Abstract. Above threshold, two superimposed sinusoidal gratings of the same spatial frequency (eg 1 cycle deg$^{-1}$), of equal moderate contrast (eg $C_1 = C_2 = 6\%$), and with orientations of $\pm45^\circ$, usually look like a compound structure containing vertical and horizontal edges (ie a blurred checkerboard). These feature orientations are very different from the dominant filter orientations in a wavelet-type (eg simple-cell) transform of the stimulus, and so present a serious challenge to conventional models of orientation coding based on labelled linear filters. Previous experiments on perceived structure in static plaids have led to the view that the outputs of tuned spatial filters are combined in a stimulus-dependent way, before features such as edges are extracted. Here an adaptation paradigm was used to investigate the cross-channel interactions that appear to underlie the spatial-filter-combination process. Reported are two aftereffects of selective adaptation: (i) adaptation to a 1 cycle deg$^{-1}$ plaid whose component orientations are intermediate to those in a 1 cycle deg$^{-1}$ test plaid 'breaks' perceptual combination of the components in the test plaid; (ii) adapting to a 3 cycles deg$^{-1}$ plaid whose component orientations match those in a 1 cycle deg$^{-1}$ test plaid facilitates perceptual combination of the components in the test plaid. The results are taken as evidence that spatial channels remote from those most responsive to a test plaid play a crucial role in determining whether the test plaid segments or coheres perceptually.

1 Introduction
1.1 Filter combination and segmentation in human vision
There is now abundant evidence that the human visual system contains a set of quasi-linear, orientation-tuned and spatial-frequency-tuned filters whose receptive fields tile the two-dimensional visual array (eg Campbell and Robson 1968; Blackmore and Campbell 1969; Watson and Robson 1981; Wilson et al 1983; Daugman 1984; Phillips and Wilson 1984; Harvey and Doan 1990). Although several authors have suggested that these filters may be responsible for encoding spatial attributes of the viewed scene (eg local orientation and size), there are at least two lines of evidence indicating that this is not so. First, the outputs of these filters are not treated independently in experiments requiring the discrimination of orientation and size (Olzak and Thomas 1991, 1992) and possibly phase (Meese 1995), suggesting that the filters cannot be accessed directly (also see Burbeck 1987; Bowne 1990; He and Nakayama 1994). Second, it is fairly straightforward to generate stimuli whose feature orientations are very different from the dominant filter orientations in a wavelet-type (eg simple-cell) transform of the stimulus (eg Meese and Georgeson 1996). For example, a two-component 1 cycle deg$^{-1}$ static plaid with component orientations at $\pm45^\circ$ (a 'standard plaid') usually appears as a blurred checkerboard with vertical and horizontal edges (see figure 1), yet, despite moderately broad orientation bandwidths at this frequency (Phillips and Wilson 1984; Snowden 1992), the most-responsive filters will be those tuned to $\pm45^\circ$. This simple observation seriously challenges conventional models of orientation coding based on labelled linear filters (eg Carpenter and Blakemore 1973).
Figure 1. A 'standard plaid' made from the superposition of a pair of sinusoidal gratings of the same contrast and spatial frequency and component orientations of ±45°. This stimulus typically looks like a blurred checkerboard with vertical and horizontal edges.

Experiments on perceived spatial structure in static plaids (Georgeson 1990, 1992, 1994, 1996; Meese and Georgeson 1991, 1992, 1996; Meese and Freeman 1995; Georgeson and Meese, 1996) have led to the view that the perceptual combination of sinusoidal components reflects the linear summation of the outputs of spatially tuned filters prior to the explicit representation of features such as edges, perhaps encoded by zero crossings (ZC; Marr and Hildreth 1980; Torre and Poggio 1986). Good evidence for this is the structural distortion found after orientation-selective adaptation (Georgeson 1992, 1996; Meese and Georgeson 1996). For example, Georgeson (1992) found that after adaptation to a sinusoidal grating whose orientation was matched to one of the components in a test plaid (like that in figure 1), the spatial structure of the plaid no longer resembled a checkerboard but, rather, appeared as a set of oblique squiggles: it was as though the contrast had been lowered for the test component co-oriented with the adapter. This asymmetric distortion could not occur if the structure of the test pattern were carried only by isotropic filters (eg Marr and Hildreth 1980; Watt 1988), but is exactly what is predicted if ZCs (or their equivalents) are extracted after the linear summation of adaptable oriented filters. In this latter case, adaptation attenuates the contrast of the test component aligned with the adapter, so producing the asymmetric distortion.

Several studies have revealed that this filter-combination process is not hard wired but stimulus dependent (Meese and Georgeson 1991, 1996; Meese 1993; Georgeson 1994, 1996; Meese and Freeman 1995; see Georgeson and Meese 1996 for a review). For example, although variability has been found across subjects (Meese 1993), the following findings broadly hold for two-component plaids at 1 cycle deg⁻¹. (i) At moderate to high contrasts, perceptual combination of components usually occurs (ie checkerboard-like percept), but at low contrasts the stimulus appears as two overlapping gratings, suggesting that filter combination has not taken place (the 'contrast effect'; figure 2a). (ii) At low contrasts, components combine less readily when the component orientations are far apart (the 'angle effect'; figure 2b). (iii) At low contrasts, components combine less readily when their orientations are balanced around oblique rather than cardinal axes of the retinae (the 'orientation effect'; figure 2c). (iv) A most compelling example of segmentation in plaids is what we shall call the 'switching effect' (figure 2d). When one, or optionally both, of the components in a standard plaid is made more like a square wave by adding a low contrast 3 cycle deg⁻¹ component,
the usual checkerboard percept switches to one of tessellating diamonds (Georgeson 1994; Georgeson and Meese 1996; Meese and Georgeson, in preparation). This result suggests that after addition of the third harmonic, the underlying filters are no longer being combined across different orientations.

Thus, in all four of these plaid effects, the manipulation of a single stimulus parameter can result in the plaid components being processed together, as a single compound stimulus, or independently, as two overlapping gratings (figure 2).

Last, our observations with plaids bear some resemblance to a recent report on the perception of textured patterns. According to the properties of two different superimposed textures, they can either combine to make a single compound texture or segment into two overlying textures (Watanabe and Cavanagh 1992).

---

**Figure 2.** Binding (checkerboard-like percept) and segmentation (components, or gingham-like percept) in static plaids. Binding occurs more readily at high stimulus contrasts (a), narrow plaid angles (b), and vertical plaid orientations (c). If one of the components of a plaid is made more like a square wave by adding a low-contrast third harmonic, then the percept switches from one of a checkerboard to tessellating diamonds (d). Note that in (b) and (c), the left-hand icon at the top of the figure should be stretched vertically. In (c) the right hand icon should first be stretched vertically, and then rotated clockwise through 45°.
1.2 Aims
The experiments outlined above have shown that the components in static plaid patterns can be segmented perceptually into two or more overlying structures, or combined to make a single structure. The process responsible for choosing between these alternatives clearly requires communication across orientation (e.g., the angle effect) and spatial frequency (e.g., the switching effect). The aim in the experiments reported here was to investigate further these lines of communication. Observers adapted to two-component plaids over a range of spatial frequencies and orientations and used a sketch-selection technique (Georgeson 1992; Meese and Freeman 1995; Meese and Georgeson 1996) to indicate whether a two-component 1 cycle deg⁻¹ test plaid appeared as two overlapping gratings or as a single, compound, checkerboard-like pattern. We found adaptation conditions that both improved and impaired the perceptual combination of components in the test plaid and we interpret these results as evidence for communication paths between spatial channels used in the perceptual processing of visual stimuli.

2 Methods
2.1 Equipment and stimulus generation
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 were generated under computer control by temporarily 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.

In experiment 3, where the two components of the adapting plaid were made from square waves with missing fundamentals (MF plaids), both of the two Picasso oscillator channels were used simultaneously. One of the channels produced square-wave modulations of the z-axis, while the other produced a sinusoidal modulation of the z-axis at the fundamental frequency of the square wave, but in antiphase. The contrast of the sinusoid was matched to that of the square-wave fundamental (i.e., it was 4/π greater than the Michelson contrast of the square wave). This had the effect of nulling the square-wave fundamental, leaving only the odd harmonics.

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 Photodyne digital photometer. The display was found to be practically linear and stable up to a contrast of 50%, considerably higher than the contrast range used in our experiments. Contrast was under computer control and was determined by a method of constant stimuli. Contrast is reported in both percent and dB (20 log₁₀C, where C is the Michelson contrast of a single sinusoidal component, expressed in percent).

Sited to the left of the plaid display 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, and was used for displaying the 'response sketches' (see section 2.3).

2.2 General conditions
Subjects had normal or corrected-to-normal vision and viewed the display binocularly with natural pupils and the aid of a chin-and-forehead rest from a viewing distance of 114 cm. The plaid display subtended 5 deg in diameter, and was surrounded by a circular black paper mask.
Each experimental session consisted of 5 min of adaptation to a plaid, followed by seventy 500 ms presentations of a test plaid interspersed with 10 s periods of top-up adaptation. There was an interstimulus interval of 500 ms between the offset of the adapter and the onset of the test plaid which was randomly selected from seven different contrast levels (ten presentations per contrast level). For all plaids, the two plaid components always had equal contrast and their orientations were 90° apart, at either 0° and 90°, or +45° and −45° (see individual experiments for more-precise descriptions of the adapting and test plaids).

Note that the brief stimulus presentations used in our experiments avoided spatial interference from retinal afterimages that, in conjunction with eye movements, can otherwise distort the perceived spatial structure of plaid patterns (Georgeson and Phillips 1980; Georgeson and 1984). To avoid the buildup of retinal afterimages during adaptation, the following 'jitter' routine was applied independently to each component of the adapter. Every 200 ms or 400 ms, selected at random, the phase of each component was translated through a phase angle selected randomly from between 90° and 270°. These random phase shifts continued for the duration of adaptation, allowing the components of the adapter to be presented always at their chosen contrast, but distributing their locations evenly over the two-dimensional phase space (Meese 1993).

2.3 Task and response procedure

Like in previous plaid-perception experiments (Georgeson 1992; Meese and Freeman 1995; Meese and Georgeson 1996), the observer's task was to respond to each test plaid by selecting which one of two different, low-contrast, computer-generated 'response sketches' was a better match for the perceived spatial structure of the test stimulus. The response sketches were displayed on the adjacent graphics screen and could be selected by pressing one of two mouse buttons (left/right). Each sketch was matched in size to the circular stimulus on the oscilloscope display. One of the sketches was generated by combining the two plaid components before searching for and marking ZCs. We refer to this as the compound sketch/response. The other sketch was generated by superimposing the pattern of ZCs found in the individual components and is referred to as the component sketch/response. Thus, these two sketches represent alternative spatial structures that might be perceived, according to whether the plaid components were combined or processed independently prior to the extraction of edge features by the visual system (Georgeson 1992).

Figure 3 shows the pair of response sketches used for a 1 cycle deg−1 test plaid with components oriented at 0° and 90° [(a) compound; (b) component].

![Figure 3](image-url)
3 Experiment 1: Adaptation can both improve and impair perceptual combination of plaid components

3.1 Method
This was the main experiment and was performed by two well-practised observers (TSM and MAG) and a naive observer (TCAF), all of whom were familiar with plaid stimuli and psychophysical experiments. For TSM and MAG, the test stimulus was a plaid with 1 cycle deg⁻¹ components oriented at 0° and 90° (ie similar to figure 1, but rotated through 45°). When this stimulus is fused perceptually, it looks like a blurred checkerboard, standing on one of its corners (see figure 3a). Seven component contrast levels were used ranging from 1.5 dB (1.2%) to 29.5 dB (9.4%) in steps of 3 dB. A preliminary experiment showed that both of the plaid components were reliably visible over this range (see Appendix).

There were three conditions of adaptation: (i) baseline condition—the adapter was a uniform, blank (0% contrast) screen of mean luminance; (ii) aligned condition—the adapter was a plaid with component orientations matched to those in the test plaid; and (iii) bisecting condition—the adapter was a plaid with both component orientations rotated through 45° relative to those in the test plaid, thus bisecting the angles between the test components. In the aligned and bisecting conditions, the adapter had a component contrast of 14 dB (5% contrast; 10% compound Michelson contrast) and the adapting-plaid spatial frequency was varied from 1 cycle deg⁻¹ to 8 cycles deg⁻¹ between sessions, though the full range was sampled by only one observer. Usually, for each adaptation condition, one session was performed at each spatial frequency, though several sessions were performed for the baseline condition. Sessions were performed in a pseudorandom order.

The naive observer (TCAF) performed only a limited selection of the conditions. Furthermore, because of known anisotropies in the perception of two-component plaids (Meese and Freeman 1995), TCAF performed this experiment with all the plaid stimuli and response sketches rotated through 45° relative to those given to TSM and MAG (eg for TCAF, the test components were at ±45°, like figure 1).

3.2 Results and discussion
As we have found previously (Meese and Freeman 1995; Meese and Georgeson 1996), fewer compound-type responses were usually made when the contrast of the test plaid was low (the contrast effect; see the appendix). This meant that for each adapting spatial frequency in each adaptation condition, we were able to use probit analysis (Finney 1971) to extract the contrast level (P50) at which the responses were split evenly between 'components' and 'compound' (see the appendix). This gives a measure of the tendency for two components to combine perceptually; if P50 is high, they do not combine readily. These contrast levels are shown for TSM in figure 4 and are plotted as a function of adapting spatial frequency. The open circles show the results from the baseline condition and serve as a reference for the other two conditions where two main aftereffects of adaptation were found.

In the bisecting condition (filled squares) when the adapting spatial frequency was 1 cycle deg⁻¹, the contrast level (P50) at which the compound sketch was selected in preference to the component sketch is markedly higher than in the baseline condition. In other words, in this condition adaptation induced a greater tendency to make component-type responses. In a previous experiment (Meese and Georgeson 1996), we found a similar aftereffect with adaptation to a grating whose orientation bisected the components in a test plaid.

In the aligned condition (filled triangles), we found a new aftereffect of adaptation tuned to 3 cycles deg⁻¹. Here, adaptation induced a greater preference for selecting the compound sketch, as shown by a reduction in the level of P50 relative to baseline
Filter combination and channel interactions

(see figure 4). In MAG’s data (not shown in figure 4), this aftereffect was so great that it was not possible to perform probit analysis. To overcome this problem the data were collapsed over contrast and expressed as the total percentage of component-type responses made for each condition (cf Meese and Freeman 1995). These results are shown in figure 5b, along with those replotted for TSM in figure 5a. A comparison between figure 4 and figure 5a shows similar trends for TSM, indicating that the method of presentation of the data does not seriously affect their interpretation. Furthermore, the main trends of MAG’s data are the same as for TSM, though the tuning functions are broader (note the difference in horizontal scale for the two subjects), and the peak aftereffect for the aligned adapter (open triangles) is shifted to the right a little.

Figure 6 shows the percentage of component-type responses made for each of the limited set of conditions performed by the naive observer (TCAF). The conditions were performed in the order shown from left to right and the baseline condition was performed twice (first and last). There is little difference between these two baseline

![Figure 4](image-url)  
**Figure 4.** Perceived spatial structure of a 1 cycle deg$^{-1}$ plaid with component orientations of 0° and 90°, after three different types of adaptation (different symbols). The ordinate shows contrast levels ($P_{50}$) at which the subject evenly split responses between component-type and compound-type sketches (figure 3). Results are for observer TSM and are plotted as a function of the spatial frequency of the adapter. Open symbols are results from a baseline condition, where the adapting stimulus was a blank uniform field of mean luminance. Filled symbols are for pattern-adaptation conditions, where the components of the adapting plaid were either at the same orientations as the test plaid (triangles) or both rotated through 45° relative to the test plaid (squares). Error bars show ±1 SE and were derived by probit analysis.

![Figure 5](image-url)  
**Figure 5.** Similar to figure 4, but the data were collapsed across contrast and expressed as the total percentage of component-type responses for each adapting spatial frequency. (a) Subject TSM; (b) subject MAG. Note the difference in horizontal scale for the two panels.
Figure 6. Percentage of component-type responses collapsed over contrast for TCAF. The conditions were performed in the order shown, from left to right. The test stimulus was a 1 cycle deg\(^{-1}\) plaid with component orientations of ±45°. 1F, 1 cycle deg\(^{-1}\); 3F, 3 cycles deg\(^{-1}\).

measures, indicating that there were no potentially confounding long-term effects of adaptation or repeated testing.

This observer clearly makes most component-type responses after adapting to a plaid whose component orientations bisect, and spatial frequencies match, those in the test plaid, and is similar to the first of the aftereffects described for TSM and MAG. This demonstrates that the aftereffect is not peculiar to test component orientations of only 0° and 90°—recall that for TCAF, the whole experiment was rotated through 45° relative to that performed by TSM and MAG.

However, TCAF’s results do not replicate the finding with the 3 cycles deg\(^{-1}\) aligned adapter. There are several reasons why this might be so. First, for TCAF, like MAG, the tuning function for this aftereffect may be at a higher spatial frequency than 3 cycles deg\(^{-1}\). Second, similar to other plaid perception experiments (Meese 1993; Meese and Freeman 1995), the presence of this effect may be subject to individual differences. Third, as the whole experiment was performed at a different orientation for TCAF, the failure to find an aftereffect for an aligned 3 cycles deg\(^{-1}\) adapter may reflect an anisotropy (though see experiments 2 and 3).

3.3 Conclusion

On the assumption that the selection of a compound or component response sketch (figure 3) indicates that oriented spatial filters are either perceptually bound or segmented (Georgeson 1992; Meese and Freeman 1995), the results of this experiment show that adaptation can influence the filter-combination process. More specifically, this experiment has revealed two main findings: (i) adapting at the same spatial frequency, but at orientations intermediate to those in a 1 cycle deg\(^{-1}\) test plaid, seriously inhibits filter combination in response to the test plaid; (ii) adapting to the same orientations as those in the test plaid, but at a higher spatial frequency—about 3 or 4 cycles deg\(^{-1}\)—strongly facilitates filter combination for the test plaid. Hereafter we will refer to the first of these findings as the bisecting component effect and the second as the aligned compound effect (see figure 9).

Subjectively, these aftereffects were extremely compelling. For example, in the aligned compound effect, not only did the plaid components cohere at lower stimulus contrasts, but the plaids also appeared less blurred and more checkerboard-like than usual. This led us to adopt the term ‘supersquare’ as a description of the percept. Indeed, contrary to the concerns of an anonymous reviewer, we are confident that these results do not reflect higher-order cognitive priming, but rather reveal cross-channel sensory interactions in the filter-combination process (Georgeson 1992). We return to this issue of priming in experiment 3.
4 Experiment 2: More evidence for the aligned compound effect

4.1 Introduction and method
In this experiment we tested three undergraduate subjects (SA9, SA10, SA11) who were psychophysically naive and unaware of the purpose in the experiments. These subjects were specifically chosen for this experiment because, unlike many other subjects we have tested, they had made almost entirely component-type responses in previous plaid-perception experiments. Thus, these subjects allowed a particularly strong test of the idea that adaptation can enhance filter combination (the aligned compound effect).

The experimental conditions were identical to those for TCAF in experiment 1 (ie the test stimulus had 1 cycle deg\(^{-1}\) components with orientations of ±45°), except that only two conditions were performed: a single baseline condition and a single aligned 3 cycles deg\(^{-1}\) condition.

4.2 Results and discussion
Figure 7 shows percentage of component-type responses collapsed over contrast for each of the naive observers. All three observers always selected the component sketch in the baseline condition, confirming previous observations for these particular subjects (Meese 1993). However, after adaptation, all three subjects showed a marked decrease in their percentage of component-type responses, hence a marked increase in compound responses. For two of the subjects (SA9 and SA11) compound-type responses increased from 0% to around 80% after adaptation. Two of the observers (SA10 and SA11) also showed an effect of contrast (not shown) on perceived plaid structure after adaptation. For these observers, probit analysis revealed P50s of 9.8 dB (SE = 1.46 dB) and 1.2 dB (SE = 2.7 dB) respectively. Taken together, these observations make it unlikely that observers were simply responding at chance in the adaptation condition but, rather, suggest that their perception of the test stimulus was genuinely changed from that of overlapping gratings to a compound, blurred checkerboard, by adapting to the aligned 3 cycles deg\(^{-1}\) plaid. Informal subjective reports by the subjects also confirmed this.

![Graph showing percentage of component-type responses](image)

Figure 7. Percentage of component-type responses collapsed over contrast for each of three naive observers (SA9, SA10, SA11). All three observers made 100% component-type responses in the baseline condition, but made considerably fewer component-type responses in the aligned 3 cycles deg\(^{-1}\) condition. The test stimulus was a 1 cycle deg\(^{-1}\) plaid with component orientations of ±45°.

(1) The plaid-perception experiments (Meese 1993) were similar to the experiments reported here, except that no adapting pattern was used and the orientations of the plaid components were varied between trials (also see Meese and Freeman 1995).
Last, the use of a test stimulus with component orientations of $\pm45^\circ$ shows that, like the bisecting component effect, the aligned compound effect is not peculiar to test component orientations of $0^\circ$ and $90^\circ$.

5 Experiment 3: The aligned compound effect depends on spatial-frequency content and not on the spatial appearance of the adapter

5.1 Introduction and method

Here we asked whether the aligned compound effect found in the previous two experiments depends on the spatial-frequency content of the 3 cycles deg$^{-1}$ adapter per se or the spatial appearance of the adapter. For example, it could be that filter combination takes place more readily for a 3 cycles deg$^{-1}$ stimulus than for a 1 cycle deg$^{-1}$ stimulus (see Meese and Freeman 1995), and that after adaptation to the 3 cycles deg$^{-1}$ plaid the perceptual experience of filter combination somehow transfers to the 1 cycle deg$^{-1}$ test plaid, by introducing response bias, for example. This is the priming hypothesis referred to in experiment 1.

To test this possibility we introduced two new conditions by using plaid adapters with components made from square waves with missing fundamentals (MF) (see section 2.1). The spatial appearance of this pattern is radically different from the 3 cycles deg$^{-1}$ plaid (for example, the periodicity of the MF pattern is one third that of the 3 cycles deg$^{-1}$ plaid, and the MF pattern contains sharp edge features aligned with the component orientations), yet both patterns have global maxima in their amplitude spectra at 3 cycles deg$^{-1}$.

The test plaid had 1 cycle deg$^{-1}$ components at $\pm45^\circ$. In one of the MF conditions, the adapting components were at the same orientations as those in the test plaid (aligned MF condition), while in the other they were rotated through $45^\circ$ relative to those in the test pattern (bisecting MF condition). The contrast of the MF stimulus was adjusted so that the effective contrast of the third harmonics were 8.3% each. This is higher than the 5% used for the 3 cycles deg$^{-1}$ adapter, but should counteract any potential effects of cross-channel inhibition from the higher harmonics in the MF condition (Klein and Stromeyer 1980). The conditions were performed in a pseudorandom order.

In addition to TSM and MAG, two naive observers also took part in this experiment. AL was a postgraduate and SA1 was an undergraduate, who, like SA9, SA10, and SA11, had made predominantly component-type responses in previous plaid perception experiments (Meese 1993).

5.2 Results and discussion

The percentages of component-type responses collapsed across contrast are shown for each of the four subjects in figure 8. Consider first the results for TSM, MAG, and AL. For all three subjects, adapting to an aligned 3 cycles deg$^{-1}$ plaid reduced the percentage of component-type responses, as before; this reduction is particularly dramatic for the naive observer, AL. Furthermore, for each subject, reductions of similar magnitude are also shown for the aligned MF condition, but not the bisecting MF condition. This result with the aligned MF adapter makes an account of our aftereffects in terms of cognitive priming seem highly unlikely. For example, why should a 3 cycles deg$^{-1}$ plaid adapter and a 1 cycle deg$^{-1}$ MF plaid adapter—stimuli that are perceptually very different—produce the same kind of priming? It is more parsimonious to suppose that the similar aftereffects came about because both stimuli maximally stimulate the same spatial channels, and that it is this sensory adaptation that is somehow responsible for the aligned compound effect.

We turn our attention now to subject SA1, who always chose the component sketch in all three of the conditions in which she performed. Given the results of the other
seven subjects reported in this paper, this was surprising. It is not clear why this subject behaved so differently from the others.\(^2\) However, in spite of this result, we are confident of our main effects: the bisecting component effect was shown by all three subjects who were tested for it (experiment 1), and six out of eight subjects showed clear evidence for the aligned compound effect (experiments 1, 2, and 3).

6 General discussion
We investigated the effects of adapting to various two-component plaids on the perceived spatial structure of two-component test plaids both for practised and for naive observers. The test plaid was always 1 cycle deg\(^{-1}\) and had component orientations that were orthogonal to one another. Subjects were required to indicate, by way of sketch selection (figure 3), whether a 500 ms test stimulus appeared as a single compound pattern or as two overlapping gratings. We varied the spatial frequency of an adapting plaid which had component orientations that were either intermediate to those in the test plaid (bisecting condition) or matched those in the test plaid (aligned condition). The results revealed two main aftereffects of adaptation. These were (i) a bisecting component effect (experiment 1), tuned to the same spatial frequency as the test plaid, where adaptation induced the plaid to appear as two overlapping gratings more often than usual, and (ii) an aligned compound effect (experiments 1, 2, and 3), tuned to a spatial frequency greater by a factor of around 3 than that of the test plaid, where adaptation induced the plaid to appear as a compound, checkerboard-like pattern more often than usual. These results are summarised schematically in figure 9.

6.1 Binding requires activity in intermediate-orientation channels
The bisecting component effect (figure 9b) provides good evidence that filters with preferred orientations intermediate to those in a test plaid play a crucial role in the filter-combination process proposed by Georgeson (1992). When intermediate filters are

\(^2\)Owing to experimental error, the length of this subject’s initial adaptation was only 3 min instead of the full 5 min. One possibility is that the length of initial adaptation is critical in observing the aligned compound effect, though in the light of the time courses of other adaptation aftereffects (e.g. Wolfe and O’Connell 1986; Greenlee et al 1991; Meese and Georgeson 1996) this seems unlikely.
Figure 9. Aftereffects of three different types of adaptation on the perception of a two-component plaid. For convenience, the test stimulus is shown with component orientations of ±45°. (a) The baseline condition. Adaptation was to a blank screen of mean luminance. As in experiments where there was no adaptation (e.g., see the appendix), the test stimulus segmented (gingham pattern) at low test contrasts but was perceived as a checkerboard at higher contrasts. (b) The bisecting component effect. Here, the orientations of the adapting components bisected those of the test stimulus, but had the same spatial frequency (1 cycle deg⁻¹). Adaptation caused segmentation to extend to higher test contrasts than in the baseline condition. (c) The aligned compound effect. In this case, the adapting components had the same orientation as those in the test stimulus but at a higher spatial frequency (3 cycles deg⁻¹). In this condition, perceptual binding (checkerboard percept) extended to lower contrasts than in the baseline condition.

adapted and so desensitized (Blakemore and Campbell 1969), the usual compound, checkerboard-like percept is 'broken' and the plaid segments into two overlapping gratings. This and other observations on plaids have led us to the 'bridge' hypothesis (Meese and Georgeson 1991). The idea is captured in figure 10. Let us designate the channel whose orientation lies midway between those most sensitive to the test components as the bridge channel. Suppose that activity in the bridge channel must exceed some threshold for filter combination—or binding—to occur. We will refer to this threshold as the filter-combination threshold (FCT) but withhold speculation on the process that may be subject to this thresholding until later in the paper. Activity in the bridge channel could be made to exceed the FCT by either increasing the stimulus contrast (figures 10a and 10b) or decreasing the angle between the two plaid components (figures 10a and 10c). This is consistent with both the contrast and the angle effect introduced earlier (figures 2a and 2b). It should be obvious that if the bridge channel(s) are desensitized by adaptation, then more test contrast would be required for activity in the bridge channel to exceed the FCT. Thus, the bridge hypothesis captures three of our effects with static plaids.

The bridge hypothesis is also reminiscent of the conclusions drawn by Meese and Freeman (1995) in their discussion of the orientation effect (figure 2c)—the finding that plaid components bind more readily when they are balanced around the cardinal rather than oblique axes of the retinae. There it was shown that the orientation effect could not be understood by considering the filters most sensitive to the plaid components, but that the orientation of the bridge channel was the crucial variable. Thus, if the
Figure 10. The bridge hypothesis. All panels show the hypothetical activity (ordinate) across orientation channels (abscissa) in response to a two-component plaid (dashed curves) and the two individual components of that plaid (filled curves). In (a), the stimulus is of low contrast and the component orientations are fairly distant. The activity in the channel intermediate to the two most active channels (the bridge channel), is lower than the filter combination threshold (FCT) and so the two response distributions are treated independently (ie segmentation occurs). In (b) the component orientations remain the same as in (a), but the contrast has been raised. The activity in the bridge channel is now greater than the FCT, and the two response distributions are perceptually bound together. This is the contrast effect (figure 2a; appendix). In (c), the contrast of the test stimulus is the same as in (a), but the component orientations are closer together. Once again, this lifts the activity in the bridge channel above the FCT, and perceptual binding occurs. This is the angle effect (figure 2b; Meese and Freeman 1995). If the bridge channel(s) were desensitised by adaptation, then segmentation would occur at higher test contrasts because greater stimulation would be required for the FCT to be exceeded. This is the bisecting component effect (figure 9b).

FCT were higher at oblique bridge-channel orientations than at cardinal orientations, this would account for the orientation effect. We shall return to this idea in section 6.4.2.

6.2 Interactions across spatial-frequency channels
At first glance, the aligned compound effect (figure 9c) seems to fit less readily into the framework considered above. However, it may not be coincidental that both this effect and the switching effect (figure 2d) appear to be tuned to a spatial frequency greater by a factor of around three than the fundamental components of the test plaid (Georgeson 1994; Meese and Georgeson, in preparation). In the switching effect, we have suggested that the addition of a third harmonic with either one (Georgeson 1994), or optionally both (Meese and Georgeson, in preparation) components of a base plaid causes the visual system to switch from combining filters across orientation (checkerboard-like percept), to combining filters across spatial frequency at a common orientation (gingham-type percept). One possibility is that there exist inhibitory connections from 3 cycles deg\(^{-1}\) channels onto 1 cycle deg\(^{-1}\) channels with orientation differences of around 45°. If this were so, then the failure for components to combine
across orientation in the switching effect might be caused by 3 cycles deg\(^{-1}\) channel activity inhibiting the bridge channel and pushing its response below the FCT. Conversely, adaptation to a 3 cycles deg\(^{-1}\) plaid would reduce the activity of the 3 cycles deg\(^{-1}\) channel and so disinhibit the bridge channel. This would raise the activity of the bridge channel, and so perceptual combination across orientation would occur more readily, as was found in the aligned compound effect.

In work performed by others, remote adaptation has been found to facilitate detection thresholds (DeValois 1977; Tolhurst and Barfield 1978; Williams et al 1982), to counteract the direct effect of adaptation (Greenlee and Magnussen 1988), and to produce illusory gratings (Georgeson 1976, 1980; Tolhurst and Barfield 1978) after the offset of the adapting stimulus. In explanations of these phenomena disinhibition between spatial channels has similarly been proposed (Georgeson 1976, 1980; DeValois 1977; Tolhurst and Barfield 1978; Greenlee and Magnussen 1988); an idea that has also received some support from single-cell recordings (DeValois and Tootell 1983). In particular, the proposal made here of connections between channels remote in both spatial frequency and orientation is supported by the results of Georgeson (1980). After adaptation to vertical gratings, Georgeson reported the presence of illusory gratings at lower spatial frequencies and with orientations about 40° either side of the adapter, suggesting direct connections between channels tuned to the adapting and illusory components.

6.3 Binding propagates around oriented filters?
We have argued above that activity in channels distant from those most sensitive to a two-component plaid [eg the bridge channel(s)] play an important role in segmentation and binding in plaids, but this in itself does not tell us how binding occurs. Why is it that when activity exceeds the putative FCT in the bridge channel, plaids become perceptually fused? One possibility is that filters which are to be perceptually grouped are somehow labelled by activity that propagates around a chain of filters. This idea is not dissimilar to that of the “association field” introduced by Field et al (1993). Those authors found that ‘snake-like’ arrays of small Gabor patches were most easily identified amongst a background of randomly oriented Gabor patches when the local orientations of the patches in the test array conformed to first-order curves (ie they were aligned with the local orientation of the ‘snake’). This led them to propose that in primary visual cortex there exist phase-invariant association fields that are subject to joint constraints of orientation and position. One possibility is that similar association fields exist in the spectral domain as well as the spatial domain. How might such fields cause segmentation and binding?

One possibility is that the substrate for these fields is a set of excitatory connections between tuned filters: those filters that ‘group’ together respond more strongly as a result of mutual excitation. This simple idea is consistent with the results of Polat and Sagi (1993, 1994) who found that detection of grating patches was facilitated by the presence of suprathreshold patches in adjacent locations, especially when the flanking patches were both coaxial and co-oriented with the test patch. However, this proposal seems flawed in at least one critical way: raised activity due to excitatory interactions would surely be confounded with perceived contrast. Indeed, upon informal inspection, Field et al’s (1993) ‘snake-like’ target arrays do not appear to have higher contrast than the background elements, suggesting that, for these stimuli, raised activity through mutual excitation is not responsible for perceptual association. A similar point has been made before (see the discussions starting at page 66 and page 188 in Bock and Goode 1994).

Perhaps one way in which this idea could be developed is to suppose that there exist two functionally distinct types of spatial filters. One set might be thought of as
Filter combination and channel interactions

Filter combination and channel interactions

‘data filters’ (eg simple cells), whose job is to carry local contrast. The second set could be viewed as ‘control units’, which mediate excitatory interactions between themselves, and have a one-to-one association with the ‘data filters’: the more strongly the ‘control units’ respond, the stronger is the binding between corresponding ‘data filters’. In this scheme, binding signals and contrast signals are kept separate, thus avoiding the confounding of grouping and contrast mentioned above. However, this proposal also suffers a weakness, one that has been referred to as the superposition catastrophe (von der Malsburg 1986). Consider a shadow contour that falls obliquely across a vertical step-edge luminance border. Typically, these two contours segment perceptually but, under the above proposal, at the point of intersection between these contours, ‘control units’ with both oblique and vertical receptive fields would be responding equally strongly. This would lead to binding across orientation instead of segmentation as required.

One way of sidestepping this problem is to suppose that there exist higher-order collator units, with elongated receptive fields, driven by arrays of lower-order spatial filters (Morgan and Hotopf 1989; Schwarz and Bolz 1991; Moulden 1994). The coactivation of different collator units centred at a common location but with different orientations could presumably be interpreted as segmentation by the visual system. Furthermore, the existence of higher-order ‘contour detectors’ is consistent with our view that ZC extraction may be used to mark luminance edges after the combination of oriented filter outputs (Georgeson 1992; Georgeson and Meese 1996). However, we have now come full circle, and return to the problem of how to label those oriented filters that are to be combined prior to the coding of edges!

6.4 Combined filters are synchronised filters?

We have no direct evidence for what follows, but the similarity between our results with plaids and recent developments in neurophysiology is sufficiently compelling for us to review briefly the relevant literature and make a tentative suggestion concerning filter combination and neural synchronisation.

Over the last five years or so there has emerged neurophysiological evidence that the neural substrate for visual scene segmentation may be the synchronised responses of cortical cells, often found to oscillate in the gamma-band region of 30–90 Hz (for reviews see Engel et al 1992; Singer 1993; Eckhorn 1994; Singer and Gray 1995; for criticisms see Tovee and Rolls 1992a; Young et al 1992; for a reply see Engel et al 1992b).

Much of the early work was performed on cat (eg Eckhorn et al 1988; Gray et al 1989, 1992; Gray and Singer 1989; Engel et al 1991b, 1991c; Eckhorn and Obermueller 1993; Koenig et al 1993, 1995; Roelfsema et al 1994), though despite initial failed attempts (eg Tovee and Rolls 1992b; Young et al 1992) similar results (Eckhorn 1994) have recently been reported for recordings made in V1, V2, and MT of awake monkey (Kreiter and Singer 1992, 1995; Eckhorn et al 1993, 1995; Frien et al 1994; Eckhorn 1995; Eckhorn and Frien 1995). For example, oscillatory activity has been found in monkey visual cortex for both slowly drifting and stationary contrast borders and gratings (Eckhorn 1995; Eckhorn and Frien 1995; Eckhorn et al 1995).

Oscillations close to 40 Hz have also been found in humans by means of magnetoencephalography and auditory stimuli (Pantev et al 1991; Ribary et al 1991; Joliot et al 1994). Moreover, evidence is also emerging that gamma-band activity in humans correlates with visual binding. In a recent preliminary report, two bursts of ca 40 Hz oscillations were found in visually evoked potentials after the presentation

(3) Tovee and Rolls (1992b) investigated activity in IT of awake monkey in response to static facial stimuli. Young et al (1992) recorded from V1, MT, and IT in anaesthetised monkey and IT in behaving monkey, using effective stimuli.

(4) For a cautionary comparison between EEG and microelectrode data see Galambos (1992).
of Kanizsa-triangle-type stimuli (Tallon-Baudry et al 1995). However, when the inducing elements were presented in a configuration that did not promote the perception of an illusory triangle—they were each rotated through 180° and so no longer perceptually bound—the second burst of gamma-band activity was no longer found. This result helps corroborate Kojo et al's (1993) speculation that synchronised gamma activity may underlie the spatial properties of Kanizsa-triangle figures.

Of particular relevance to our plaid-perception experiments (eg Georgeson 1992, 1994, 1996; Meese and Freeman 1995; Meese and Georgeson 1996) is the stimulus-dependent synchronisation and desynchronisation of cortical cells found by Engel et al (1991b) in cat area 17. In that study, the authors made multiple-electrode recordings from cortical cells with different preferred orientations but overlapping receptive fields. When a single oriented light bar was drifted over their receptive fields, many cells responded in synchrony, regardless of whether their response was optimal. However, when the stimulus was a pair of drifting light bars with different orientations, the cells formed two groups with preferred orientations balanced around those of the two stimulus bars; within each group, oscillations were synchronised, but across groups, the responses were asynchronous. A similar result has recently been reported for monkey MT (Kreiter and Singer 1995; Singer and Gray 1995).

Importantly, the phase locking described above is unrelated to the temporal structure of the stimulus (Gray and Singer 1989), implying that the oscillations are of neural origin. Furthermore, the finding that abolition of interhemispheric synchronisation occurs when the corpus callosum was sectioned in cat suggests that cortical connections are involved in establishing synchronisation (Engel et al 1991a).

The idea of using temporal synchronisation to bind together cortical responses to common stimulus structure was discussed by von der Malsburg and Schneider (1986) and is particularly attractive in that it not only solves the 'superposition catastrophe' (von der Malsburg 1986) but also avoids the ambiguity between stimulus cohesion and stimulus contrast discussed earlier (see section 6.3). This, taken with the evidence reviewed above, brings to mind the possibility that the way in which plaid components are labelled for perceptual combination is that corresponding spatial filters respond in synchrony. This synchronisation might be passed around a chain of interconnected oscillators (König and Schillen 1991) with overlapping, tuned receptive fields at neighbouring orientations (Schillen and König 1991, 1994). This idea is clearly compatible with the bridge hypothesis outlined earlier and provides a reasonable interpretation of the FCT. That is, the FCT might be the contrast level required for synchronised oscillations to be successfully propagated across the bridge channel (König and Schillen 1991; Grossberg and Somers 1991).

Field et al (1993) and Eckhorn (1994) similarly speculated that synchronised oscillations might underlie the “association fields” implied by Field et al's psychophysical work (see section 6.3).

6.4.1 Neurophysiological predictions. The idea that synchronised oscillations are the neural analogue of binding in the perception of plaid structure leads us to a specific prediction for multiple-cell recordings from oriented cells in primary visual cortex. When a high-contrast plaid is used as a stimulus, our working hypothesis predicts that, unlike in the results of Engel et al (1991b; see section 6.4), sufficiently active cells in V1 will all respond in synchrony because this stimulus appears perceptually bound. However, when one or both of the two plaid components are made more like square waves by adding third harmonics, the stimulus segments perceptually (the switching effect; figure 2d), and so our hypothesis predicts that, like in the results of Engel et al, neurons in V1 should organise into two synchronous groups that are uncorrelated with respect to each other. Of course, the broad-band stimuli used by Engel et al bear
more resemblance (both spectrally and perceptually) to our quasi-square-wave plaids than our sine-wave plaids (Albrecht et al. 1980), and so Engel et al.'s results go some way to supporting the second of our predictions. Our case would be strengthened considerably if the first prediction were also borne out.

6.4.2 Visual experience and synchronised activity. Meese and Freeman (1995) reported that component-type percepts were more common for plaids whose component orientations were balanced around oblique, as opposed to cardinal, retinal axes (the orientation effect; figure 2c). They were able to show that the anisotropy was not due to different response characteristics of the filters most sensitive to the test components, and suggested that it may somehow reflect the anisotropy in the Fourier amplitude spectrum found in carpentered environments at low spatial frequencies (Switkes et al. 1978; also see Baddeley and Hancock 1991). More specifically, they suggested that coactivated filters may learn to combine their outputs more readily on future occasions: “neurons wire together if they fire together” (Löwel and Singer 1992; Singer 1995). Under this hypothesis, it would be filters that are balanced around vertical and horizontal orientations that would learn to combine most readily because of the prominence of these orientations in the visual world. Thus, one might expect a stimulus-driven learning process to promote stronger (or farther-reaching) connections (i.e., lower FCTs) between filters balanced around vertical and horizontal than those balanced around obliques. This would be in accordance with the orientation effect for plaids (Meese and Freeman 1995).

Furthermore, there is evidence to support the idea that visual experience is important in establishing the cortical conditions needed for synchronised activity. Artificially induced strabismic cats developed amblyopia and were tested for synchronised activity in cortical cells driven by either the normal or the amblyopic eye. Although the amplitude of response was the same for each eye, neurons driven by the normal eye displayed stronger synchronisation in response to drifting bars and gratings than those driven by the amblyopic eye (Roelfsema et al. 1994; also see Löwel and Singer 1992 and König et al. 1993 for related studies). The result with gratings was most pronounced at high spatial frequencies and fits nicely with reports (e.g., Hess et al. 1990) that human amblyopes experience spatial jitter-type distortions (e.g., perceptual edge misalignments) at high but not low spatial frequencies when the stimulus is viewed through their amblyopic eye alone. Taken together, these two sets of results suggest that amblyopic spatial vision is more fragmented because neural responses are less well bound together across space.

6.5 Summary and conclusions

Static plaid patterns made from two sinusoidal components of matched spatial frequency (1 cycle deg⁻¹) can look like either (i) a single compound structure (checkerboard-like percept) or (ii) two overlapping gratings (components percept). For example, at very low contrasts the components percept is more common, though as the contrast is increased, the compound percept dominates (Meese and Georgeson 1991, 1996; Meese and Freeman 1995). Using a sketch-selection paradigm (Georgeson 1992) to measure these perceptions, we replicated the effect of contrast on perceived spatial structure (see the appendix) and found two new aftereffects of selective adaptation. In the first case (the bisecting component effect), we found a marked increase in the components percept after adaptation to a plaid whose component orientations were intermediate to those in the test plaid. This aftereffect appeared to be tuned to an adapting spatial frequency close to that of the test plaid (1 cycle deg⁻¹). In the second case (the aligned compound effect), we found a marked increase in the compound percept after adaptation to a plaid whose components were at the same orientations as
those in the test plaid. This aftereffect appeared to be tuned to an adapting spatial frequency about three times that of the test plaid (3 cycles deg⁻¹).

We took these results as evidence that activity in spatial channels that are distant to those most sensitive to the test components in a two-component plaid are important in determining whether that plaid binds or segments perceptually. We introduced the bridge hypothesis (figure 10) as a way of formulating a total of six experimental effects (see figures 2 and 9) within a single conceptual framework. Three of these effects were easily accounted for (the contrast, angle, and bisecting component effects) and a fourth (the orientation effect) required only a minor modification of the bridge hypothesis. The last two effects (the switching and aligned compound effect) required a further assumption about interactions across spatial frequency and orientation channels.

While the bridge hypothesis was useful in showing the relations between the effects that we have found with plaids, it did not in itself provide an explanation of how spatial filters might be bound or segmented perceptually. A firm conclusion on this issue awaits substantial work, though we were able to offer one plausible though speculative suggestion. We conjectured that 'synchronised filters' (Singer and Gray 1995) may be 'perceptually combined filters', and that a network of spatially tuned oscillators (Schillen and Koenig 1994) may be responsible for implementing the 'grouping rules' posited by Georgeson (1992): "neurons that hum together, sum together".

Acknowledgement. Some of the results were reported at the 14th European Conference on Visual Perception, Vilnius (Meese and Georgeson 1991).

References
Bowne S F, 1990 “Contrast discrimination cannot explain spatial frequency, orientation or temporal frequency discrimination” Vision Research 30 449–461
DeValois K K, 1977 “Spatial frequency adaptation can enhance contrast sensitivity” Vision Research 17 1057–1065
Eckhorn R, 1994 “Oscillatory and non-oscillatory synchronization in the visual cortex and their possible roles in associations of visual features” Progress in Brain Research 102 405–426
Eckhorn R, Obermueller A, 1993 “Single neurons are differently involved in stimulus-specific oscillations in cat visual cortex” Experimental Brain Research 95 177–182
Galambos R, 1992 “A comparison of certain gamma band (40 Hz) brain rhythms in cat and man”, in Induced Rhythms in the Brain Eds E Başar, T H Bullock (Boston, MA: Birkhäuser) pp 201–216
Georgeson M A, 1976 “Psychophysical hallucinations of orientation and spatial frequency” Perception 5 99–111
Georgeson M A, 1980 “The perceived spatial frequency, contrast, and orientation of illusory gratings” Perception 9 695–712
Georgeson M A 1990 “Human vision combines oriented filters to compute edges” Perception 19 154
Greenlee M W, Magnussen S, 1988 “Interactions among spatial frequency and orientation channels adapted concurrently” Vision Research 28 1303–1310
Grossberg S, Somers D, 1991 “Synchronized oscillations during cooperative feature linking in a cortical model of visual perception” Neural Networks 4 453–466
He Z J, Nakayama K, 1994 “Perceiving textures: beyond filtering” Vision Research 34 151–162
Löwel S, Singer W, 1992 “Selection of intrinsic horizontal connections in the visual cortex by correlated neuronal activity” Science 255 209–212
Meese T S, 1993 Feature Coding in Human Pattern Vision PhD Thesis, University of Bristol, UK
Meese T S, 1995 “Phase-reversal discrimination in one and two dimensions: performance is limited by spatial repetition, not spatial frequency content” Vision Research 35 2157–2167
Polat U, Sagi D, 1993 “Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments” *Vision Research* 33 993–999
Polat U, Sagi D, 1994 “The architecture of perceptual spatial interactions” *Vision Research* 34 73–78
Tovee M J, Rolls E T, 1992b “Oscillatory activity is not evident in the primate temporal visual cortex with static stimuli” *Neuroreport* 3 369–372
APPENDIX
Here we present the results of a preliminary experiment in which it was established that both components in our plaid stimuli were well above detection threshold (for TSM). Thus, the contrast effect for plaid perception—the finding that two-component plaids tend to segment more readily at low test contrasts—is not due to a failure to detect one of the test components.

A.1 Methods
Equipment and general conditions were identical to those in the main experiments.

A.1.1 Plaid perception
Plaid stimuli had components oriented at ±45° and spatial frequencies of 1 cycle deg⁻¹. Stimuli were presented for 500 ms at eight different levels of component contrast ranging from 1.5 dB (1.2%) to 26 dB (20%) in 3.5 dB steps. In a single session, each contrast level was presented ten times in a random order. Results are the means from two sessions. As in the main experiments, responses were made by selecting either a compound-type or a component-type sketch. These sketches were similar to those shown in figure 3, but were rotated through 45° so as to be appropriate for the stimuli used in this experiment.

A.1.2 Detection of plaid components
We used a two-interval forced-choice technique and a method of constant stimuli to measure the detection threshold for a single component of a plaid. Sinusoidal test gratings with a spatial frequency of 1 cycle deg⁻¹ were presented for 500 ms in one of two temporal intervals at contrast levels from −16 dB (0.16%) to 1.5 dB (1.2%) in steps of 3.5 dB. The other interval was blank, and each interval was marked by the onset of a short tone. For each contrast level, ten presentations were made at orientations of both +45° and −45°. On each trial, orientation, contrast, and interval were chosen randomly. The observer’s task was to select the interval containing the test grating by pressing one of two buttons. Two sessions were performed and results were collapsed across grating orientation, giving a total of forty observations at each of six contrast levels.

A.2 Results and discussion
The detection data were corrected for guessing by using Abbott’s (1925) formula:

\[ P(d) = \frac{P(c) - g}{1 - g} \]

where \( P(d) \) is the proportion of grating stimuli that were detected, \( P(c) \) is the proportion of correct responses at each contrast level and \( g \) is the guess rate, which for a two-interval forced choice is 0.5.

Results are shown for TSM in figure A1. Open symbols are for the grating-detection experiment and show proportion detected after correcting for guessing [\( P(d) \); left-hand ordinate]. The filled symbols are for the plaid-perception experiment and show the percentage of compound-type responses indicated by the right-hand ordinate. The solid curves through these data are normal ogives derived by probit analysis (Finney 1971). The dashed curve is a theoretical prediction for the proportion of trials in which both components of a plaid would be detected with the assumption of probability summation between a pair of independent channels (Georgeson and Shackleton 1994). This curve was generated by correcting the

\(^{(A1)}\) Previously, and in the main experiments reported here, we have plotted the percentage of component-type responses instead (eg Meese and Freeman 1995; Meese and Georgeson 1996).
Figure A1. Grating-detection data (open circles and left ordinate) and plaid-perception data (filled squares and right ordinate) for TSM. The stimulus components had a spatial frequency of 1 cycle deg⁻¹, and orientations of ±45°. For plaid perception, both components were presented at the same time and the observer made sketch selections to indicate whether the stimulus appeared as a compound (i.e., checkerboard-like) or two overlapping gratings. For grating detection, only one of the components was presented, and observers chose in which of two temporal intervals it was contained. The solid curves are probit fits to the respective data. The dashed curve is the predicted psychometric function for detecting both components of a plaid simultaneously, on the assumption that each component is detected by independent channels (see text for derivation). Detection threshold (50% detected; 75% correct) of a single grating was $-10.2\, \text{dB} (0.31\%)$. The contrast level at which both components in a plaid were detected was $-6.7\, \text{dB} (0.46\%)$. This is considerably lower than the 50% point ($P_{50}$) of 11 dB (3.55%) for plaid perception.

The grating-detection data for guessing and then squaring to give probabilities of detecting both components. Probit analysis was then performed on the transformed data.

From the plaid-perception data in figure A1 it is clear that TSM made component-type responses at low stimulus contrasts, but as the contrast was increased, responses changed to compound-type. This is the contrast effect that we have reported previously (Meese and Freeman 1995; Meese and Georgeson 1996).

This result might be expected if both of the plaid components were not reliably detected at low contrasts; the oblique zero crossings of a single component would be more similar to the oblique features in a component sketch than to the vertical and horizontal features of the compound sketch. However, we can reject this hypothesis because from figure A1 it is clear that both components (dashed curve) are reliably detected over the full range of contrasts used in the plaid-perception experiment.