Edge computation in human vision: 
anisotropy in the combining of oriented filters

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Received 17 October 1994, in revised form 24 January 1995

Abstract. Above threshold, two superimposed sinusoidal gratings of the same spatial frequency (eg 1 cycle deg⁻¹) and equal contrasts, and with orientations balanced around vertical, usually look like a compound structure containing vertical and horizontal edges. However, at large plaid angles (ie large differences between component orientations) and low plaid contrasts there is a tendency for the stimulus to appear as two overlapping gratings (component structure) with obliquely oriented edges. These dependencies of perceived spatial structure in plaids are incompatible with an edge-coding scheme that uses only circular filters to compute zero-crossings, but instead support the idea that different oriented filters can (compound percept) or cannot (component percept) be combined before edges are represented. Here, further evidence is presented in support of this hypothesis. Two-component plaid stimuli had plaid angles of 45° or 90°, and a range of plaid orientations (ie a range of orientations around which the plaid components were balanced). Observers indicated whether each stimulus was perceived as a compound or component structure for a range of plaid contrasts. In addition to angle and contrast effects, perceived spatial structure was also found to depend on plaid orientation: compound structures were perceived more often when the plaid components were balanced around the cardinal axes of the retina. It is suggested that the principles governing the combination of oriented-filter outputs might be learnt during the development of the visual system by using a Hebb-type rule: coactivated filters are more likely to combine their outputs when activated on future occasions. Given the prominence of vertical and horizontal orientations in a carpentered environment, this simple rule promotes a network that combines filters balanced around cardinal axes more readily than oblique axes, in agreement with the results.

1 Introduction
1.1 Aims
The main aim in this paper is to report a spatial anisotropy found in the perceived spatial structure of two-component, static plaid stimuli. This effect is interpreted in the context of the edge-coding scheme proposed by Georgeson (1992), where the outputs of oriented spatial filters are selectively combined prior to the coding of edge location by the extraction of zero-crossings (or their equivalents).

1.2 Edge coding in human vision
The locations of rapid spatial changes in the luminance profile of a stimulus generally correspond to useful features in the viewed scene (eg object boundaries and shadows). It is widely believed that one of the early requirements of both human and machine vision is the explicit coding of these luminance edges (eg Marr and Hildreth 1980; Haralick 1984; Watt and Morgan 1985; Canny 1986; Spacek 1986; Torre and Poggio 1986; Morrone and Owens 1987; Burr and Morrone 1992; Georgeson 1992; Malik and Perona 1992; Morrone and Burr 1993). For example, by generating a spatial edge map, a meaningful and compressed code is made available for use by later vision modules, such as those responsible for performing object recognition (see Marr 1982).
1.3 Perceived orientation in plaids is not given by orientation-labelled linear filters

One common view in the experimental-vision literature is that oriented luminance contours are coded by the distribution of activity across orientation-labelled linear filters (e.g., Coltheart 1971; Carpenter and Blakemore 1973). However, it is fairly straightforward to generate stimuli whose perceived contours cannot be signalled by such filters. For example, Meese and Georgeson (1991) found that at contrasts above a few percent, a static plaid with two 1 cycle deg⁻¹ components oriented at ±45° from vertical looks like a blurred checkerboard consisting of horizontal and vertical edges, despite having no Fourier energy at those orientations (cf DeValois et al. 1979). Current estimates of orientation half-bandwidths of early spatial filters are about 30° at 1 cycle deg⁻¹ (e.g., Phillips and Wilson 1984), so the most responsive filters for this plaid stimulus have the same preferred orientations as the stimulus components themselves (i.e., ±45°) and not 0° and 90°, as is required if the filter orientations are to accord with perceived orientation.

This psychophysical evidence implies the existence of a nonlinear stage of visual processing. One candidate stage is the coding of zero-crossing (ZC) locations in the linearly filtered output of the stimulus. Indeed, a search for ZCs in the second derivative of the luminance profile has been suggested as an edge-coding algorithm by several authors (e.g., Marr et al. 1979; Marr and Hildreth 1980; Torre and Poggio 1986; Clark 1989). A convenient front end for this scheme is (circular) Laplacian-of-a-Gaussian (linear) filtering (Marr and Hildreth 1980; Hildreth 1983; Watt 1988). Indeed, this idea is biologically plausible (Marr and Hildreth 1980), because the Mexican-hat-shaped sensitivity profile of a Laplacian-of-a-Gaussian (LoG) operator is well approximated by a difference-of-Gaussians (DoG) operator, which in turn bears a close resemblance to the receptive-field profiles of retinal ganglion cells (Rodieck 1965; Enroth-Cugell and Robson 1966; though see Young 1987 for alternative receptive-field models of the retina).

In support of this view, Georgeson (1992) used a sketch-selection technique and showed that naive observers readily associate the perceived spatial structure of test plaids with outline sketches depicting the appropriate ZCs after LoG filtering. The plaids were composed of two or three gratings with identical spatial frequency and contrast but differing orientation and phase. This result supports the earlier finding (Georgeson 1990; Meese and Georgeson 1991) with ±45° plaids (see above), where the compound checkerboard structure is also given by the spatial distribution of ZCs across the LoG filtered stimulus.

1.4 Evidence against the use of circular filters for edge coding in human vision

Despite the apparent success of the circular-filter model (e.g., Marr and Hildreth 1980; Watt 1988), recent evidence suggests that circular symmetric filters (e.g., LoG filters) are not used in human vision by the putative edge-coding process (Georgeson 1990, 1992; Meese and Georgeson 1991, 1992; Georgeson and Meese 1992). Rather, it has been argued that the outputs of oriented spatial filters (Blakemore and Campbell 1969; Phillips and Wilson 1984) are combined before searching for ZCs, or their equivalents (Georgeson 1992). Crucial to this conclusion is the finding that forward masking or adaptation to one of the components in a two-component plaid produces asymmetric distortions in the resultant perceived structure: the percept is similar to that produced by physically lowering the contrast of one of the components (Georgeson 1992). These orientation-dependent distortions of perceived spatial structure cannot be mediated by nonoriented (i.e., circular) spatial filters (Georgeson 1992).

Georgeson and Meese (1992) and Meese and Georgeson (submitted) extended this work by adapting to a vertical test grating and viewing a ±45°, 1 cycle deg⁻¹ test plaid. At high test contrasts, the usual tessellating squares were no longer seen,
but, rather, the stimulus appeared as tessellating rectangles stretched in a direction orthogonal to that of the adapter. This two-dimensional version of the tilt aftereffect produces a percept similar to that found when the plaid components are physically tilted further apart. Again, such a distortion could not arise from circular filtering.

1.5 Oriented-filter combination takes place before edge coding

The above findings imply that the outputs of oriented spatial filters can be combined prior to the extraction of ZCs or their equivalents (Georgeson 1990, 1992). A schematic account is shown in figure 1 (adapted from Georgeson 1992). The model depicts a series of processing stages with receptive fields shown here at just a single spatial location. Spatial filtering takes place at the first stage of the model, and is performed by a two-dimensional array of cosine filters, tuned for spatial frequency and orientation (Campbell and Robson 1968; Blakemore and Campbell 1969; Blakemore and Sutton 1969; Movshon and Blakemore 1973; Wilson et al 1983; Phillips and Wilson 1984). The second stage is a ‘grouping matrix’, where the outputs of the spatial filters are selectively switched into one or more ‘feature groups’ (Georgeson 1990, 1994). After linear summation of the filter outputs, edges are coded by searching for ZCs within each ‘feature group’, and then finally superimposed to produce a global feature map.

**Figure 1.** The grouping model, adapted from Georgeson (1992). The outputs of spatially tuned filters are selectively combined (grouping matrix) to produce between 1 and \( n \) feature groups. Within each feature group, the filter outputs are linearly summed and then examined by a nonlinear ZC-extraction process. The ZCs indicate the presence of edge features within each feature group. The superposition of the feature maps from each feature group produces a global feature map that describes the viewed scene. The architecture shown here allows a wide variety of filters (e.g. circular filters, and oriented filters of different orientation and spatial frequency bandwidths) to be synthesised from a much smaller set of basis filters. In the discussion we suggest that the rules governing stimulus-driven filter synthesis may be determined by visual experience of the environment during development.
1.5.1 Segmentation in plaid perception. Some progress has been made towards understanding the rules governing the grouping matrix, which can be otherwise considered as segmentation in the (piecewise) Fourier domain. For instance, it seems that the switching is not always ‘hard’; under certain conditions the output of a single filter may be shared between two ‘feature groups’ (Meese and Georgeson 1992). Moreover, there are several conditions under which common grouping of filter outputs does not seem to occur (Georgeson 1990, 1994; Meese and Georgeson 1991, 1992). In particular, Meese and Georgeson (1991) found two-component plaid perception to be nonlinear with contrast: at low contrasts observers tend to choose sketches depicting superimposed ZCs of the individual components, while at higher contrasts they tend to choose a ‘compound’ sketch, where component combination takes place before ZC extraction (see figures 2a and 2b, section 3.1 for example sketches). A similar change in spatial structure is found when the plaid angle (defined as the smaller of the two angles between the components) is manipulated: more component-type responses are observed at broader plaid angles (Meese and Georgeson 1991).

1.6 A further investigation into the perceived spatial structure of plaids

The main purpose in this paper was to explore further the grouping rules shown in figure 1 by extending the parametric study of Meese and Georgeson (1991). Here, we manipulated the orientation around which the components in a two-component plaid were balanced. Thus, the test plaids were characterised by (i) their plaid angle (see figure 3, section 3.1) and (ii) the orientation that bisects the plaid angle, which we term plaid orientation (see figure 3). Like Meese and Georgeson (1991), we also used a two-sketch paradigm, where the sketches depicted compound and component spatial structures for two-component plaids (see figure 2).

If an anisotropy in the perception of two-component plaids were found, then this would stand as further evidence against the use of isotropic (ie circular) filters in edge coding by the human visual system. In the main experiments reported here (experiments 1, 2, and 3), we found a pronounced effect of plaid orientation on response type for plaid angles of both 45° and 90°—more compound responses were made for plaids whose orientation was vertical or horizontal than for obliquely oriented plaids. In experiment 1 this effect is shown in a well-practised observer, in experiment 2 the effect is replicated in a group of naive observers, and in experiment 3 it is shown that the effect is tied to retinal coordinates as opposed to a gravitational frame of reference. Last, we show in experiment 4 that the results of experiments 1 and 3 cannot be understood in terms of an anisotropy for grating detection. In section 7 we argue that the anisotropy for plaid perception is not related to the individual response characteristics of spatial filters and account for our results in terms of a network that learns to combine the outputs of filters that tend to be coactivated.

2 Equipment and general conditions

Stimuli were generated by means of an Inisfree Picasso Image Synthesizer with a frame rate of 242 Hz under the experimental control of an Acorn Archimedes 440 computer and displayed on a Tektronix 608 oscilloscope with green phosphor (P31). The sinusoidal stimulus components were produced by modulating the z-axis of the oscilloscope at a spatial frequency determined by the manual setting of vernier dials on the fascia of the Picasso. Plaid stimuli consisted of two superimposed sinusoidal components, whereas grating stimuli consisted of a single component. Component orientation was under computer control and was achieved by rotating the raster scan to the desired orientation. Plaid stimuli were generated by temporally interleaving two stimulus components, which required the raster scan to be rotated between frames. It took the software two frames to calculate the required rotation and instruct the hardware, giving
a picture refresh rate for two-component plaids of 60 Hz. Component contrast was also under computer control and in the plaid-perception experiments was determined each trial by a method of constant stimuli, whereas in a grating-detection experiment, it was adjusted by a randomly interleaved staircase (see experiment 4).

Contrast is reported in dB, and is equal to $20 \log_{10} C$ where $C$ is the Michelson contrast of a single sinusoidal component in percent. In plaid stimuli, the contrasts of the two components were always equal.

The display field had a mean luminance of 17 cd m$^{-2}$, and routine calibration of the contrast and luminance linearity of the display was performed by using a Photo-dyne digital photometer. The display was found to be practically linear and stable up to a contrast of 50%, thus setting an upper limit for the contrast levels used in our experiments.

For both plaid perception and grating detection the diameter of the display field was adjusted to accommodate 5 full cycles of one of the stimulus components. Thus, for spatial frequencies of 1, 2, 4, and 8 cycles deg$^{-1}$, the field diameters were 5, 2.5, 1.25, and 0.625 deg, respectively. The immediate surround of the circular display window was black. Experiments were performed in a darkened room at a viewing distance of either 114 cm or 228 cm. Subjects with normal or corrected-to-normal vision viewed the display binocularly with natural pupils and the aid of a chin-and-forehead rest. Stimulus presentation was 500 ms and the phase of the stimulus was selected randomly on each trial.

3 Experiment 1: An orientation effect for plaid perception over a range of spatial frequencies

3.1 Method

3.1.1 Equipment and response procedure. Sited to the left of the display monitor and at approximately the same height was a computer graphics screen 24 cm wide and 19 cm tall which was matched approximately in colour and luminance to the stimulus display. A pair of computer-generated sketches were displayed on the graphics screen and could be selected by moving a mouse pointer into a box containing the required sketch. The response box into which each sketch was placed was chosen randomly each trial. When the required sketch was selected, the response was recorded by clicking a mouse button. Each sketch was matched in size to the circular stimulus on the display monitor. For each trial, one of the sketches was the pattern of ZCs produced by the output of a circular filter (or equivalently, the sum of oriented filters) applied to the plaid stimulus (compound sketch/response), while the other was the pattern of ZCs produced by the individual components (component sketch/response). Figure 2 shows two pairs of response sketches: one for a plaid angle of 90°, oriented at 0° (top row), and one for a plaid angle of 45°, oriented at 45° (bottom row). Figures 2a and 2c show the compound-response sketches and figures 2b and 2d show the component-response sketches. The response sketches were turned on immediately after the offset of the stimulus, and turned off again as soon as the observer made a response.

3.1.2 Stimuli and experimental procedure. A single session consisted of eleven contiguous blocks of stimulus presentations (one practice block plus ten test blocks), where a single block contained five component contrast levels and five orientations (twenty-five trials in all) in a random order. A practice block was included to give subjects time to establish their response criteria, and in subsequent analyses the data from these blocks were always discarded. Previous work (Meese and Georgeson 1991) has shown that it is important to include several levels of contrast in plaid-perception experiments in order to avoid ceiling and floor effects.
The stimulus was always a two-component plaid whose components had common spatial frequency and contrast. The plaid angle was either 45° or 90°, but was fixed within a single session. For the condition with 45° plaid angle, the five plaid orientations were 0°, 22.5°, 45°, 67.5°, and 90°. For the 90° plaid angle, the plaid orientations were 0°, 11.25°, 22.5°, 33.75°, and 45°. Examples of these ten plaids are shown in figure 3. In experiment 1, the plaid orientations were also counterbalanced around vertical (i.e. mirror reversed). For example, if a plaid with angle of 45° and component contrast of \(c\) dB was presented at an orientation of 22.5° in one block, it was presented at an orientation of −22.5° in the next block, then back at 22.5°, and so on. The initial direction of orientation [clockwise (+) or anticlockwise (−)] was chosen randomly for each of the twenty-five stimuli in the first block. This method ensured that spatial channels at all orientations in steps of 22.5° for the 45° angle plaid and steps of 11.25° for the 90° angle plaid were stimulated over the duration of the experiment. However, in later experiments, this counterbalancing procedure was abandoned in favour of always presenting the stimuli in the clockwise orientation (see experiment 2).

For component spatial frequencies of 1 and 2 cycles deg\(^{-1}\), the minimum component contrast was 6 dB, while for spatial frequencies of 4 and 8 cycles deg\(^{-1}\), the minimum component contrast was 8 dB. Note that for each spatial frequency these contrast levels are well above TSM’s detection thresholds for a single component (see experiment 4, figure 10). For all conditions, the spacing between contrast levels was 5 dB.

Sessions of different spatial frequencies and plaid angles were interleaved in a pseudorandom order, and at least two sessions were performed for each condition. This gave at least twenty trials at each contrast level for each plaid orientation, plaid angle, and spatial frequency.

The full set of conditions defined in experiment 1 was completed by a single well-practised observer who was one of the authors (TSM).

Figure 2. Two pairs of response sketches: (a) and (b) are ZC sketches for a two-component plaid stimulus oriented at 0°, with a plaid angle of 90°; (c) and (d) are for a plaid angle of 45°, oriented at 45°. (a) and (c) are compound response sketches, and are generated by grouping the components prior to ZC extraction; (b) and (d) are component sketches, and are generated by superimposing the ZCs of the individual components (see figure 1). The stimuli that correspond to these sketch pairs are shown in figure 3, at top right and middle left, respectively.
3.2 Results

A preliminary inspection of the data supported our expectation that there would be no systematic difference between the mirror-reversed conditions (clockwise and anticlockwise orientations). Therefore, data were collapsed over mirror-reversed trials for each plaid angle and spatial frequency.

Figure 4 shows the percentage of component-type responses as a function of component contrast for a plaid angle of 45° and a spatial frequency of 1 cycle deg⁻¹ for each of the five different conditions of plaid orientation. For each condition, the percentage of component responses decreases as the contrast is increased, confirming the contrast effect reported elsewhere (Meese and Georgeson 1991, submitted). Plots of this kind were generated for each spatial frequency and at both plaid angles, and probit analysis (Finney 1971) was used to calculate the contrast level ($P50$) at which responses were split evenly between the two response categories. These $P50$ levels...
are plotted relative to grating-detection thresholds (measured in experiment 4) in figure 5. Thus, 0 dB indicates grating detection threshold, and each increase of 6 dB indicates a doubling of this threshold.

In the top panel of figure 5 (plaid angle 90°), the data from the 4 cycle deg\(^{-1}\) condition are omitted because in general they showed little evidence of the contrast effect and so yield rather meaningless results from probit analysis. In the lower panel of figure 5 (plaid angle 45°) probit analysis was not possible at plaid orientations of 0° and 90° for a spatial frequency of 2 cycles deg\(^{-1}\) because insufficient component-type responses were made. The corresponding data points have been set arbitrarily to -12 dB.

![Figure 4](image)

**Figure 4.** Percentage of component responses made by TSM at five different plaid orientations as a function of component contrast. The plaid angle was 45° and the component spatial frequency was 1 cycle deg\(^{-1}\).

![Figure 5](image)

**Figure 5.** The contrast levels at which responses were split evenly between the two response categories (P50) plotted relative to grating-detection thresholds as a function of plaid orientation (degrees from vertical) for different spatial frequencies. (0 dB represents grating-detection threshold). Where larger than the data symbols, error bars show ±1 SE derived by probit analysis (see text for details). Plaid angles were 90° (top panel) and 45° (bottom panel).
For spatial frequencies of 1, 2, and 8 cycles deg$^{-1}$ at plaid angles of both 45° and 90°, there is a clear effect of plaid orientation on the perceived spatial structure of two component plaids (see figure 5). In general, the P50 level is greater for oblique plaid orientations (eg 45°) than for vertical and horizontal orientations (0° and 90°). This is illustrated by the overall positive slope of the data in the top panel of figure 5 (plaid angle 90°) and the inverted-U form of the data in the lower panel of figure 5 (plaid angle 45°). On the other hand, the data from the 90°-plaid-angle condition are not monotonic, but instead dip back down after 33.75°. We return to this point in section 7.

Figure 6 shows an alternative presentation of the data: results are collapsed across contrast and plotted as the percentage of component-type responses for each condition. In both panels of figure 6 (plaid angle 90° and plaid angle 45°), an orientation effect is now also revealed for the 4 cycles deg$^{-1}$ condition, though for a plaid angle of 45° it is rather small. Note however, that the shapes of each individual data set in figure 6 are remarkably similar to those in figure 5. As this method of data presentation does not rely on the existence of a contrast effect, and as this experiment revealed that the contrast effect is not found for all conditions, we adopt this method of data presentation for the remainder of the paper.

![Figure 6. Percentage of component responses made by TSM at four spatial frequencies as a function of plaid orientation (in degrees from vertical) for plaid angles of 90° (top panel) and 45° (bottom panel). Data are collapsed over contrast.](image)

4 Experiment 2: An orientation effect for plaid perception with naive observers

4.1 Introduction and method

The aim in this experiment was to see whether TSM's results generalised to a group of naive subjects. The methods were the same as for experiment 1, with a few minor differences outlined below.

In previous work on the contrast and angle effects (Meese 1993), individual differences were found for the contrast level at which responses switched from component-type to compound-type (ie P50). Moreover, some subjects continued to make component responses over the whole range of contrast levels used [up to 20%
component contrast (26 dB)]. Therefore, in order to avoid a ceiling effect in this experiment, data collection was terminated prematurely for those observers who made more than 90% component responses in their first session with a plaid stimulus of 1 cycle deg$^{-1}$ and 45° plaid angle. This screening procedure removed two of the twelve naive subjects who took part in the study. All ten of the remaining subjects took part in plaid-angle conditions of both 45° and 90° with a plaid spatial frequency of 1 cycle deg$^{-1}$, and the first seven of these subjects also took part in a condition where the plaid spatial frequency was 4 cycles deg$^{-1}$ for both plaid angles. The minimum contrast level for all observers and all conditions was 8 dB. All observers performed at least two sessions for each condition.

4.1.1 Orientation counterbalancing. For plaid orientations of 0° and 90° and a plaid angle of 45°, together with plaid orientations of 0° and 45° and a plaid angle of 90°, mirror reversal has no effect on spatial structure. This introduces a bias in the number of presentations of these stimuli. To investigate whether such a bias might account for the plaid-orientation effect, three out of ten of the naive observers undertook the experiment with no orientation counterbalancing. No obvious differences were found between this group and the remaining observers who undertook the experiment with counterbalancing. This was supported by additional data collected from TSM (not shown), who repeated the whole of experiment 1 without counterbalancing. Consequently, all ten naive observers were treated as a single group in the subsequent statistical analyses.

4.2 Results
Consider first the results for a spatial frequency of 1 cycle deg$^{-1}$ (figure 7). The general trends for each subject were remarkably similar, despite quite large individual differences (not shown) in the average percentage of component responses collapsed across conditions (eg individual averages varied from around 30% to around 90%). In figure 7 the group results are plotted as the mean percentage of component responses as functions of plaid orientation, and are for a plaid angle of 45° (open symbols) and a plaid angle of 90° (filled symbols). The main findings of experiment 1 are clearly replicated by naive observers: the data for a plaid angle of 45° have an inverted U-form, and those for a plaid angle of 90° have a positive slope.

A two-way ANOVA (contrast and plaid orientation) revealed a highly significant main effect for plaid orientation, for both a plaid angle of 45° ($F_{4,144} = 11.77$,
$p < 0.0005$) and a plaid angle of $90^\circ$ ($F_{4,144} = 5.56, p = 0.001$). Significant main effects were also found for plaid contrast for each plaid angle [$F_{4,144} = 12.81$, $p < 0.0005$ (plaid angle $45^\circ$); $F_{4,144} = 2.89, p = 0.036$ (plaid angle $90^\circ$)], once again confirming the contrast effect (Meese and Georgeson 1991).

Figure 7 also illustrates the angle effect (Meese and Georgeson 1991): more component responses were made for the $90^\circ$-plaid-angle condition than for the $45^\circ$-plaid-angle condition.

The results for the 4 cycles deg$^{-1}$ condition are shown in figure 8. Here a two-way ANOVA revealed no main effect for plaid orientation at either plaid angle, though there was a highly significant main effect for contrast at a plaid angle of $45^\circ$ ($F_{4,96} = 7.07, p = 0.001$) but not for a plaid angle of $90^\circ$ ($F_{4,96} = 0.51, p = 0.729$). The absence of the contrast effect in this one condition is similar to that found for TSM in the previous experiment. However, unlike the naive observers, TSM also showed a systematic effect of plaid orientation at 4 cycles deg$^{-1}$, though recall that this effect was rather weak at a plaid angle of $45^\circ$ (see figure 6, lower panel). We return to these data for 4 cycles deg$^{-1}$ in section 7.

At neither spatial frequency were there significant interactions between plaid orientation and contrast at either plaid angle.

**Figure 8.** Mean percentage of component responses collapsed over contrast and made by seven naive observers, plotted as a function of plaid orientation (in degrees from vertical) for plaids with component spatial frequencies of 4 cycles deg$^{-1}$. There is no systematic effect of plaid orientation on perceived spatial structure for plaid angles of either $90^\circ$ (filled squares) or $45^\circ$ (open squares). However, more component responses are made in the $90^\circ$-plaid-angle condition than in the $45^\circ$-plaid angle condition.

**5 Experiment 3: The plaid-orientation effect is tied to retinal coordinates not external coordinates**

5.1 Introduction and method

The aim in this experiment was to discover whether the orientation effect revealed in experiments 1 and 2 is tied to a retinal coordinate system or an external coordinate system (eg that defined by gravity). To achieve this, experiment 1 was repeated by TSM with a plaid spatial frequency of 1 cycle deg$^{-1}$ and plaid angle of $45^\circ$ in two different conditions of head orientation. In an oblique head condition, the head rest was tilted at $45^\circ$, and in a vertical head condition the head rest was vertical ($0^\circ$). In both conditions, the head rest was firm enough to hold the head at the required orientation to within a few degrees of accuracy. Plaids were presented in the usual way at five orientations relative to the orientation of the observer’s head and no orientation counterbalancing was employed (see section 4.1.1). TSM performed two
sessions for each condition of head orientation, giving one hundred responses for each orientation tested within each condition.

5.2 Results and discussion
Figure 9 shows the results for both the oblique head condition and the vertical head condition. The percentage of component responses is plotted as a function of plaid orientation, relative to the orientation of the observer's head. The two sets of results are remarkably similar when plotted this way, demonstrating that the plaid-orientation effect depends on the orientation of the stimulus on the observer's retinas and not on an external coordinate system. A comparison of these results in terms of P50 contrast levels (not shown) revealed a similar result.

6 Experiment 4: Oriented-grating detection
6.1 Oblique effects in vision
Oblique effects are well documented in the literature (e.g., see Appelle 1972 and Essock 1980). One possibility is that the lower sensitivity of the visual system to oblique gratings relative to vertical and horizontal gratings (Campbell et al. 1966; Kelly 1975; Camisa et al. 1977; Blake and Holopigian 1985; Kitterle and Kaye 1985) might in some way underlie the orientation effect for plaid perception. To consider this further, we also measured contrast-detection thresholds for gratings over a range of orientations and for the same range of spatial frequencies used in the plaid-perception experiments (1 cycle deg\(^{-1}\)–8 cycles deg\(^{-1}\)).

6.2 Methods
Detection thresholds were measured by means of a two-interval forced-choice paradigm, with a staircase configured to converge on the 79.4% correct point (Wetherill and Levitt 1965). Each trial consisted of two 500 ms intervals, one of which contained a sinusoidal grating while the other was a blank field of mean luminance. Each interval was indicated by the onset of an audible tone and had equal probability of containing the grating. The observer's task was to identify which of the two intervals contained the grating by pressing one of two buttons. The initial contrast step size used for the staircase was 4 dB, but was reduced to 2 dB after the first staircase reversal. Thresholds were determined by calculating the mean of the staircase reversals (Wetherill and Chen 1964) between and including the third and the twelfth reversals. The initial stimulus level for all orientations was set to be a few dB above a best guess of threshold for each spatial frequency tested.
Within a given session, thresholds were measured simultaneously for five different grating orientations (0°, 22.5°, 45°, 67.5°, and 90°), by means of five randomly interleaved staircases. This whole procedure was repeated for spatial frequencies of 1, 2, 4, and 8 cycles deg⁻¹.

The experiment was performed by the same observer who took part in experiments 1 and 3 (TSM). This observer was well practised in two-interval forced-choice detection experiments over a variety of spatial frequencies and orientations.

6.3 Results and discussion

Grating-detection thresholds are shown in figure 10 as a function of grating orientation, and for spatial frequencies of 1, 2, 4, and 8 cycles deg⁻¹. The results for the 8 cycles deg⁻¹ condition are means of three experimental sessions, while those for the other three conditions are from a single session. Although gratings of different spatial frequencies produced different detection thresholds, there is no systematic effect of orientation. The absence of an oblique effect for TSM is perhaps surprising, particularly at a high spatial frequency (8 cycles deg⁻¹), where an effect is usually found (Campbell et al 1966; Camisa et al 1977; Kitterle and Kaye 1985). On the other hand, individual differences in the magnitude of the oblique effect were found by Kitterle and Kaye (1985).

As no oblique effect was found, mean grating-detection thresholds were calculated for each spatial frequency by combining the data from each of the five different orientations. These thresholds are shown on the far right of figure 10 and replicate earlier findings for the same observer (Meese 1993).¹ Note that it is the mean grating-detection thresholds shown in figure 10 that were used as a reference for the P50 data shown in figure 5.

![Figure 10](image)

Figure 10. Mean two-interval forced-choice grating-detection thresholds (79.4% correct point determined by a converging staircase) for four different spatial frequencies as a function of grating orientation. As orientation had no obvious effect at any of the four frequencies, the data symbols at the right of the figure show the mean detection threshold for each frequency collapsed across orientation.

¹ Of passing interest is the observation that the usual roll off of the contrast sensitivity function at low spatial frequencies (eg Blakemore and Campbell 1969) was not found. At least in part, this is probably because in our own grating-detection experiments, the size of the display was adjusted so that the same number of grating cycles was displayed for each spatial frequency (five full cycles: also see Howell and Hess 1978). In comparison with an experiment where the field size remained fixed (eg Blakemore and Campbell 1969), this would lower the detection thresholds for the higher spatial frequencies owing to a reduction in spatial probability summation (Howell and Hess 1978; Legge 1978; Robson and Graham 1981).
The results of this experiment indicate that, for TSM at least, an account of the orientation effect for plaid perception cannot be couched in terms of different channel-response thresholds.

7 General discussion
The experiments reported in this paper were designed to investigate whether the perceived spatial structure of two-component plaids is invariant with plaid orientation. We found that this was not the case. Since circular filters could not produce an orientation anisotropy (by definition), our results stand as further evidence against the direct use of circular filters in edge coding.

7.1 Contrast and angle effects for plaid perception
Overall, both the angle and the contrast effects found by Meese and Georgeson (1991) were replicated here for most conditions. However, peculiar to a spatial frequency of 4 cycles deg\(^{-1}\), the contrast effect was not found for either TSM (plaid angle of 90°) or a group of naive observers (plaid angles of 45° and 90°). In this respect, it remains unclear why the results for this spatial frequency are different from the others.

7.2 An orientation effect for the perception of two-component plaids
The main new finding reported here is that of an orientation effect for plaid perception: two-component plaids oriented either vertically or horizontally appear as a compound structure more often than those oriented obliquely. We interpret this as an anisotropy in the visual system's preference for combining the outputs of oriented filters (see figure 1); filters balanced around cardinal axes are combined more readily than those balanced around oblique axes.\(^{(2)}\) At a spatial frequency of 1 cycle deg\(^{-1}\), this effect was found for both a group of ten naive observers (experiment 2) and a single practised observer, TSM (experiment 1), at plaid angles of both 45° and 90°. Furthermore, the effect is tied to retinal coordinates not external coordinates (experiment 3), suggesting that the cause of the effect may be at an early stage of processing (Essock 1980).

7.2.1 The orientation effect for plaid perception does not depend on individual filter characteristics. One important observation is that the orientation effect for plaid perception is not related to the individual response characteristics (eg bandwidth, threshold, contrast nonlinearity) of the filters most sensitive to the individual plaid components. To see this, consider a pair of 45° angle plaids oriented at 0° and 90°. A schematic illustration is shown in figure 11, where the plaid components are grouped by the open ellipses and the component orientations are indicated by the four crossed lines. Now consider the component orientations of a second pair of 45°

\(^{(2)}\)The following alternative account is based on a suggestion made by an anonymous referee. First assume that edge features are coded by either one or the other of two different sets of oriented spatial filters. The first set are band-pass linear filters and, accordingly, are sensitive to Fourier orientation. The second set are nonlinear, and sensitive to the orientations of the ZCs in the compound stimuli. Further suppose that these two sets of filters are in competition with one another, and that the winning set codes perceived orientation. If the nonlinear filters are relatively underrepresented at oblique orientations, and so less competitive at those orientations, then the compound percept will occur less readily for obliquely oriented plaids. Although this is in agreement with the orientation effect reported in this paper, the scheme fits less readily with the perceptions of other plaid stimuli that we have used. For example, when plaid stimuli are made from three sine-phase components that are evenly spaced in the orientation domain, the stimulus components never seem to dominate but, rather, the stimulus appears as a compound structure made from tessellating triangles (eg Georgeson 1992). These triangles contain obliquely oriented contours, which, according to the above hypothesis, should give way to a component percept. They do not.
angle plaids, oriented at $+45^\circ$ and $-45^\circ$. In figure 11 these are grouped by the filled ellipses; the component orientations for this second pair of plaids are identical to those of the first pair of plaids. However, the results of experiments 1 and 2 showed that more component-type responses were made for the second pair than for the first pair. This means that the plaid-orientation effect does not depend upon the individual component orientations but, rather, implies that it is plaid orientation per se that is the important variable.

There are two obvious ways in which this dependency could be realised. First, it could be that the characteristics of filters at and orthogonal to the plaid orientation are in some way involved in the perceptual processing of the stimulus. Given that estimates of the orientation half bandwidths of visual mechanisms are moderately broad—between about $15^\circ$ and $35^\circ$ depending on the spatial and temporal frequency of the test pattern (Phillips and Wilson 1984; Blake and Holopigian 1985; Harvey and Doan 1990; Snowden 1992), it is likely that there will be some activity in the filters at these orientations. A second possibility is that perhaps what matters is the activation of specific pairs (or groups) of filters or channels: the orientation effect reflects an anisotropy in postfilter processing.

We consider the first of these alternatives in the next subsection, and the second in the remainder of section 7.

**Figure 11.** The orientation effect for plaid perception is not dependent on the characteristics of linear filters most sensitive to the plaid components. The filled ellipses group together the orientations of the four filters most sensitive to the components in a pair of plaids oriented at $45^\circ$ and $-45^\circ$, and with a plaid angle of $45^\circ$. The open ellipses group together the orientations of the four filters most sensitive to the components in a similar pair of plaids oriented at $0^\circ$ and $90^\circ$. Although the results of experiments 1 and 2 show that more component responses were made for the first pair of plaids, each plaid pair maximally activates the same four spatial filters.

7.2.2 Filter bandwidth and detection thresholds. In considering the first hypothesis we might ask whether there are any known anisotropies that could account for our result. One well-known visual anisotropy is that found in grating-detection studies. However, it seems highly unlikely that an anisotropy in the detection thresholds of filters at and orthogonal to the plaid orientation can account for our results. For example, TSM showed no anisotropy for grating detection in experiment 4, but did show an anisotropy for plaid perception in experiments 1 and 3. Furthermore, when an oblique effect is found for grating detection (eg Campbell et al 1966; Blake and Holopigian 1985; Kitterle and Kaye 1985), then it is typically found at high spatial frequencies.
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(eg >4 cycles deg⁻¹), but not at 1 cycle deg⁻¹, where the orientation effect for plaid perception was found amongst naive observers (experiment 2, see figure 7).

Perhaps what matters is the orientation bandwidth of the filters at the plaid orientation. Those studying this issue either have found no anisotropy (Phillips and Wilson 1984; Blake and Hologpian 1985) or have estimated oblique bandwidths to be broader than those at vertical and horizontal (Campbell and Kulikowski 1966; Rose and Blakemore 1974; Harvey and Doan 1990). However, if this is indeed the case, then oblique channels would be sensitive to a broader range of component orientations than those orientated at vertical and horizontal. This suggests that perceptual combination should occur most readily for obliquely oriented plaids. Our results show exactly the opposite, suggesting that an anisotropy in the orientation bandwidths of early visual mechanisms does not underlie the plaid-orientation effect.

7.2.3 Environmental statistics may underlie the plaid-orientation effect. The experimental results presented here suggest that oriented-filter combination occurs more readily when the stimulus components are balanced around vertical and horizontal than when they are balanced around oblique orientations. From the spectral analyses of photographs, Switkes et al (1978) found that both indoor and outdoor carpentered worlds contained markedly more spectral power at vertical and horizontal orientations than at oblique orientations, presumably reflecting the predominance of vertical and horizontal edges in buildings, furniture, and so forth. Furthermore, there is ample evidence that the development of the visual system continues after birth (eg Braddick et al 1986; Morrone and Burr 1986) and is dependent upon the environment (eg Blakemore and Cooper 1970; Wiesel 1982). Now, suppose that the likelihood of filter combination is related to a Hebb-type learning process that takes place during development. That is to say, a set of filters that respond at the same time as one another are more likely to combine their outputs thereafter. Given the observations of Switkes et al (1978), this simple proposition readily accounts for the orientation effect for plaid perception. For example, suppose that most of the length of a vertical or horizontal edge occurs away from T-junctions, cross points, and corners. These edges will result in activity in vertical (or horizontal) filters, but not simultaneously in horizontal (or vertical) filters. Therefore, the outputs of filters at vertical and horizontal orientations will tend not to be encouraged to combine and so will be processed independently. On the other hand, filters whose orientations are close to vertical or horizontal (ie those filters balanced around vertical and horizontal orientations), will also respond to vertical and horizontal edges, and so the outputs of these filters will tend to combine. Note that this account also explains the angle effect for plaid perception: spatial filters at closer orientations are more likely to be coactivated. However, in order to explain the contrast effect—filter combination occurs less readily at low contrasts—it is also necessary to assume a contrast-related nonlinearity in the combination process.

Another finding of Switkes et al (1978) was that for carpentered environments the prominence of vertical and horizontal power over oblique power was most marked at low spatial frequencies. This could explain why the orientation effect was found only for the naive observers at low spatial frequencies (ie 1 cycle deg⁻¹) but not at a higher spatial frequency (ie 4 cycles deg⁻¹), though this does not explain why an orientation effect was found for TSM at 4 cycles deg⁻¹ and 8 cycles deg⁻¹ in some conditions.

(3) Note that for cosine-phase filters, this activity will take place away from the edge at some distance that is dependent upon the size of the receptive field.

(4) Switkes et al compared the orientation spectra of spatial frequency ranges of 1–25 cycles deg⁻¹ and 5–25 cycles deg⁻¹.
Several others have also considered networks involving communication between oriented filters. For example, Heeger (1992) and Wilson and Humanski (1993) have proposed contrast-gain-control circuits that employ inhibitory feedback from groups of oriented filters, in order that individual simple cells (oriented filters) should maintain stimulus selectivity, despite having limited dynamic range. Closer to our own proposal, however, is that of Schillen and König (1991) (see also König and Schillen 1991), who used communication between filters at neighbouring orientations to demonstrate how the oscillatory responses of cortical cells (Eckhorn et al 1988; Gray and Singer 1989; Engel et al 1991; Kreiter and Singer 1992) may synchronise (group) their outputs in order to solve the 'binding' problem (von der Malsburg and Schneider 1986; Engel et al 1992; Singer 1993).

7.2.4 Can the grouping rules be modified through experience? So far, we have assumed that the learning process takes place only during development of the visual system. Such learning could involve both changes in synaptic weights and the pruning of synaptic connections (eg see Singer et al 1990). A further possibility is that once the architecture has been put in place, there may remain a degree of plasticity (achieved by changing the weights at synaptic connections, for example), allowing the system to self-calibrate, perhaps necessitated by changes in the environment, or within the system itself (eg cell death). Certainly, stimulus-specific learning (eg specific to orientation or size) has been found in grating-discrimination experiments (Fiorentini and Berardi 1981) and hyperacuity (Fahle and Adelman 1993; Saarinen and Levi 1995).

Before performing the experiments reported here, TSM had experienced several thousand trials of two-component plaid presentations during other experiments and software development. Most of these trials employed two-component stimuli of various plaid angles, balanced around a vertical orientation, or a plaid angle of 90°, oriented at 45°. If a learning process similar to that discussed above continues to operate into adult life then this might explain the idiosyncratic form of TSM's data for the 90° plaid angle—the data dip back down at a plaid orientation of 45° (see figure 4b) because TSM had had more experience with this stimulus, and so the corresponding filters (vertical and horizontal) learned to combine more readily. This issue remains to be addressed.

8 Summary and conclusions
The finding of an anisotropy in the perception of two-component plaids (experiments 1–3) stands as further evidence against the use of isotropic (ie circular) filters in edge coding by the human visual system. We found that plaids oriented along the cardinal retinal axes tend to be perceived as a compound structure more often than those oriented along oblique retinal axes. We considered this finding in the context of the filter-combination model proposed by Georgeson (1990, 1992).

We ruled out the possibility that the plaid-orientation effect was somehow related to the oblique effect for grating detection because no oblique effect was found for TSM, though that subject showed a clear anisotropy for plaid perception. We also rejected the hypothesis that the anisotropy is in some way related to the characteristics of the individual filters that are most sensitive to the plaid components (see section 7.2.1) and concluded instead that the anisotropy is related to plaid orientation per se. Specific pairs (or groups) of coactivated filters may be processed differently from other pairs (or groups). For example, the processing of the output of a filter oriented at 22.5° depends upon the relative activity of other filters—if additional activity is centred at –22.5°, then filter combination is likely, whereas if additional activity is centred at 67.5°, then filter combination is less likely. Indeed, we account for the plaid-orientation effect by proposing that during development, a Hebb-type learning process causes...
filters whose outputs are coactivated to be more likely to combine their outputs on future occasions. Effectively, this results in the synthesis of a pair of oriented linear filters that operate in horizontal and vertical directions (also see Foster and Ward 1991a, 1991b), reflecting the dominance of these orientations in carpentered environments (Switkes et al 1978).

Acknowledgments. We would like to thank Mark Georgeson for numerous helpful discussions during the period in which this work was completed. This work was supported in part by a studentship from Bristol University awarded to Tim Meese.

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