Fixation of tissues in situ for electron microscopy was accomplished by (i) intra-arterial perfusion with glutaraldehyde as used previously (3) or (ii) filling the peritoneal cavity with the fixative. After 20 to 30 minutes of fixation, the animals were killed and tissue was removed from the middle of each horn. These tissues were fixed (2 percent glutaraldehyde and 4.5 percent sucrose in 0.075*M* cacodylate buffer, *p*H 7.4) for an additional 2 hours. After the initial fixation in glutaraldehyde, the tissues were washed in buffer for 60 minutes and fixed for another 90 minutes in 1 percent osmium tetroxide (in cacodylate buffer, 0.05*M*, *p*H 7.4). All tissues were stained en block with saturated uranyl acetate for 30 minutes, dehydrated in graded alcohols, and embedded in Spurr. The tissues were oriented in molds so that either the outer longitudinal or inner circular muscle layers would be cut in cross section.
6. Eight to 12 nonoverlapping photographs from one section of each tissue were taken of smooth muscle cut in cross section and examined at ×11,000. The negatives were enlarged three times (×33,000) and printed on 20 by 28 cm paper. A map tracing compass (Selsi, West Germany) was used to trace along the surface of each smooth muscle cell in the photograph. Each suspected gap junction observed in the photograph at ×33,000 was further enlarged to ×100,000 magnification for identification and length measurements. Cell-to-cell contacts were identified as nexuses or gap junctions at the higher magnification if they showed a five-lined structure or a seven-lined structure with a 2-nm gap between outer membrane leaflets.
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Optical Transforms and the "Pincushion Grid" Illusion?

Schachar (*1*) has presented experimental evidence which he contends contradicts the theory that the visual system performs two-dimensional Fourier transformations of observed patterns. He does this on the basis of the "pincushion grid" illusion in which diagonal lines are seen when one views a square grid of lines. Schachar presents what he claims to be an optical transform of the grid, and since no diagonal components appear in his optical transform, he contends that the visual system does not perform a Fourier transformation of the observed grid.

In this communication I raise two objections to Schachar's report.

First, his optical transform is not that from a grid. The optical transform, or optical diffraction pattern, of a square grid is well known to be a square array of spots. The theory is developed in many standard texts [see, for example, Ditchburn (*2*)] and is easily demonstrated with a laser. Figure 1 is a photographic enlargement of a grid whose actual spacing is 0.085 mm. The beam of a helium-neon laser was directed onto the grid, and the diffraction pattern, intercepted by photographic paper at approximately 2 m from the grid, is reproduced in Fig. 2. The spot pattern is clearly evident and includes diagonal components.

The photograph presented by Schachar in his figure 1 does not exhibit any of the spots characteristic of the diffraction pattern of a grid, neither on the major axes nor on the diagonal. It appears to be the pattern observed when a laser beam passes through photographic film of approximately even density. Schachar does not give the spacing of the grid used for the diffraction experiment, but if the cover of *Science* is a one-step photographic enlargement of the 35-mm slide mentioned in the article, then the actual grid spacing on the slide would have been on the order of 1 mm, about the size of a typical laser beam, and there would not have been a repeating object to produce a diffraction pattern.

Second, a more fundamental question arises concerning the applicability of optical diffraction patterns as an analogy for the Fourier transformation that is postulated to occur in the visual processing system. A diffraction pattern is not a Fourier transform, but is the complex square of the Fourier transform and is not unambiguously related to the diffracting object. It is this ambiguity that makes the determination of crystal structure from x-ray diffraction patterns a complicated task.

One specific form of this ambiguity relates to an observation by Schachar. He mentions that "a negative of the pincushion grid (black pincushions separated by white spaces) produces the illusion of diagonal black lines." If the visual system uses diffraction transforms, not true Fourier transforms, this observation of the reversal of the color of the illusion would be in contradiction to Babinet's principle (*3*), which states that complementary objects, that is, those that have reversed contrast, give identical diffraction patterns. Schachar's observation of reversed color of the illusion when complementary grids were used, violates Babinet's principle and demonstrates that the visual system does not behave as though it used diffraction transforms. This neither proves nor disproves that Fourier transforms are used by the visual system, but it does show that Schachar's basic assumption, that an optical transform can be used as an analogy for possible Fourier transformations in the visual system, is not valid.

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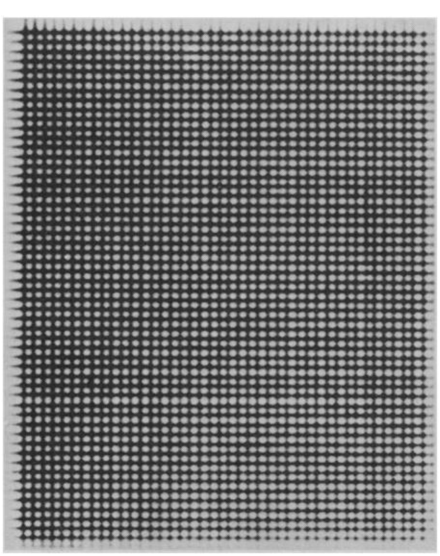

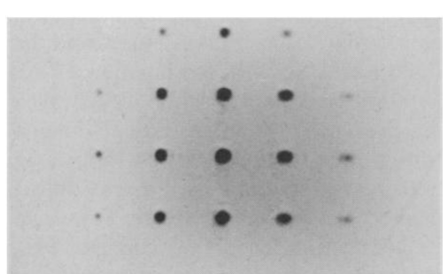

Fig. 1 (left). Photographic enlargement of a diffraction grating. The grating was produced by ruling black lines on white paper and producing a photographic reduction on a glass-supported emulsion. The actual spacing was 0.085 mm. Fig. 2 (right). An optical diffraction pattern produced by directing a helium-neon laser beam through the grating produced in Fig. 1.

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Schachar (*1*) failed to observe diagonal spatial frequencies in the optical Fourier transform of a "pincushion grid." This implied that the illusion of diagonal lines that are observed in such a pattern cannot be attributed to two-dimensional Fourier analysis by the human visual

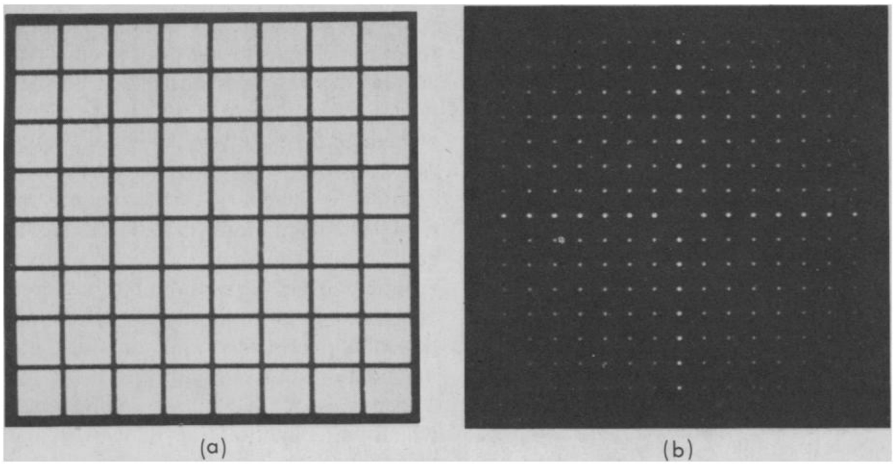

Fig. 1. Original pincushion grid (a) and its power spectrum (b). The discrete diagonal frequencies are apparent.

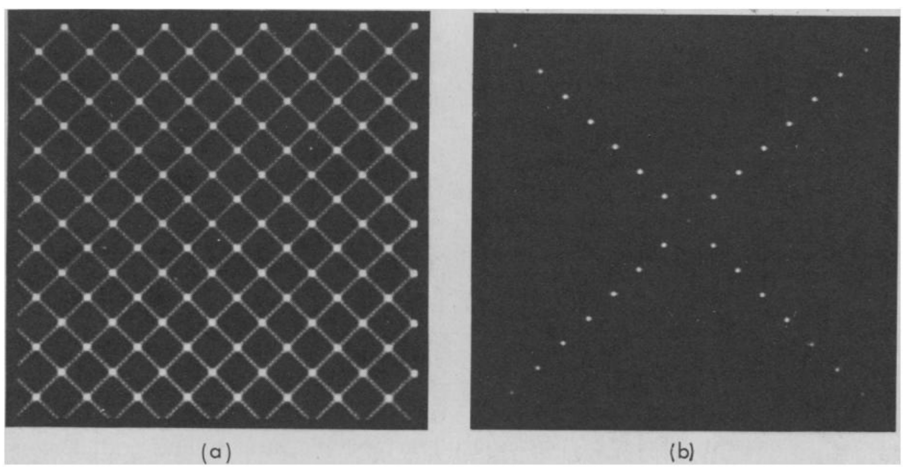

Fig. 2. The pincushion grid (a) and its power spectrum (b) after filtration to retain only spatial frequencies along the central diagonal axes. Both the diagonal-line and the pincushion illusions are produced.

system. We show that a pincushion grid does possess diagonal spatial frequencies and that these components can account for both the diagonal-line and the pincushion illusions.

A binary pincushion grid similar to that in (*1*) was generated over a 128- by 128-element grid by means of a digital computer (Fig. 1a). The average d-c level was removed, and the two-dimensional digital power spectrum was calculated. The logarithm of this power spectrum is shown in Fig. 1b. The absence of the very large d-c component (which can cause considerable interference in an optical Fourier transform) and the dynamic-range compression achieved by the logarithmic display reveals discrete spatial frequencies along the diagonal axes.

The corresponding diagonal lines present in the pincushion grid can be observed by retaining only spatial frequencies along the central diagonal axes. The pincushion grid and its power spectrum are shown in Fig. 2, a and b, after such directional filtering. The points of the pincushion are observed where the diagonal lines cross and their amplitudes add.

The appearance of diagonal lines in a pincushion grid can therefore be expected from its two-dimensional Fourier transform; the effect does not exclude the possibility that frequency-domain analysis is involved in human vision.

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Schachar's report suggested that an illusion generated by a "pincushion grid" is not predicted from the two-dimensional Fourier transform of the grid (*1*). The implication was that the visual system may not perform a two-dimensional Fourier transform of observed patterns. These conclusions were based on the belief that there were no diagonal components present in an optical Fourier transform of the pincushion grid. However, the pincushion grid does have diagonal Fourier-transform components that can be observed in a photograph, provided that the appropriate scaling of the transform and several exposure times for the film are used.

The two-dimensional Fourier transforms of a 35-mm slide of the pincushion grid were obtained from a laser optical Fourier-transform device (Fig. 1, a and b). The diagonal components are clearly visible. Now that we know what the diagonal components look like, a return to Fig. 1 of the recent letter will, under careful observation, reveal diagonal components just visible in the noise of the poor photograph.

In order to observe better the diagonal components without the noise that is present in the photographs of the transform, digital Fourier transforms of a coarsely digitized version of a two by two section of the pincushion grid have been produced and are shown in Fig. 2, a and b.

These transforms should not be too surprising. The Fourier transform is a linear reversible process that can neither add or subtract nor, in any way, can it change the spatial information contained in the original pattern without some kind of filtering. The diagonal transform components reflect the even symmetry of the diagonal components of the pincushion grid. The magnitude of the diagonal components, when compared to the on-axis components, will increase and decrease as the pincushion effect increases and decreases.

It should be stressed that neither the presence of the diagonal components in the transform nor the illusory diagonal lines that are observed in the pincushion grid prove or disprove that the visual system performs a two-dimensional Fourier transform of the pattern. Nor do statements like "the points of the pincushion grid suggest a line to the visual cortex and the illusion of a line occurs" explain the illusion. It merely states what we see. The sides of the pincushion grid would also suggest lines across each grid to the visual cortex, but we don't "see" these lines.

There are other observations in addition to those reported in the recent letter that suggest a more quantitative physiological explanation for the illusion. First of all, the illusion depends upon viewing distance, being strongest when the size of each grid ranges from about 0.39 to 6.2 cycles per degree. Second, the illusion is not seen with the fovea at closer viewing distances, but rather in the parafovea and is strongest when eye-movements are made. Third, the illusory

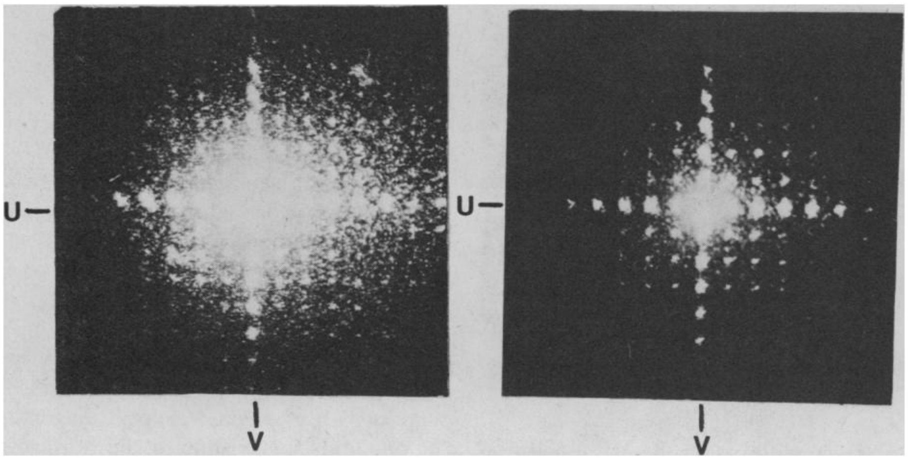

Fig. 1. Optical Fourier transforms of the "pincushion grid." The diagonal transform components in (a) can be seen more readily by using a shorter exposure time as seen in (b).

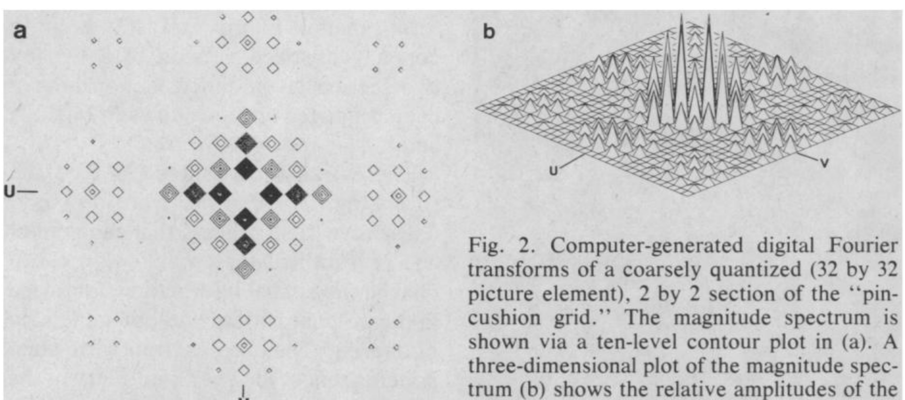

Fig. 2. Computer-generated digital Fourier transforms of a coarsely quantized (32 by 32 picture element), 2 by 2 section of the "pincushion grid." The magnitude spectrum is shown via a ten-level contour plot in (a). A three-dimensional plot of the magnitude spectrum (b) shows the relative amplitudes of the diagonal components. The d-c component (the central maximum in the optical transforms) has been removed to increase the relative amplitude of the other transform components in the computer plots. The different number of harmonics between the optical and the computer transforms are due to the different line width ratios of the original and digitized tiles. The computer plots also show more high spatial frequencies than that shown in the optical pictures.

lines do not appear to go all the way across the diagonals of the grids at closer viewing distances, but rather are strongest for only about one-third of the distance away from the intersection.

Finally, the strength of the illusion depends upon contrast and the shape of the lines at the intersection. The illusion appears strongest at a middle range of contrast from about 49 to 10 percent and when the pincushion effect is greatest, that is, when the lines are thinnest at their intersection. At higher and lower contrasts and with thicker lines at the intersection, the "pincushion illusion" appears minimal. However, under conditions of high contrast and decreased pincushion effect, there are diffused circles of opposite contrast to the lines at the intersection which is the Hering grid illusion. This latter illusion can be shown to be due to the filtering of the pattern by the visual system.

Such results, and the fact that the pincushion illusion changes as a function of orientation (*1*), suggests that the illusory lines are physically present because of the two-dimensional spatial filtering characteristics of the visual system.

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The optical Fourier transform of the "pincushion grid" (*1*) definitely has diagonal components. However, the presence of diagonal Fourier components in the pincushion grid does not necessarily account for the presence of the illusory diagonal lines nor prove that the visual system performs a two-dimensional Fourier transform.

Rudee is correct that whenever the optical wave-amplitude transform is recorded on any medium, it becomes an energy spectrum: amplitudes are squared and phase information is lost. Of course this nonlinear transformation does not invalidate it as a method of locating the frequencies of the Fourier components, which was our intention. However, the fact that the sign of the illusion follows the sign of the stimulus does indicate that the visual system retains phase information.

Using a straight-line approximation to the original pincushion grid, we have decomposed this stimulus into two component patterns—one with no off-axis Fourier terms, and the other containing all the off-axis terms. We have found (*2*) that *neither* of these component patterns produce the illusory diagonal lines, although their linear combination does. Therefore, there must be more to this illusion than a straightforward filtering of Fourier components by the visual system.

In conclusion, the two-dimensional Fourier transform of both the pincushion grid and the straight-line grid demonstrates that the two-dimensional Fourier transform contains all of the information about an object, including its features and periodicity; however, the finding of Fourier components which correspond to certain illusions does not necessarily imply that the visual system does Fourier-transform analysis nor allow for prediction by Fourier theory without knowledge of the other properties of the visual system.

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