrations of α-pinene caused tassel-eared squirrels to reduce their intake of a preferred foodstuff.

Thus the amount of α-pinene is important in choosing which ponderosa pine trees are to be used as food sources by tassel-eared squirrels. Other factors that may affect twig preferences are nutritional quality of the cortical tissue and possible synergisms between nutrients and combinations of secondary compounds (mono- and sesquiterpenes). Contextual factors such as the visual appearance of the trees, presence of conspecifics, and pheromonal cues may also act as determinants in feeding tree selection if the chemistry of the tree is acceptable.

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3. Feeding trees were determined in the field by extensiveness of defoliation and number of freshly clipped needle clusters; the nearest neighbor of the same age and size as the feeding tree that did not show evidence of squirrel-caused defoliation was designated as a nonfeeding tree. In choice experiments and monoterpene analysis, twigs from a specific feeding tree were compared with twigs from its counterpart nonfeeding tree.
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6. A 2.0-g sample of cortical tissue was frozen under liquid nitrogen, ground to a powder, transferred with 50 ml of distilled water, and steam-distilled with *n*-pentane for 1 hour. The pentane extract was dried over anhydrous Na_2SO_4, and the pentane was removed (micro Vigreaux column). When the volume of the extract was less than 0.1 ml, an internal standard of 10.0 μl of *n*-tetradecane in *n*-heptane (200 μl of $C_{14}H_{30}$ in 10 ml of C_7H_{16}) wa added, and the volume was then increased to 0.1 ml with *n*-heptane. The concentrated extract was analyzed by gas chromatography (F and M model 810), with dual-flame ionization detection and a 104-m glass capillary column coated with Carbowax 20M). A 5.0-μl sample of the concentrated extract with added internal standard was injected into a glass-lined injection port at a split ratio of approximately 100 : 1. The oven conditions were 5 minutes at 65°C, then increased 1° per minute to 165°C, and isothermal thereafter. Helium make-up gas was supplied at 30 ml/min at the exit end of the glass capillary column. The data were recorded on a Varian CDS-111 chromatography data system, which gave the area percent composition for the various components and the area of each component relative to 10 percent of the area of the internal standard. Presentation of data in this manner permitted the evaluation of amounts of each component in the samples relative to the internal standard as well as the determination of the (relative) total amounts of all monoterpenes in each sample. Kovats' indices were determined on the glass capillary Carbowax 20M column at 70°C for the monoterpenes, and mass spectra were obtained from the total essential oil with a Carbowax 20M glass capillary column in a quadrupole gas chromatography–mass spectrometer (Finnigan model 1015C) with a model 6000 data system [H. Maarse and R. E. Kepner, *J. Agric. Food Chem.* **18**, 1095 (1970)].
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8. For the December data, a stepwise regression analysis, with the MAXR option of the SAS statistical package [J. H. Goodnight, in *SAS User's Guide*, J. T. Helwig and K. A.Council, Eds. (SAS Institute, Raleigh, N.C., 1979)], indicated that α-pinene accounted for 29.5 percent of the variance ($P = .013$); the semipartials (SR^2) for 3-carene, β-pinene, and limonene were not significant ($P > .25$). Similar results were obtained for the seasonally combined data with α-pinene accounting for 34.5 percent of the variance ($P = .006$); again the semipartials for 3-carene, β-pinene, and limonene were not significant ($P > .25$).
9. The mash consisted of 50 percent ground sunflower seeds and 50 percent mouse food (Charles River); 5 ml of safflower oil was added to each 100 g of mash. The mash containing monoterpene was made up in concentrations of 0.1, 0.3, and 0.5 ml of α-pinene per 100 g of mash. On each testing day, after 23 hours of food deprivation, each squirrel was given two food dishes; one contained 20 g of plain mash, the other 20 g of mash laced with α-pinene. Once a squirrel began to feed from either dish, it was given 20 minutes to eat; then both dishes were removed and the amount of each type of food eaten was recorded. Each squirrel received five trials at each of the three concentration levels. The monoterpene was obtained from Glidden, Organic Chemicals Division, SCM Corporation, Jacksonville, Fla.
10. We thank J. R. McKnight, J. C. Pederson, R. M. Potter, and K. Wuensch for their help with the study and A. J. Cooper, S. D. Berry, A. J. Pantle, and J. C. Jahnke for reading the manuscript. Supported by NSF grants BNS 76-05069 and DEB 76-80423.
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23 October 1980

Spatial Knowledge and Geometric Representation in a Child Blind from Birth

Abstract. *A series of experiments demonstrated that a congenitally blind 2½-year-old child—as well as sighted but blindfolded children and adults—can determine the appropriate path between two objects after traveling to each of those objects from a third object. This task requires that the child detect the distances and the angular relationship of the familiar paths and that she derive therefrom the angle of the new path. Our research indicates that the locomotion of the young blind child is guided by knowledge of the Euclidean properties of a spatial layout and by principles for making inferences based on those properties.*

We have had the opportunity to study the spatially guided locomotion of one 2½-year-old blind child in several experimental settings. After the child had been taken along several paths connecting four objects in a small room, she was able to move directly between the objects along paths she had never taken. Sighted adults and 3-year-old children, all blindfolded, performed with similar accuracy. These observations demonstrate that the locomotion of children, with or without visual experience, is guided by metric knowledge of space. This knowledge makes possible the derivation of further spatial information.

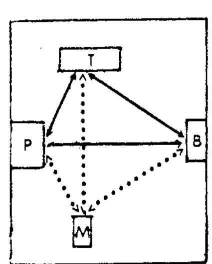

Fig. 1. Room layout for spatial inference experiment. The room measured 2.44 m by 3.05 m. Dashed lines, trained routes; solid lines, test routes. Landmarks: *M*, mother; *P*, pillows; *T*, table; *B*, basket.

These observations were undertaken to address a classical issue in psychology, the development of human knowledge of space. Descartes (*1*) suggested that the geometric principles underlying spatial knowledge are innate and accessible to any perceptual mode. He offered the example of a blind man exploring objects with a stick. For the man to discover the shapes and arrangement of those objects, he must refer each tactual

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impression to a unitary spatial framework, structured by the principles of Euclidean geometry. Descartes proposed that any perceiver, exploring the world through any mode, faces the blind man's problem, and must draw on tacit knowledge of geometry to solve it. Descartes further reasoned that geometric principles must be innate: since those principles structure any perceptual experience, they cannot themselves be acquired through experience. These arguments form part of the core of the rationalist tradition in psychology (*2*).

Descartes's analysis can be contrasted with two major subsequent developments. First, Helmholtz (*3*), extending the arguments of British empiricism, rejected Descartes's claim of innateness. Helmholtz suggested that the geometric principles underlying space perception can be acquired. Perceivers need be endowed only with a set of general, nonspatial inference rules. They will deduce the principles of Euclidean geometry as they apply these inference rules to the sensory information that the environment provides. Second, Gibson (*4*) proposed that no geometric principles whatever need structure one's sensory impressions. The spatial properties of objects are specified by higher-order relationships in spatially and temporally extended arrays of stimulation. Space perception depends on mechanisms that detect these relationships.

We have attempted to address these issues by extending Descartes's example. We focused on the attempts of a young blind child to discover the spatial layout of objects in a room from limited, temporally extended encounters with those objects and with paths between them. We investigated whether this child could make spatial deductions that rely on information about Euclidean angles and distances.

Our principal subject was Kelli, a child born 3 months prematurely and blinded shortly after birth as a result of retrolental fibroplasia. She is totally blind (*5*). After spending the first 5 months in the hospital, primarily in an isolette, Kelli was discharged with a developmental status of newborn.

When Kelli was 32 months old, she was brought into an unfamiliar laboratory playroom, 2.44 m by 3.05 m. The room contained four landmarks in a diamond shaped array: her mother seated on a chair (M), a stack of pillows (P), a basket of toys (B), and a table (T) (Fig. 1). In experiment 1, we placed her at M and walked her from there to P and back, twice; from M to T and back, twice; and from M to B and back, twice. Each time, Kelli felt the object while facing it, and she might have thus determined the orientation of the object relative to the trained path. We then induced her to find the routes between P, T, and B on her own, by giving her such simple commands as "Go to the toybasket" or "Go to the pillows." Kelli was followed as she moved until she reached the goal or

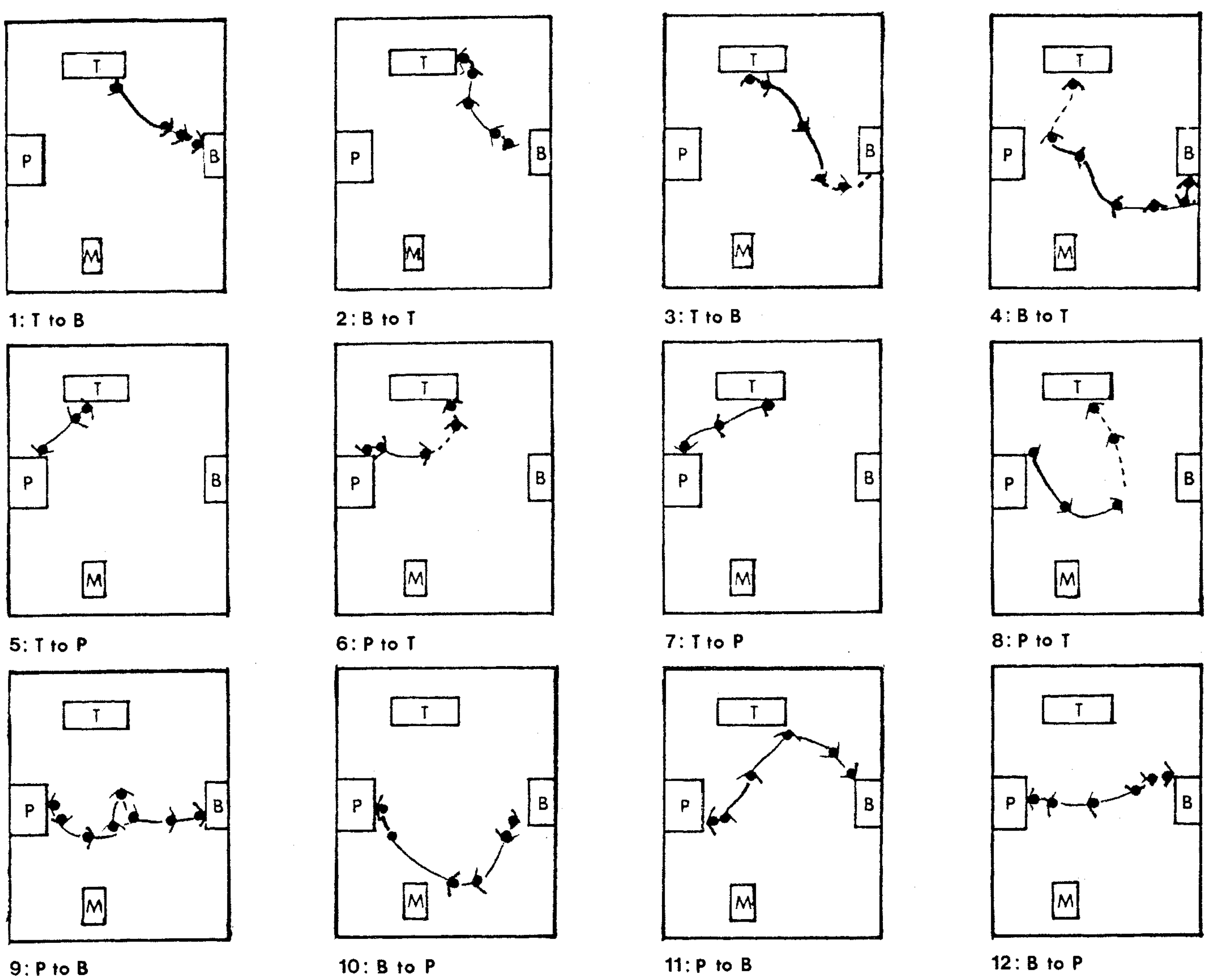

Fig. 2. Performance on test trials. Solid line, independent movement by child; dashed line, experimenter aided child.

expressed confusion. In the latter case, the trial was ended, and she was taken to the goal. Each route was tested twice, for a total of 12 trials, in the following order: T–B, B–T, T–B, B–T; T–P, P–T, T–P, P–T; P–B, B–P, P–B, B–P. Her route was plotted from a videotaped record by observing her position and frontal direction at 3-second intervals, and joining these points with a line representing her path of movement.

Kelli's performance on each test trial is shown in Fig. 2. To test the null hypothesis that Kelli moved randomly to some stopping point, we measured her position just before reaching the target or before the trial was ended. The circle that surrounded her starting position was divided into nine 40° segments, and each trial was treated as a success if her final position fell within the 40° segment containing the target (which subtended an angle of about that magnitude). The random probability of success is .11, but Kelli's actual performance was much higher: there were eight successes and four failures (binomial test, $P = .0001$). Two of the failures were errors of 15° or less.

Kelli did not move ballistically toward the target. Instead, she seemed to adjust her movements, as she went, towards the target. At successive intervals of 0.61 m. from her starting position, we compared her frontal direction at the beginning of the interval to her position at the end of the interval and computed the average degrees of self-correction toward the target for each trial. She adjusted her direction toward the target on 11 trials, and away from the target on 1 of the 12 trials ($P = .003$) (*6*).

Kelli's performance might have been caused by the use of subtle acoustic cues to orient her toward the different landmarks. Experiment 2 tested for this possibility. Its procedure was identical to that of experiment 1 with one exception: after the first six test trials, Kelli was carried out of the room, and the array of objects was rotated 90°. Kelli was then carried back in and placed facing one of the objects. She then received eight test trials with the rotated array. The rotation preserved the spatial relationships among objects, but it changed the absolute position of each object within the room. Thus, if Kelli used acoustic information from the room as spatial landmarks or beacons, she would be expected to move incorrectly between objects, since spatial information about the objects and about the room conflicted. Kelli's level of accuracy after this rotation was close to what it had been before. She moved successfully to the target on five of eight trials ($P = .0008$). More important, on only one of the eight trials could her direction of movement be accounted for by the orientation of the room, a nonsignificant proportion ($P = .38$).

A third experiment was conducted with five sighted 3-year-old children and six sighted adults, all of whom wore opaque goggles to block their vision of the room. The accuracy of the child subjects was similar to that of Kelli, with a mean of 8.2 successes in 12 trials. The adult subjects performed somewhat better, with a mean of 11.0 successes.

These experiments indicate that a young blind child is able to set a course between objects along a route she has never followed, after moving to each object from a third point. In order to accomplish this, the child must have access to information about the lengths of the two connecting routes travelled during training and the angular separation of those routes. From this information, the child can derive new angular relationships: the angular direction of one object from the other. Angle and distance information are properties that are preserved in metric geometries, such as Euclidean geometry; they are not properties of nonmetric geometries, such as the projective or topological. Furthermore, the axioms and theorems of Euclidean geometry are sufficient for the derivation of the new angular information, whereas those of the other geometries are not (*7*). We conclude that this blind child, and sighted controls, know about some of the metric properties of space, probably Euclidean properties.

Our findings do not distinguish conclusively between the Cartesian, Helmholtzian, and Gibsonian approaches, but they do help to sharpen the theoretical issues and clarify the empirical tasks facing proponents of each tradition. The Cartesian psychologist might propose that Euclidean geometry is innate. The task is then to discover the psychologically appropriate axiomatization of that geometry and to characterize the processes of inference based on a Euclidean representation. The Helmholtzian psychologist might propose that Euclidean principles can be induced in the first $2\frac{1}{2}$ years by a child who applies innate nonspatial inference rules to correlated patterns of sensation, whether visual or nonvisual. The burden of a Helmholtzian is to describe these rules and the learning processes that lead to the development of a Euclidean representation and its associated inference rules, using sense information. Finally, the Gibsonian psychologist might propose that the child made no inferences at all in our task; rather, her actions may have been guided by a perceptual mechanism that detected invariant tactual relationships as she actively locomoted. Such a mechanism might be sensitive to Euclidean relationships, yielding the perception of further Euclidean relationships without producing a spatial representation to which inference rules are explicitly applied. The Gibsonian burden is to provide a general characterization of the invariants that perceivers detect and of the mechanisms that detect them—a characterization that can encompass the performance of the blind child traveling along a limited set of paths.

A young blind child exploring an environment was able to gain knowledge of certain spatial relationships between objects. Moreover, she could use these relationships to derive further knowledge about the spatial properties of that layout. Our observations indicate that metric properties of space can be appreciated by children at an early age. They further indicate that vision plays no essential role in the early development of knowledge of such properties.

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5. Cases of severe prematurity are at risk for a variety of problems. Kelli has been assessed yearly since the beginning of the study and does not show any significant deficiencies relative to norms for sighted or blind children.
6. Had Kelli been moving constantly straight ahead, she would not have performed well, since her starting position varied on each trial. For example, on trial 2, she would have moved toward M from her starting position; on trial 3, she would have moved straight into T from her starting position.
7. Three different metric geometries could support the inferences of the blind child: Euclidean, hyperbolic, and Riemannian geometries. These geometries are empirically indistinguishable over the range of distances that humans can negotiate. Other geometries, such as topology and projective geometry, have been proposed to characterize the child's spatial knowledge; see J. Piaget and B. Inhelder, *The Child's Conception of Space* (Norton, New York, 1967; orig-

inally published in 1948). These geometries cannot support the inferences we have studied, however, for they preserve no metric properties [R. Courant and H. Robbins, *What is Mathematics?* (Oxford Univ. Press, New York, 1941)].
8. We thank C. R. Gallistel, for focusing our attention on formal geometric analysis of our experiment, for suggesting important controls and variations on the basic experimental paradigm, and for suggesting a statistical analysis derived from the avian navigation literature; L. R. Gleitman for extensive overall conceptual guidance; U. Neisser for comments on a previous draft of this paper; and K. Feldman for running sighted control subjects and transcribing the videotaped sessions. This work was aided by a social and behavioral sciences research grant from the National Foundation–March of Dimes and a William T. Carter Foundation grant, both to L. R. Gleitman.

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Staining of Blue-Sensitive Cones of the Macaque Retina by a Fluorescent Dye

Abstract. *Intravitreal injection of a fluorescent dye, Procion yellow, results in the complete and systematic staining of a cone population in the monkey retina. These cones form an approximately regular array whose separation varies with retinal eccentricity. They are absent in the very center of the fovea, and their density peaks at 1°. The distribution of stained cones resembles that reported for blue-sensitive cones of other primates and, consistent with such an identification, they are found with less incidence in species having lower concentrations of blue cones.*

The neural retina is a highly organized structure with a crystalline-like array of tightly packed cones and rods in a two-dimensional matrix. Microspectrophotometric work has provided evidence of three cone types in the primate retina, each having peak sensitivity at a different part of the spectrum (*1*)—"blue-," "green-," and "red-sensitive" cones. To our knowledge, morphological differences among these cone types have not been reported in primates. Functionally, however, blue cones have unique properties. In humans and (Old World) macaque monkeys, the green and red cone systems have similar electrophysiological and psychophysical properties, whereas those of the blue cone system are different (*2*). There are also differences between dysfunctions of these cone systems leading to color vision disorders. Congenital disorders of the green and red cone systems correspond to sex-linked inheritance, whereas those of the blue cone system correspond to autosomal inheritance (*3*). In addition, blue cones are often involved in acquired color vision disorders secondary to retinal disease [Köllner's rule (*4*)], indicating an undue vulnerability to retinal insult.

In 1970, Laties and Liebman (*5*) reported that the intravitreal injection of a tissue-reactive fluorescent dye, Procion yellow, stained the outer segments of cones, but not of rods, in the amphibian retina. Using greater amounts of the dye, we have obtained a striking result. In the retina of the monkey, not only are all cone outer segments stained with Procion yellow, but the entire soma of some cones is completely stained by the dye, producing a Golgi-like silhouette. Such cones are organized in a rather regular array and have a characteristic retinal distribution.

Procion yellow M4RAN (Polysciences), 5 to 7 percent in deionized water, was injected (0.15 ml) intravitreally into the eye of anesthetized rhesus and cynomolgus monkeys. Leakage of dye was reduced by the slow removal of the needle. In some animals we also injected Lucifer yellow (Polysciences) (*6*) simultaneously with or subsequently to the Procion dye in a weight ratio of 1:50 to 1:100 of Lucifer to Procion yellow. Except for one monkey, which was kept in the dark during and after the injection, the animals were kept in a normal light (200 trolands): dark cycle for 18 to 30 hours (*7*). The animals were then killed with an overdose of pentobarbital. The eyes were fixed, often by arterial perfu-

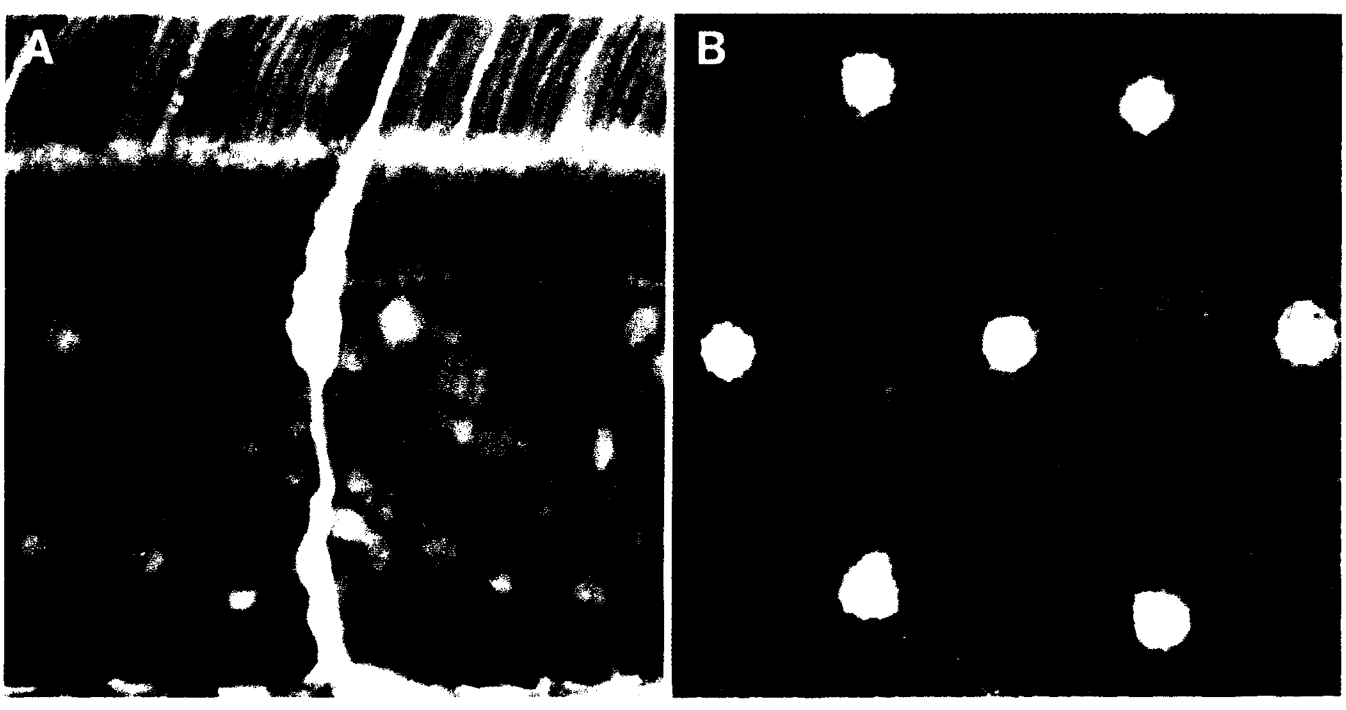

Fig. 1. (A) Radial section of rhesus monkey retina (~ 20° eccentricity) showing a cone completely stained by Procion yellow among other cones unstained except for their outer segments. (B) Tangential section passing through the outer limiting membrane showing a regular array of stained cones; unstained cones and rods appear as holes in the stained mesh of the outer limiting membrane.