of 5-HT) injected 1 h before the critical period blocked progesterone induced ovulation (group E). Conversely, by shifting the balance of monoamines in favour of CA, ovulation ought to be restored even in the presence of high levels of 5-HT. The inhibitory effect of 5-HT was completely blocked by a simultaneous injection of LSD (group G), a potent antagonist of 5-HT[15], or by dopamine (group H). These data should not necessarily be interpreted to mean that dopamine as such overcomes the inhibitory effect of 5-HT. It is equally possible that its metabolites adrenaline or noradrenaline may be involved. The possibility that the intraventricularly administered monoamines act on the pituitary can be excluded because monoamines do not inhibit the response of the pituitary to gonadotrophin releasing factors *in vitro*[16], nor do they significantly affect discharge of gonadotrophins from the pituitary when infused directly into the portal vessels in the pituitary stalk[3]. Body weight was unaffected by these treatments, so the nonspecific stress of the drugs cannot account for the observed effects. In fact, starving the animals beginning at the time of PMSG injection until autopsy, which caused a considerable loss of weight, failed to interfere with the facilitatory effect of progesterone on ovulation (group I).

Our results provide evidence for the first time that the inhibitory effect of 5-HT on ovulation can be overcome by a catecholamine and suggest that the balance between these contrasting influences is crucial in ovulation. These findings further reinforce the theory of dual hypothalamic control of ovulation postulated earlier[6].

This study was supported in part by a grant from the Ford Foundation.

A. ZOLOVICK
A. P. LABHSETWAR*
Worcester Foundation for Experimental Biology, Shrewsbury, Massachusetts 01545

Received April 16; revised May 21, 1973.

* Please address reprint requests to A. P. L.

1 Schneider, H. P. G., and McCann, S. M., *Endocrinology*, **86**, 1127 (1970).
2 Kamberi, I. A., Mical, R. S., and Porter, J. C., *Endocrinology*, **87**, 1 (1970).
3 Kamberi, I. A., Mical, R. S., and Porter, J. C., *Endocrinology*, **88**, 1288 (1971).
4 Brown, P. S., *J. Endocr.*, **37**, 327 (1967).
5 Kordon, C., *Neuroendocrinology*, **4**, 129 (1969).
6 Labhsetwar, A. P., *Acta Endocr. Kbh.*, **68**, 334 (1971).
7 Labhsetwar, A. P., *J. Endocr.*, **54**, 269 (1972).
8 Rubinstein, L., and Sawyer, C. W., *Endocrinology*, **86**, 988 (1970).
9 Lippman, W., *Nature*, **218**, 173 (1968).
10 Kordon, C., and Glowinski, J., *Endocrinology*, **85**, 924 (1969).
11 Carrer, H. F., and Taleisnik, S., *J. Endocr.*, **48**, 527 (1970).
12 McCormack, C. E., and Meyer, R. K., *Gen. comp. Endocr.*, **3**, 300 (1963).
13 Ying, S., and Meyer, R. K., *Endocrinology*, **84**, 1466 (1969).
14 Gallo, R. V., and Zarrow, M. K., *Endocrinology*, **86**, 296 (1970).
15 Cooper, J. R., Bloom, F. E., and Roth, R. H., *The Biochemical Basis of Neuropharmacology* (Oxford University Press, New York, 1970).
16 Schneider, H. P. G., and McCann, S. M., in *Aspects of Neurosecretion* (edit. by Bargman, W., and Scharrer, B.), 177 (Springer, Berlin, 1970).

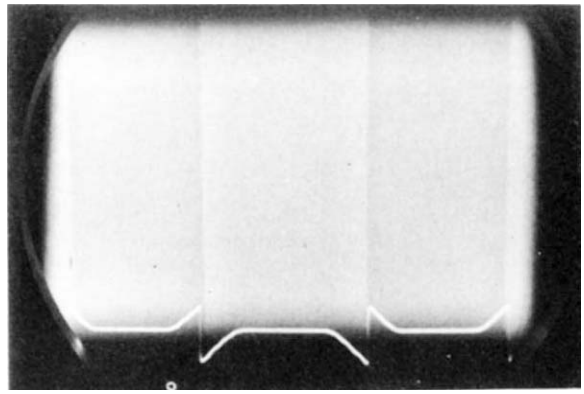

Fig. 1 Lateral interaction between channels sensitive to luminance. This figure illustrates the well-known enhancement of brightness produced when a given luminous area is flanked by regions whose luminance profile is as shown at the foot. (Downward deflexion represents increased luminance.) The role of the transition regions in generating the illusion is strikingly demonstrated by covering them with strips of plain paper.

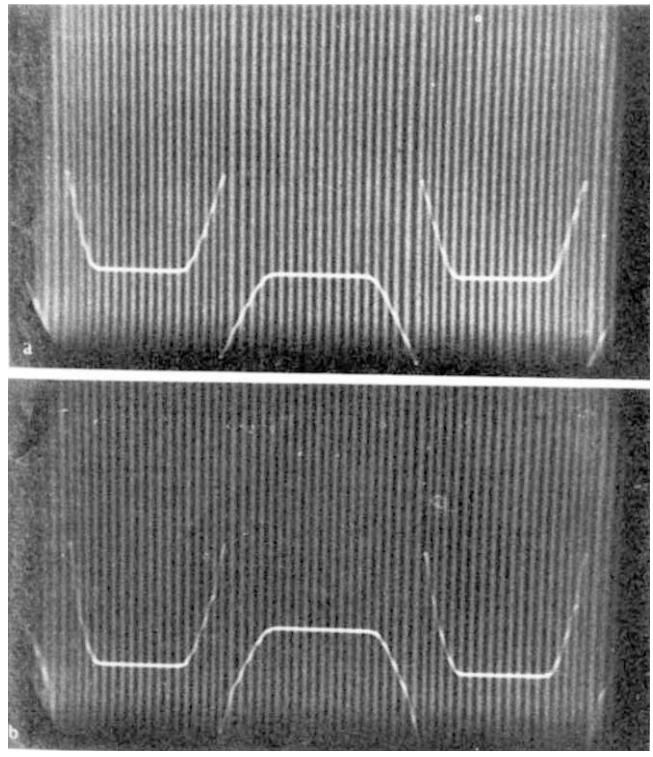

Fig. 2 Lateral interaction between channels sensitive to texture density. (a) The texture density (spatial frequency) of each pattern of lines is modulated in the same way as luminance was in Fig. 1. The height of the superimposed oscilloscope trace is linearly related to spatial frequency (upward deflexion for increased frequency). Closely analogous contrast enhancement effects can be observed. (b) By adding a central "pedestal" to the controlling waveform, the effect can be annulled and so quantified.

Lateral Interaction between Neural Channels sensitive to Texture Density?

A NUMBER of well-known visual phenomena, including Mach Bands[1] and the related illusion[2] shown in Fig. 1 are interpretable as evidence of lateral interaction between adjacent neural channels sensitive to retinal luminance. Inhibitory interaction would lead to disproportionate weight being given to sharp discontinuities in luminance. This can be taken to explain why the middle panel in Fig. 1 (when viewed from the right distance) is seen as brighter overall than its neighbours, though objectively all three have the same luminance at their centres. The limited retinal range of the interactive process responsible is shown by the gradual disappearance of the illusion as the viewing distance is increased.

Gibson[3] and others have shown psychophysically that the gradient of density of visual texture is an important clue to the orientation in depth of textured surfaces. This suggests that the visual nervous system might also have a gradient-enhancing process acting among elements sensitive to density of texture[4]. If so, one might expect analogous border contrast effects to those of Fig. 1 in the spatial-frequency domain giving rise to illusory spatial frequency shifts near discontinuities of texture density. In the experiments to be described these expectations were confirmed.

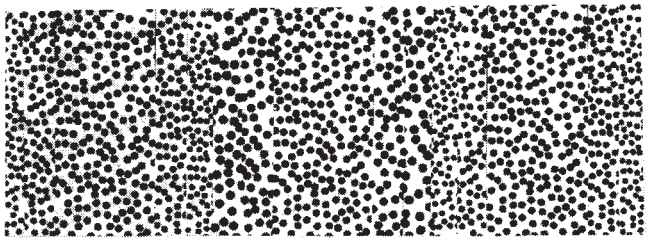

Fig. 3 A static visual noise field with similar variations in texture density to those in Fig. 2a.

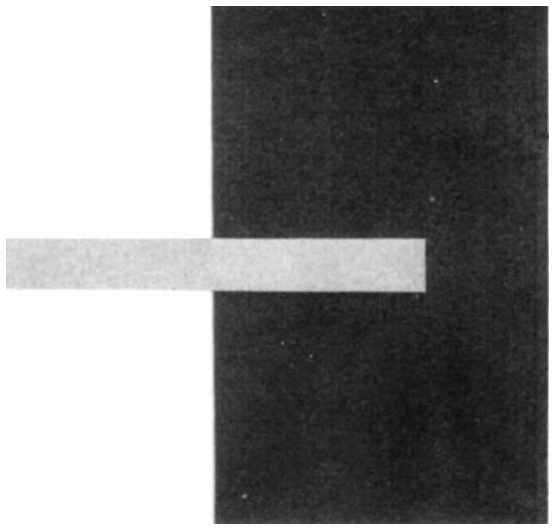

Fig. 4 Simultaneous contrast of brightness. A thin black line bisecting the test strip enhances the effect. If the line is moved transversely to and fro it seems to draw the light/dark boundary with it.

For ease of adjustment the first stimulus used consisted of a frequency modulated grating (Fig. 2a) on the screen of a cathode ray tube. X-Deflexion was provided by a normal time-base generator at 50 Hz. A 100 kHz triangular waveform provided Y-deflexion. Trace brightness was modulated by a periodic trapezoidal waveform whose frequency was varied electronically with X-coordinate according to the profile shown at the foot of Fig. 2a. This arrangement avoided any change in mean luminance with spatial frequency, which might otherwise have produced confusing side effects.

The resulting pattern in Fig. 2a produces the expected illusion of spatial frequency shift, the central panel appearing 5–10% lower in spatial frequency than its neighbours. To quantify this effect, the difference between resting levels of the modulating waveform was made adjustable by a smooth knob, which the subject was asked to turn until the line densities at the centres of all three panels looked the same. A typical stimulus approximately adjusted for perceived equality is shown in Fig. 2b, with its actual density profile at the foot for comparison. As with Fig. 1, the strength of the illusion can be seen to depend on the visual angle subtended by the transition regions. With the profiles shown, a subtense of about 0.5° per region seems optimal. Interestingly, the effect is less when the figure is turned through a right angle.

To test the generality of this effect, a random dot field with roughly similar gradations of texture density was constructed from a series of strips printed at different magnifications (Fig. 3). This gives only a crude stepwise approximation to the texture density profile of Fig. 2a; but for most observers it produces a weak illusion in the same direction. The middle panel seems coarser in texture than its neighbours, though in fact the central regions of all are identical. In most cases the strongest effect was observed when the transition region subtended about 1° at the eye.

The phenomenon of "simultaneous contrast" illustrated in Fig. 4 has long been taken as evidence of lateral inhibition between luminance-sensitive channels. Left and right halves of the central test strip, identical in luminance, look different in brightness. Analogous test patterns were therefore prepared in which contrasting densities of texture were juxtaposed. Inspection of Fig. 5 shows that (a) enhancement of texture

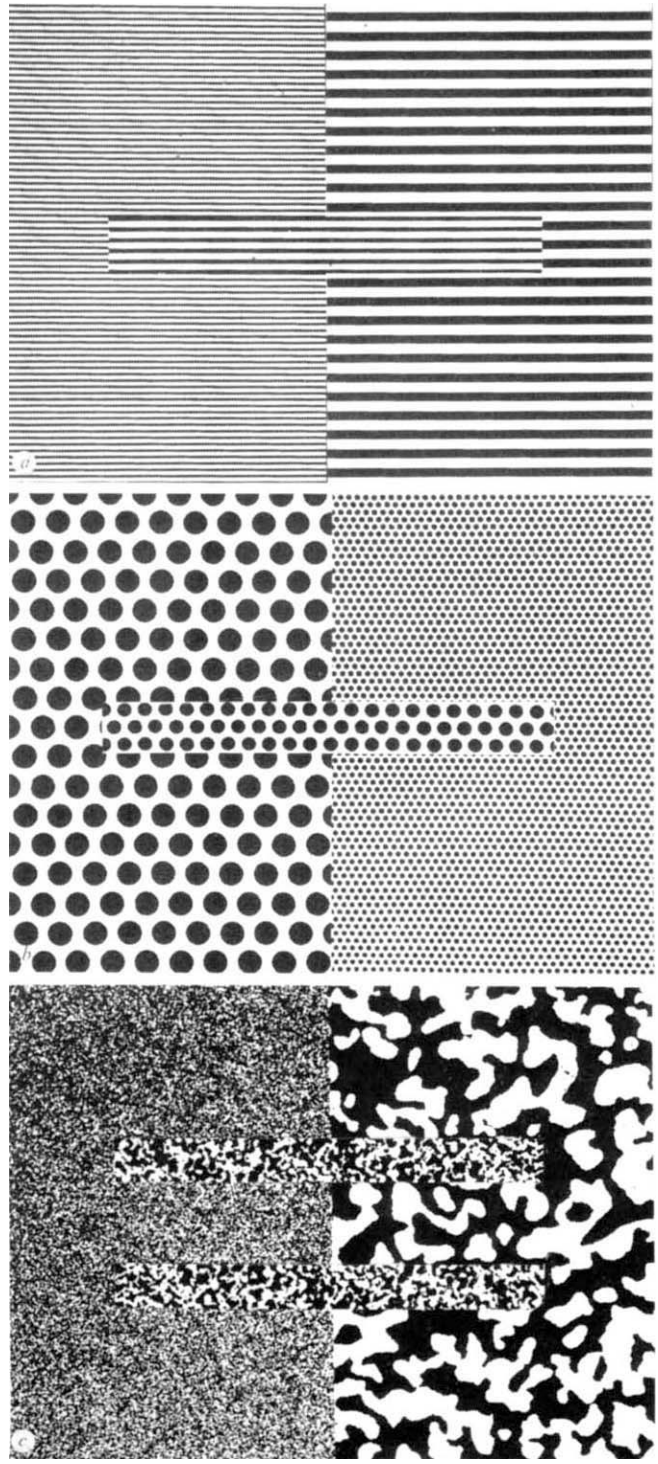

Fig. 5 Simultaneous contrast of density of texture. Moving a dividing line over the test strip has analogous effects in each case. Note that (*c*) has two identical half strips lying in opposite directions for comparison.

contrast does occur, and obeys laws closely analogous to those of brightness contrast; and (b) such phenomena are not peculiar to stimuli with well-defined spatially periodic and oriented components. In both cases, the contrast seen is enhanced if a thin black dividing line (such as a piece of wire) is placed along the vertical mid-line of the figure. If the line is moved to and fro it "draws" the area of magnified or minified texture density with it.

The contrast can be further enhanced by moving the whole figure up and down while the eye is held stationary. This suggests that the neural channels involved (like many feature-sensitive units already identified physiologically) are more responsive to moving than to stationary retinal images.

If the central "test strip" of one of these figures is presented to one eye and the remainder to the other, it is possible with practice to combine the images dichoptically. No significant contrast effect is then observed. This suggests that the abstraction of texture density takes place at a relatively early stage in the neural processing of retinal signals, and that the lateral inhibitory mechanisms presumably responsible for these contrast enhancements are located mainly in the uniocular systems before binocular fusion.

In summary, it seems from these experiments that the visual system may have channels that signal local density of texture, and interact to enhance local gradients of texture density, in ways somewhat analogous to the channels that are sensitive to retinal illumination and its gradients. Such "texture" channels would not require to be "space-frequency tuned" like those postulated by Campbell and Robson[5]. They might, however, play a part in the "binocular perception of depth without geometrical cues" described recently by Fiorentini and Maffei[6], who found that changes in contrast in one eye could produce similar effects to changes in spatial periodicity. This, like the effects described here, would be readily understandable if the channels concerned respond monotonically to density of texture elements over a certain range. Some geniculate cells recently discovered[7] seem to have properties of this general kind.

I thank MRC and SRC for support.

D. M. MacKay

Research Department of Communication,
University of Keele,
Staffordshire ST5 5BG

Received June 1; revised August 9, 1973.

1 Ratliff, F., *Mach Bands* (Holden-Day, San Francisco, California, 1965).
2 O'Brien, V., *J. opt. Soc. Am.*, **48**, 112 (1958).
3 Gibson, J. J., *The Perception of the Visual World* (Houghton, Boston, Mass., 1950).
4 MacKay, D. M., *J. gen. Psychol.*, **72**, 181 (1965).
5 Campbell, F. W., and Robson, J. G., *J. Physiol. Lond.*, **197**, 551 (1968).
6 Fiorentini, Adriana, and Maffei, L., *Vision Res.*, **11**, 1299 (1971).
7 Levick, W. R., Cleland, B. G., and Dubin, M. W., *Invest. Ophthalmol.*, **11**, 302 (1972).

Transcellular Strands of Cytoplasm in Sieve Tubes of Squash

The mechanism of long-distance phloem translocation is the subject of several hypotheses based on different concepts of structure and function in sieve tubes[1]. One of us (R. T.)[2–4] has proposed that transcellular strands of cytoplasm, continuous from one sieve element to the next through the sieve pores, provide a basis for the development of the physical force required for movement and pathways for translocation. The hypothetical model of a transcellular strand[5] consists of closely packed filaments of phloem filament (PF)-protein which form a tubular boundary enclosing cytoplasmic particles and a substructure of one or more tubules parallel with the outer boundary and formed from endoplasmic membranes. The

Fig. 1 A longitudinal section (18 μm thick) of a sieve tube viewed in the Nomarski microscope and showing parallel strands of cytoplasm, one of which (⊣⊢) is easily followed through the sieve pore. The bar represents 10 μm.

number of tubules in each strand depends on the diameter of the sieve pores filled by a single strand. Should a conformational change[6] occur in the outer boundary and cause a constriction which travelled as a wave in response to the propagation of electrical impulses of regular periodicity, this peristaltic pumping action could impel solution through the enclosed subtubules.

Aikman and Anderson's theoretical analysis[7] shows that the capacity and energy requirements of the strand system are consistent with measurements obtained from physiological experiments, but recent reviews[1,8–10] question the evidence of transcellular strands in sieve elements and a number of research workers[11–17] are convinced these structures do not exist. Their main criticisms are that evidence in favour of transcellular strands is sparse and is largely from light micrographs of fresh hand sections and that electron microscopy of the sieve elements has failed to provide evidence of highly organized transcellular strands. Lee *et al.*[18] did not see transcellular strands when they used the differential diffraction microscope (Nomarski) to observe sieve tubes of *Heracleum mantegazzianum* which were in narrow bands displaced from surrounding tissues with both ends attached to a petiole. In a study of freeze-etched sieve tubes Johnson[19] reports transcellular strands. He presents evidence of parallel groups of filaments at sieve pores and in the lumina of sieve elements, but contrary to the model described above he found no membranes.

Here observations of transcellular strands, obtained from cryostat sections in transmitted light[20,21], are extended using the