Table 1 Colour Rivalry in Gratings of Opponent Colours

	1 Black/white	2 Blue/green	3 Yellow/red	4 Green/yellow	5 Blue/red	6 Green/red	7 Blue/yellow
F. W. C.	12.8±1.0	12.8±0.6	20.6±1.4	23.4±1.4	21.7±1.2	33.3±0.7	35.7±1.6
J. A.	6.8±0.7	18.4±0.9	21.0±0.4	19.1±0.4	20.9±0.6	24.1±0.7	22.4±0.6
J. P. J. R.	12.2±0.6	14.7±0.8	16.4±0.4	20.0±0.9	19.8±1.4	27.7±1.5	33.3±1.2
J. M.	4.8±0.4	13.2±0.9	20.7±1.0	19.8±0.8	22.9±0.8	23.4±1.1	27.6±1.3
Mean	9.1±2.0	14.8±1.3	19.7±1.1	20.6±1.0	21.3±0.7	27.1±2.3	29.8±3.0

Results are for four subjects: mean ± s.e.

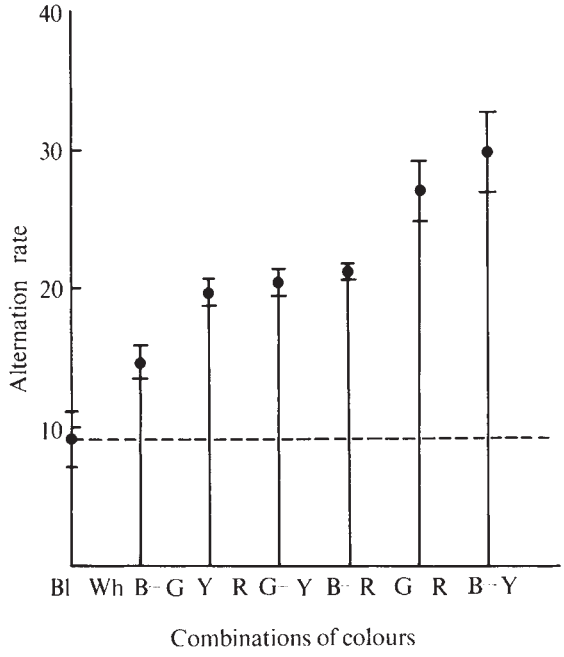

Fig. 1 The height of each line indicates the mean rate of alternation for each colour combination. The bars indicate ±1 s.e.

The luminance of the gratings did not seem to be critical provided that it was comfortably within the photopic range. For each colour combination the gratings were matched for apparent contrast; the contrast was approximately 0.3. The observer was asked to record each time there was a change from one grating dominating to the other. This rate of rivalry was measured for 1 min for each combination of colours. Nine 1-min runs were recorded for each combination in a quasi-random sequence and the mean and its s.e. calculated for each combination (Table 1). The pooled means of these results are shown at the foot of Table 1.

For crossed black and white gratings the mean rivalry rate was 9.1 changes per min (column 1). For all four subjects the rivalry rate for crossed green/red or blue/yellow gratings was much higher, giving means of 27.1 and 29.8 (columns 6 and 7). The rivalry rates for other colour combinations (columns 2 to 5) were intermediate between the black/white and green/red or blue/yellow results.

These results can be better assessed by inspecting Fig. 1. Here the pooled means ±1 s.e. are displayed. A dotted line is drawn through the mean rivalry rate for black/white gratings, below this line rivalry must be due only to the difference in orientation between the gratings. The additional rivalry caused by colour differences is shown by the height above the dotted line. The rates for green/red and blue/yellow are significantly greater than for any other combination.

Binocular rivalry thus depends not only upon the relative orientation but also the colour of the sine gratings. The differences in rivalry rates for different colour combinations cannot be due to accommodation or chromatic aberration for presbyopic and atropinized observers show the same magnitude of rivalry as observers with normal accommodation.

Nor can the difference be due to the absolute difference in wavelength of the pairs of filters used, for if this were the case the blue/red combination (wavelength difference 166 nm [column 5]) should rival more than the blue/yellow combination (wavelength difference 101 nm [column 7]) and this is not so for any observer; in fact the reverse is found. Further, the difference in wavelength for the green/yellow combination is 49 nm, for the yellow/red combination 65 nm and for the blue/red combination 166 nm yet the rivalry rates for these three observations are not significantly different from one another (Fig. 1).

It seems likely therefore that monocular rivalry involves colour opponent mechanisms in human vision and the results are thus evidence for colour neurones in man which operate on a green-red, blue-yellow opponent system. Because the effect also depends on the orientation of the gratings these colour selective neurones must be as central, or more central, than the first orientationally selective neurones[2,4].

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Spatial Frequency Selectivity of a Visual Tilt Illusion

ONE of the most consistent findings in neurophysiology[1,2] and psychophysics[3] has been that, in both human and animal visual systems, there exist neural mechanisms tuned to the orientation of a stimulus. It has been suggested that the selectivity of these orientation-sensitive detectors is sharpened by inhibitory interaction between them[4,5], and that illusions and distortions of apparent orientation occur as a consequence of that interaction[5–8].

There are strong indications that "channels" selective for orientation are also selective for a fairly narrow band of spatial frequencies[9,10]. I have now investigated the visual tilt illusion[5] in a new format which provides the first evidence that, in man, orientation-specific inhibition operates between channels that have similar optimal spatial frequencies, and declines as the difference in frequency increases.

The stimulus display is shown in Fig. 1. It was presented against a dim background, for 0.5 s every 2 s during each

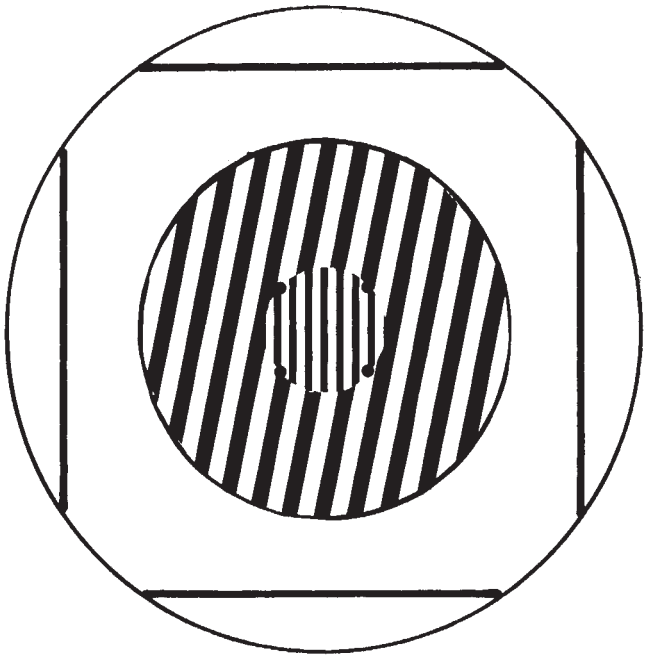

Fig. 1 The display as seen by the observer. The centre grating was 1.5 degrees in diameter with contrast=0.35, and the surrounding grating was 4.5 degrees in diameter, with contrast about 0.8. The dark horizontal and vertical lines surrounding the gratings provided the orientation reference. These reference lines were 5 min wide and their mid-points were 1 degree from the boundary of the outer grating. Four red spots, optically superimposed on the circumference of the centre grating, acted as a stimulus for accommodation when the display itself was off, but were not visible when it was on. All gratings in the experiment were sinusoidal photographs (though shown above, for convenience, as square waves). The mean luminance of each part of the display was 12 cd m^{-2}.

trial, to prevent the build-up of spatial-adaptation effects[9]. Each subject viewed the display with his left eye, without artificial pupil, and with his head supported by chin and temple rests. He was instructed to adjust the orientation of the gratings (whose relative angle was constant during a trial) until the centre grating appeared to be parallel to the fixed vertical reference lines (see Fig. 1). Use of a "subjective vertical" criterion was discouraged, to rule out Gibsonian "normalization" effects[11], but eye movements were allowed. Each setting of the motor-driven display took 15–30 s. Before each trial the display was offset by 10–15 degrees, alternately clockwise and anti-clockwise from the vertical.

For each run of five trials, the spatial frequency of the surround (2.5, 5, or 10 c per degree) and the angle between the gratings (+10, 0 or −10 degrees) were held constant, while the spatial frequency of the centre grating was varied in ascending or descending steps. The angle between the gratings was changed after each run, and the surrounding spatial frequency was changed after every three runs. The order of the different conditions was randomized within and between sessions.

Result were obtained from two male students who did not know the purpose of the experiment. In the control condition (0 degrees between the gratings) neither subject showed any significant response bias as a function of the spatial frequency of centre or surround gratings. Only for subject J. W. was there a small anti-clockwise bias of all control settings, with a mean shift of 0.6 degrees from true vertical. With ±10 degrees between the gratings, however, the subjects' settings indicated that, as expected, the apparent orientation of the test grating was biased away from that of the surround. The extent of this induced-tilt effect is shown in Fig. 2 (*a* and *b*). The illusion has been plotted as half the difference between mean settings made in the +10, and in the −10 degree conditions. This procedure eliminated the small baseline errors mentioned above, and also smoothed out any left-right asymmetries in the data.

For both 5 and 10 c per degree surrounds the tilt effect was maximum when the spatial frequencies of the test and surround gratings were equal. For the 2.5 c per degree surround, however, the curve peaked at a test frequency of 5 c per degree. An extra condition for subject H. G., with 1.25 c per degree surround, confirmed this low-frequency anomaly. Analysis of variance on the data of Fig. 2 (excluding the 1.25 c per degree condition) showed no significant difference between the subjects, but significant effects of test frequency, and of surround frequency (both with $P<0.01$), and a significant interaction of test frequency with surround frequency ($P<0.05$).

These results are very similar to those found for spatial-frequency specific after-effects[9]. In the case of after-effects with adapting frequencies greater than 3–4 c per degree, threshold elevation and the spatial-frequency shift are tuned to the adapting frequency, but with lower adapting frequencies the effects are tuned around 3–4 c per degree, with progressively lower amplitude. Similarly, in this experiment, results with 2.5 and 1.25 c per degree surrounds appear to be attenuated versions of the 5 c per degree curve. This is illustrated in Fig. 2*c*, where data averaged over the two subjects have been replotted as percentages of the peak value for each curve, against a normalized spatial-frequency axis, on which the test frequency is expressed in octaves, relative to the test frequency at which the maximum occurred. Also shown are data confirming the frequency-specific tilt effect with 5 and 10 c per degree surrounds, averaged over three other subjects for whom centre and surround contrasts were reduced by a factor of four, and display was continuous during a trial which took about 5 s. The results, therefore, did not depend upon having high contrast or flashing stimuli.

It thus seems that spatial-frequency selective channels[9,12] are operative in this simultaneously induced tilt illusion. If a channel with a particular optimal orientation is inhibited

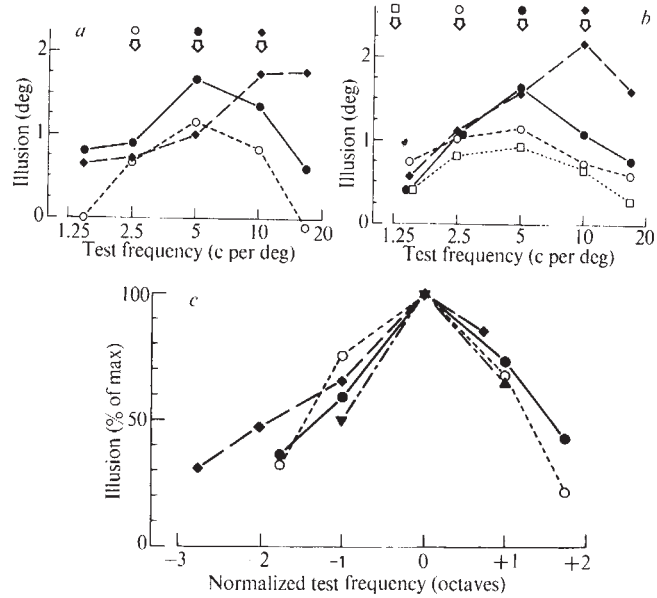

Fig. 2 *a*, Amount of illusion plotted as a function of test spatial frequency. Symbols denote surround frequency: 2.5 c per degree (○), 5 c per degree (●), 10 c per degree (◆). Arrows indicate where the peak of each curve would lie if the illusion were spatial frequency specific for all values of surround frequency. Each point was based on sixteen trials. Subject: J. W. *b*, As for *a*, but including data with a surrounding grating of 1.25 c per degree (□). Subject: H. G. *c*, Data from *a* and *b* averaged, and re-scaled so that each curve is superimposed at 100% (see text). The illusion has very similar tuning characteristics for all surround frequencies. Also shown are similar results from three other subjects, as described in the text: 5 c per degree surround (▲), 10 c per degree surround (▼). Other symbols as in *a*.

only by channels with the same or nearby orientations, then tilt contrast is predicted when spatially adjacent stimuli differ in orientation by a suitable amount[5]. The spatial-frequency specific tilt effect obtained here implies that such orientation-selective inhibition operates maximally between channels with similar frequency selectivities, and hardly at all between those tuned two octaves apart.

Blakemore and Tobin[13] recently found complex units which were inhibited by gratings at or near the preferred orientation, placed outside the conventional receptive field. Bishop *et al.*[11] have shown that simple cells are inhibited by lines tilted away from the preferred orientation, even when the line is strictly confined to the discharge centre of the receptive field. The function of such feature-specific inhibition[15] may be to enhance, or even produce[16], the selectivity of visual neurones along important stimulus dimensions. In systems of neurones possessing a degree of wired-in specificity, the development of inhibition between neighbouring neurones would be an economical method of sharpening the selectivity of the units, provided that the dimensions for which the units were selective was topologically mapped in the cortex[17]. Just such a precise spatial organization of orientation-selective cells exists in the monkey's striate cortex. Oblique penetrations of the microelectrode revealed ordered arrays of units, with the axis of each successive receptive field rotated by about 10 degrees from that of the previous unit[1].

There is thus strong physiological support now for the inhibitory explanation of tilt illusions[5]. My results raise the possibility that spatial-frequency channels are similarly organized in the human brain such that physically adjacent channels respond best to neighbouring frequencies, and that their frequency selectivity is enhanced by mutual inhibition. Such a system could overcome the problem of having rather coarse spatial tuning of units at earlier levels in the visual pathway[18,19].

In view of recent reports that the tilt after-effect does not depend on spatial frequency[20,21], the finding of a simultaneous tilt illusion selective for spatial frequency supports the proposal[22] that there is an inhibitory process in the spatial frequency domain which is different from the mechanism of adaptation to prolonged stimulation.

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Steroid Hormone Production by Pig Blastocysts

A LONG-STANDING problem in reproductive biology is that of the maternal recognition of pregnancy, the mechanism by which the developing conceptus signals its presence to the mother. An essential requirement for the establishment and maintenance of pregnancy is that the normal ovarian cycle should be arrested and the activity of the corpus luteum prolonged. In the sheep and pig, the recognition signal has been transmitted even before the embryonic tissue becomes intimately attached to the uterine epithelium and is therefore clearly distinct from implantation. In species such as the pig the blastocyst, while it remains free in the uterine lumen, may produce some substance that is capable of diffusing into uterine "milk" and across the lumen, exerting a local effect on the uterine tissues.

Huff and Eik-Nes[1] showed that rabbit blastocysts contain enzyme systems capable of synthesizing cholesterol and pregnenolone from acetate and of metabolizing various steroid substances. Other workers[2,3] have found a significant concentration of progesterone and smaller amounts of 20α-dihydroprogesterone and 17α-hydroxyprogesterone in the blastocyst and blastocoel fluid. Seamark and Lutwak-Mann[3] suggested that the progestagens in blastocysts "are not necessarily synthesized by the embryos, but may be conveyed to them by the endometrial secretion". Work in this laboratory has demonstrated the presence of unconjugated oestrogens as well as progesterone in pig blastocysts, and so we decided to investigate the possibility that steroid hormones are produced by the blastocyst of this species. Such local steroid production may well have an essential role in the material recognition of pregnancy or in the process of implantation.

Some time before attachment to the endometrium, the blastocysts of the pig elongate enormously and occupy a large proportion of the length of the uterine horn. This elongation[4] coincides closely with the time of the recognition of pregnancy[5]. About 3 d later, tenuous attachment occurs at isolated points along the length of the blastocyst, but the definitive attachment by interlocking microvilli is not seen until about 18 d after copulation (p.c.)[6]. Blastocysts were recovered by flushing the uterine horns with a large volume of sterile medium. The concentration of total unconjugated oestrogens[7] and progesterone[8,9] was determined by radioimmunoassay. The antiserum used for the estimation of total unconjugated oestrogens (SLC 6X) had a high cross-reactivity with oestradiol-17β and oestrone[10], whereas that used for progesterone (S49 No. 6) reacted predominantly with progesterone, 17α-hydroxyprogesterone and 11-deoxycortisol[9]. Steroids were extracted from the blastocyst tissue with diethyl ether in the oestrogen assay and petroleum ether in the progesterone assay and they were not subjected to a separation procedure before radioimmunoassay.

Uterine flushings were centrifuged (2,000 r.p.m. for 5 min) and the weight of the residue, consisting predominantly of fragmented blastocysts, was taken as the original wet weight of the blastocysts. The concentration of total unconjugated oestrogens at days 14 and 17 was 2.23 and 0.86 ng g^{-1} wet tissue, respectively, and that of progesterone at days 14 and 16 was 6.8 and 9.8 ng g^{-1} wet tissue. During this period of pregnancy, the peripheral plasma concentration of progesterone is about 10 to 20 ng ml^{-1} whereas that of total unconjugated oestrogens is less than 0.1 ng ml^{-1}.

To determine whether the blastocyst was actively synthesizing steroids or accumulating steroids derived from the mother, blastocyst tissue was incubated with appropriate precursors. Blastocysts (0.2 to 0.5 g wet weight), endometrial tissue (0.2 g) and uterine washings (3.0 ml) were incubated separately under sterile conditions in either a total volume of 4 ml of Medium 199 or Brinster's medium[11] for 3 h at 37° C and gassed with 95% oxygen:5% CO_2. The incubation medium was prepared with a recently purified ^{3}H-labelled