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Thresholds for the Identification of the Direction of Motion of Plaid Patterns Defined by Luminance or Chromatic Contrast

KARL R. GEGENFURTNER*

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Contrast thresholds for identification of the direction of motion were determined for sinusoidal gratings and plaid patterns moving in eight possible directions. Since plaid patterns are the sum of two component gratings, a prediction of the thresholds for plaids can be made by assuming that the motions of both component gratings are independently identified (probability summation). In agreement with standard two-stage models of plaid perception, our results show that for stimuli defined by luminance contrast, plaid direction thresholds can be predicted well from the component thresholds. This also holds for fast-moving isoluminant plaid patterns, but for slowly moving (<4 Hz) isoluminant plaids, direction thresholds were substantially higher than the prediction from the components. In the latter case, subjects frequently were unable to identify the motion of the plaid in the pattern direction, even when the direction of motion of both components could be reliably identified. Different mechanisms might underlie the perception of luminance and isoluminant plaids at slow speeds. © 1998 Elsevier Science Ltd. All rights reserved.

Color Isoluminance Motion Plaids

INTRODUCTION

Plaid patterns consist of two superimposed sinusoidal gratings of different orientations. When the component gratings move, the plaid may be seen to move coherently in a direction different from either one of the component directions. The discovery of a correspondence between the subjective coherence of moving plaid patterns (Adelson & Movshon, 1982) and properties of neurons in the middle temporal area (MT) of macaque monkeys (Movshon, Adelson, Gizzi & Newsome, 1985) marked a milestone in the search for neural substrates of perceptual phenomena. It motivated numerous psychophysical experiments which studied further aspects of plaid perception (for a review see Noest & van den Berg, 1993). Many of these studies were concerned with the validity of a simple two-stage model of plaid processing (Adelson & Movshon, 1982), which assumes that the one-dimensional components are processed separately from each other and separately from the two-dimensional motion. Numerous experimenters addressed the question whether perceptual aspects of the plaid, such as its coherence, speed or direction of motion, can be predicted from the perception of the components.

Whereas most of these experiments used stimuli at high levels of contrast, I concentrated on the mechanisms underlying the identification of the direction of motion of plaids at contrast threshold. Interestingly, if both component gratings are defined by isoluminant sinewave gratings, a coherently moving plaid is perceived as well. It is known that neurons in MT show rather poor sensitivity to isoluminant stimuli (Gegenfurtner, Kiper, Beusmans, Carandini, Zaidi & Movshon, 1994) and therefore area MT is assumed to be of little or no importance for the analysis of color (Zeki, 1978). So far, area MT has been the only area in primate visual cortex where a significant proportion of cells (15%) has been found that could possibly underlie the perception of plaids (Movshon *et al.*, 1985). Therefore, I investigated the mechanism for determining the direction of motion of threshold level plaids defined by luminance or chromatic contrast.

METHODS

Equipment

Stimuli were displayed on an EIZO RGB monitor (T560i) driven by a Cambridge Research Systems VSG 2/3 graphics board with a refresh rate of 120 Hz non-interlaced. Each gun of the CRT was linearized by a look-up table to give a 12 bit intensity resolution. A Photo Research Model 703-PC spectroradiometer was used to calibrate the display screen. The display was 12.5 deg × 9.375 deg at the viewing distance of 137 cm

*Max-Planck-Institute für biologische Kybernetik, Spemannstr. 38, 72076 Tübingen, Germany [*Tel*: +49 7071 601 607; *Fax*: +49 7071 601 616; *Email*: karl@mpik-tueb.mpg.de].

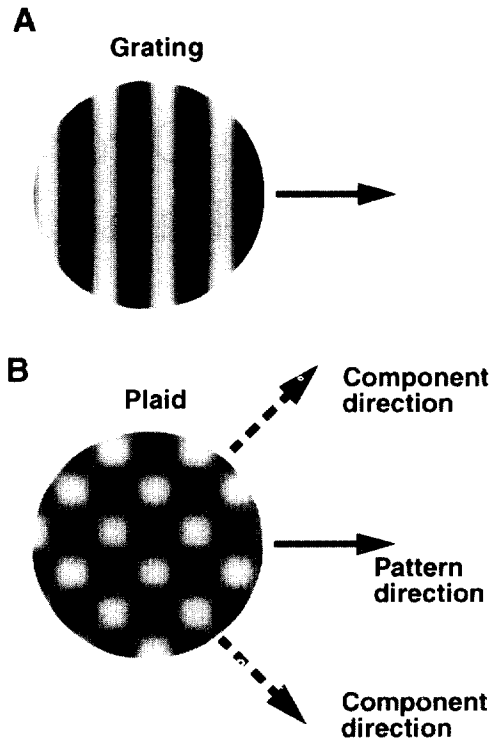

FIGURE 1. Illustration of the stimuli used in these experiments. The observer had to indicate in which of eight possible directions of motion the stimuli were moving. (A) Sinusoidal grating. (B) Plaid pattern made by adding two sinusoidal gratings of identical spatial frequency, temporal frequency, and contrast. When the components move in the directions indicated by the dashed arrows, the plaid is usually seen to move in the direction indicated by the continuous arrow.

and had a mean luminance of 50 cd/m^{-2}. Subjects were seated with their heads resting on a chin-rest and viewed the screen binocularly through natural pupils.

Subjects

The author (KG) and three subjects, who were naïve with respect to the experiments, participated in this study. All had normal vision and normal color vision, as determined in earlier experiments.

Stimuli

Two classes of stimuli were used: sinewave gratings and plaids. The two types of stimuli are illustrated in Fig. 1. They were presented within a circular aperture of 4 deg diameter for 500 msec on top of a uniform gray background extending over the whole monitor screen. The grating stimuli had a spatial frequency of 1 c/deg and could move in one out of eight possible directions, equally spaced between 0 and 360 deg in steps of 45 deg. Plaid stimuli were constructed by the superposition of two of the sinusoidal gratings, which had identical spatial frequency, temporal frequency and contrast, but whose orientations differed by 90 deg. At high contrast, the plaid stimuli always produced a coherent perception of motion in the direction intermediate to those of its two component gratings. It could move in one of eight directions, which were identical to the directions of the single grating stimuli. The superposition of the two component gratings was done by rapidly alternating them on the display screen, which reduced the effective frame rate to 60 Hz. Component gratings instead were alternated with a blank frame, thus reducing their nominal contrast by a factor of two. When specifying the contrast of the plaid patterns, the contrast of one of its component gratings was used, even though the Weber contrast of the peaks and troughs of the plaid was twice as high.

The luminance modulation of the sinusoids making up gratings and plaids was around a neutral gray background with the C.I.E. *xyY* coordinates (0.30, 0.35, 50). The red–green isoluminant axis that was used to modulate gratings and plaids went from red (0.36, 0.32, 50) to green (0.22, 0.39, 50) through the gray background defined above. The red–green axis differentially excites the second-stage mechanism defined by opponent long wavelength sensitive (L) and middle wavelength sensitive (M) cone inputs (MacLeod & Boynton, 1979; Krauskopf, Williams & Heeley, 1982; Derrington, Krauskopf & Lennie, 1984). We define contrast as the RMS cone contrast of the L- and M-cones. For luminance stimuli, this is identical to the standard Weber contrast, since L- and M-cone contrasts are equal and of equal sign for such stimuli. For isoluminant stimuli, it results in a contrast intermediate between L- and M-cone contrasts. The maximum L-cone contrast for isoluminant modulations was 7% and the maximum M-cone contrast was 11.7% for symmetric modulations around the given white point, resulting in an RMS cone contrast of 9.7% for the maximally obtainable isoluminant modulation at the mean luminance of 50 cd/m^2 of the monitor.

Procedure

The method of constant stimuli was used to determine the contrast required for observers to correctly identify the direction of motion of each stimulus. Typically five to eight different component contrast levels were chosen for one session, and 40 trials were run for each grating and plaid stimulus. On each trial, the stimulus was randomly chosen to be either a plaid or a grating, and the direction of motion was randomly chosen from eight constant directions. The observer responded by pressing one of eight keys, which were arranged on a keypad to correspond to the movement directions of the stimuli. No feedback regarding the correctness of the response was given. Before each trial a short signal tone alerted the observer.

Within each session the temporal frequency and color of the stimuli was fixed. Subjects ran sessions for black & white luminance stimuli and for red & green isoluminant stimuli at the following six temporal frequencies: 0.5, 1, 2, 4, 8 and 16 Hz. Since the spatial frequency was constant at 1 c/deg for all stimuli, the values for the temporal frequencies are equivalent to the velocities of the stimuli in deg/sec.

Data analysis

For each contrast level, the number of correct responses was counted. For plaid patterns, a response

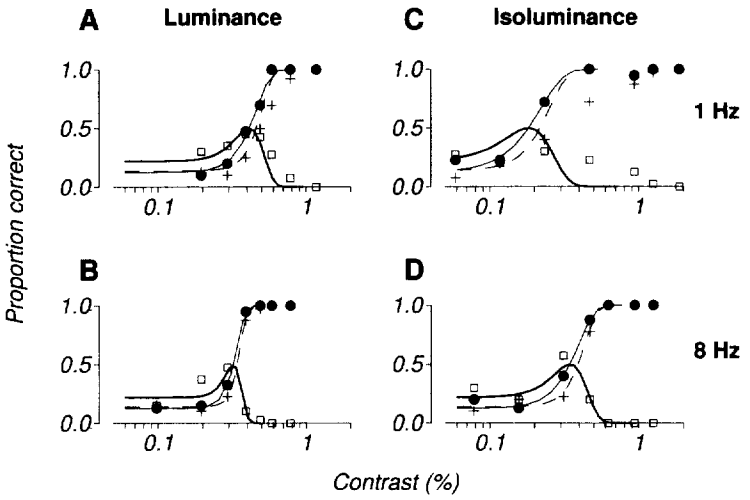

FIGURE 2. Proportion of correct responses as a function of contrast. Each data point is based on 40 trials. The filled circles indicate the proportion correctly identifying the direction of motion of a single grating. The thin continuous curve through these data points shows the best-fitting Weibull function. The plus signs indicate the proportion of correct responses identifying the direction of motion of a plaid made up of two components, each having the contrast indicated on the x-axis. The dashed thin curve shows the performance for the plaids, as predicted by probability summation of the two components. The open squares show the proportion of trials in which the observer indicated the motion in the direction of one of the components of a plaid. The heavy continuous curve shows the proportion of trials in which such a component response would be predicted from probability summation. Data for a single observer, KG. (A) Luminance stimuli moving at a temporal frequency of 1 Hz. (B) Luminance stimuli moving at a temporal frequency of 8 Hz. (C) Isoluminant stimuli moving at a temporal frequency of 1 Hz. (D) Isoluminant stimuli moving at a temporal frequency of 8 Hz.

was correct when the observer correctly indicated the direction of the pattern, not of the components. A Weibull function was then fitted to the data relating contrast and proportion correct for gratings:

$$P_g(C) = P_{\text{guess}} + (1 - P_{\text{guess}})(1 - \exp(-(C/\alpha)^{\beta})),$$

where $P_g(C)$ is the probability of obtaining a correct response at a contrast level C. P_{guess} is the probability of correctly guessing, which was set to 1/8; α and β are parameters identifying the position and slope of the psychometric curve. Threshold was defined as the point where $C = \alpha$, and where, as a consequence, $P_g(C) = 0.678$. A similar function was then fitted to the plaid responses to obtain the probability $P_p(C)$, with which the observer correctly identifies the direction of motion of the plaid pattern, and the corresponding thresholds.

In order to account for summation effects between the two components of the plaid, we adopted the high threshold model of probability summation. This particular model was chosen for its simplicity and because it has been used successfully in a large variety of experiments (for a complete review, see Graham, 1989). The proportion of responses in the pattern direction, for a plaid consisting of two components with contrast C, can be predicted as the product of the probabilities with which the observer correctly identifies the motion of each the component gratings:

$$P_{\text{pred}}(C) = P_{\text{guess}} + (1 - P_{\text{guess}})(1 - \exp(-(C/\alpha)^{\beta}))^2.$$

Here α and β are the parameters of the psychometric functions for the component gratings and C is the contrast of the component gratings.

We also counted how often the observer gave a response in one of the directions of the components when a plaid pattern was presented. The above model of probability summation assumes that this would happen if the observer correctly identified one of the component gratings, but failed to detect the other component grating. The predicted proportion $P_c(C)$ of times the direction of motion of a single grating (component response) was observed is given by:

$$P_c(C) = P_g(C)(1 - P_g(C)) + P_g(C)(1 - P_g(C)),$$

since there are two possible ways to achieve this outcome. Note that the term for guessing is already included in $P_g(C)$. At low contrasts, $P_c(C)$ will be equal to the probability of correctly guessing the direction of either one of the components, which is 0.25. At high level of contrasts $P_c(C)$ goes towards 0, since the directions of both components will be reliably detected.

RESULTS

Figure 2 shows results from observer KG for luminance and isoluminant stimuli at two different temporal frequencies (1 and 8 Hz). The x-axis in all graphs represents RMS contrast and the y-axis the proportion of correct responses. The filled circles indicate the proportion of correct identification of the direction of a moving single grating. The thin continuous curve through these data points shows the best-fitting Weibull function. The plus signs indicate the proportion of

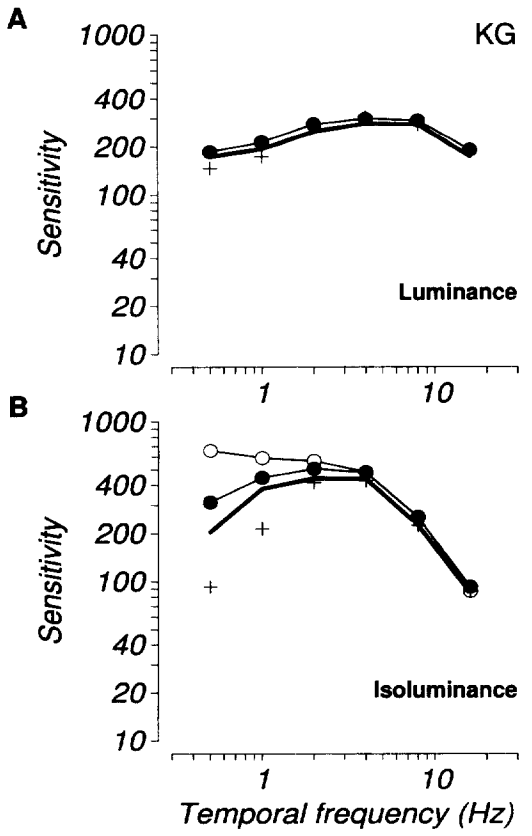

FIGURE 3. Sensitivity of observer KG as a function of temporal frequency for (A) luminance; and (B) isoluminant stimuli. Filled circles indicate sensitivity to the direction of motion of gratings, plus signs sensitivity to plaids. The lower thin curve shows the sensitivity for plaids, as predicted from independent summation of the components. The open circles in (B) show sensitivity to the orientation of the isoluminant gratings.

correctly identifying the pattern motion of a plaid composed of two gratings, each having the contrast indicated on the x-axis. The dashed thin curve shows the predicted proportion of pattern responses to the corresponding plaid stimuli, generated using probability summation of the two components. The open squares show the proportion of responses to plaids, in which the observer indicated the motion in the direction of one of its components. Finally, the heavy continuous curve shows the proportion of trials in which such a component response would be predicted from probability summation.

For luminance defined stimuli, shown in Fig. 2(A) and (B), the data follow the predictions quite well. For fast-moving stimuli [8 Hz, Fig. 2(B)] the correspondence is quite precise. For the slower moving stimuli [1 Hz, Fig. 2(A)] the observed plaid responses deviate slightly at the highestet contrasts from the predictions based on the component responses. The predicted plaid threshold was at a component contrast of 0.51%, whereas the observed threshold was at a contrast of 0.57%. Although small, this difference was statistically significant. Fitting the observed proportions with the predicted psychometric function led to a significant value of χ^2 for all four observers.

For fast-moving isoluminant stimuli [8 Hz, Fig. 2(D)], the data for the plaids were also predicted quite accurately by the component summation model. However, for slowly moving isoluminant stimuli the prediction for the plaids failed dramatically. Even though the direction of motion of the components could be identified at a RMS cone contrast of 0.22%, plaid threshold was as high as 0.47%, much higher than the predicted 0.26%. The slope of the psychometric function for identifying the direction of motion of the plaids was noticeably shallower than predicted. Interestingly, the threshold (in RMS cone contrast) was similar in that case to the threshold for the corresponding slowly moving luminance plaids. This raises the possibility that the direction of motion of both types of plaid patterns is detected by a luminance-based mechanism. However, the slope of the two functions for slowly moving luminance and isoluminant plaids are distinctly different, 4.42 for slowly moving luminance plaids, and 1.51 for the slowly moving isoluminant plaids.

Figure 2(A, B and D) shows, that for luminance plaids and fast moving isoluminant plaids the model also predicts quite well the proportion of trials when one of the component directions is identified. This happened most frequently when the component gratings were just below threshold. When the direction of each one of the components is identified correctly 50% of the time, then the probability of a component response is also 50%. For slowly moving isoluminant plaids, as shown in Fig. 2(C), the observer gives more responses in the direction of one of the components than predicted by the model. Even when the direction of motion of the components alone could be identified perfectly, for example, at a contrast of 0.5%, the plaid was frequently seen to move in one of the component directions. This is hard to reconcile with any summation rule for combining information about the component gratings.

Figures 3 and 4 compare the sensitivities of two observers, KG and BL, for identifying the direction of motion of gratings and plaids, and the predicted sensitivity for the direction of the plaids as a function of temporal frequency. The filled circles show sensitivity to the direction of gratings, and the plus signs sensitivity to plaids. The heavy curve shows the predicted sensitivity for the plaid patterns. For isoluminant stimuli the sensitivities for identifying the orientation of the grating stimuli are also shown [open circles in Fig. 3(B) and Fig. 4(B)]. These orientation thresholds were derived from the individual responses in the direction identification task and not measured separately. Thresholds for such coarse orientation judgments represent good upper bounds for the estimates of detection threshold. For isoluminant stimuli, thresholds for detection and thresholds for the identification of the direction of motion are different at low temporal frequencies (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991), as can be seen in Fig. 3(B) and Fig. 4(B). For luminance stimuli we do not show separate detection thresholds, since in that case they are equal to thresholds for identifying the direction of motion

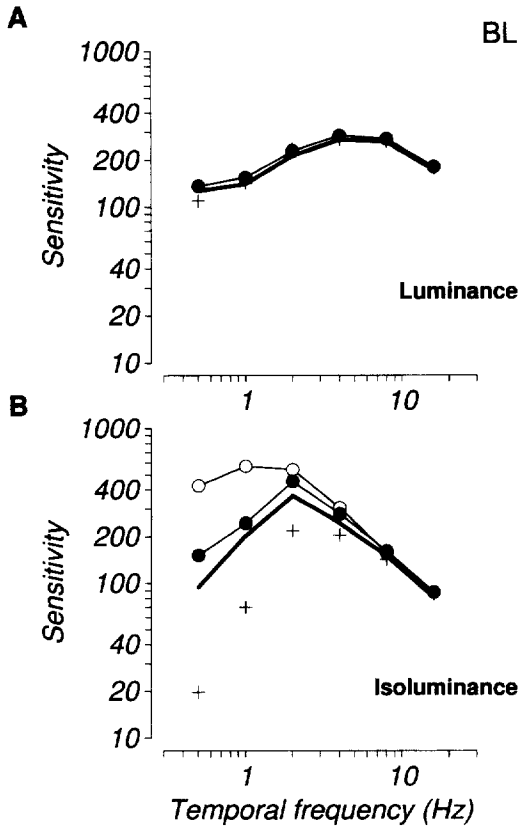

FIGURE 4. Sensitivity of observer BL as a function of temporal frequency for (A) luminance; and (B) isoluminant stimuli. Symbols as in Fig. 3.

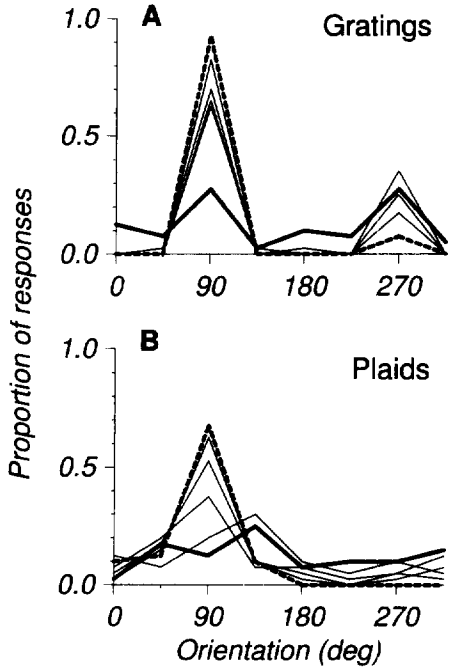

FIGURE 5. Proportion of responses at different orientations to (A) isoluminant gratings; and (B) isoluminant plaids with a temporal frequency of 0.5 Hz. The different curves indicate different contrast levels, from 0.12% cone contrast (heavy continuous line) to 1.875% cone contrast (heavy dashed line). Stimuli were actually moving in different directions. We plot the responses relative to the direction of the stimulus motion, which is arbitrarily set to 90 deg. Results are for observer KG. Each data point is based on 40 trials.

(Watson, Thompson, Murphy & Nachmias, 1980). For luminance stimuli, the temporal contrast sensitivity curve for luminance has a typical bandpass shape with a peak between 4 and 8 Hz [Fig. 3(A)]. The observed sensitivities for the plaids (plus-signs) follow the predictions (solid line) quite closely. Only at the very low temporal frequencies is there is a small deviation. Between 0.5 and 1 Hz, the observed sensitivity for plaid direction is not quite as high as predicted. These reductions of sensitivity, although systematic, are relatively small. Almost identical results are seen for a second observer [Fig. 4(A)].

Under conditions of isoluminance, shown in Fig. 3(B), the deviations at low temporal frequencies of 2 Hz and below are quite large. At higher temporal frequencies, observations and predictions correspond quite well. At temporal frequencies at or below 2 Hz the predicted performance for the plaids is far better than the observed performance. Interestingly, for the same range of temporal frequencies, the sensitivities for correctly detecting the orientation of the single gratings (open symbols) exceed the direction of motion thresholds. Similar results were obtained for a second observer, as shown in Fig. 4(B), and for two other observers, whose data are not shown. The critical temporal frequency range seems to be around 2–4 Hz, below which the predictions for the isoluminant plaids fail.

There are several possible explanations for the failure of probability summation for slowly moving isoluminant plaids. One is that the mechanism underlying the detection of motion of plaids could not receive input from the preceding stages at which the direction of motion of the isoluminant component gratings is identified. Another possibility is that the mechanism detecting the plaids is less directionally selective than the mechanisms detecting the component gratings. It is well established that the direction of slowly moving isoluminant gratings cannot be identified at detection threshold (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991). If the pattern mechanism is even less directionally selective than the component mechanisms, a lower sensitivity for direction of motion of plaids than predicted from the components would be expected.

These different possibilities can to some degree be differentiated by looking at the distribution of individual direction judgments relative to the direction of motion. Figure 5(A) shows the proportion of responses at each direction to an isoluminant grating stimuli with a temporal frequency of 0.5 Hz. Direction is relative to the direction in which the grating moved, which was arbitrarily set to 90 deg in Fig. 5. The various lines show response curves at six different contrast levels, from 0.12% RMS cone contrast (heavy continuous line) up to 1.875% cone contrast (heavy dashed line). At 0.12% contrast the observer (KG) responds about equally often in the correct direction and in the opposite direction. The direction of motion cannot be reliably identified, even though the orientation is perceived correctly above

chance level. This difference between detection and direction of motion thresholds is well documented (for a recent review, see Gegenfurtner & Hawken, 1996). What becomes clear from these results is that not only can these stimuli be detected at low cone contrasts, but also that their orientation can be identified close to or at detection threshold (Webster, De Valois & Switkes, 1990). At 0.23% contrast there are hardly any responses in directions other than the correct one and the one opposite to it. The orientation bandwidth of the detection mechanisms must be considerably below 45 deg, or else responses would be seen in the directions neighboring the correct one. At higher contrasts the number of responses in the correct direction increased and the number of responses in the opposite direction decreased, and at the highest contrast tested, 1.875%, there are hardly any incorrect responses (dashed line). As a consequence, if both of the component gratings making up a plaid pattern have such a high contrast, their direction of motion should be identified and the plaid pattern be perceived to move in the resultant direction.

As was shown earlier [Fig. 2(C), Fig. 3(B), Fig. 4(B)], this was not the case. Figure 5(B) shows responses to plaid patterns consisting of components with the same contrasts as in Fig. 5(A). In this graph, the direction of the plaid pattern was normalized to be at 90 deg. Therefore, responses in the 45 and 135 deg direction indicate responses to the component gratings. At the lowest contrasts (heavy continuous line) only the responses in these component directions lay above chance level. At slightly higher contrasts the combined number of component responses is still higher than the number of pattern responses. The threshold for the direction of motion of the plaids is reached only at a cone contrast of 1.08%. At that contrast the observer was near perfect in identifying the direction of motion of the components.

It is informative to look at the directions in which the observer gave the incorrect responses to the plaids in Fig. 5(B). There were virtually no responses in the direction opposite to the direction of the plaid pattern. Incorrect responses were almost exclusively in the component directions. Therefore, the higher direction thresholds for the plaids were not caused by a less directionally selective underlying mechanism. The results for the other three observers showed a similar pattern.

DISCUSSION

In summary, thresholds for identifying the direction of motion of plaids can be predicted quite well from the direction thresholds of the components for luminance stimuli and for fast-moving isoluminant stimuli. For slowly moving isoluminant stimuli the prediction fails. Sensitivity for the direction of motion of plaid patterns is much lower than predicted from component sensitivity.

Models of plaid perception

The probability summation model specifies that the observer will give a response to a plaid in the pattern direction only if both component gratings are above threshold. This means that performance for the plaid will always be worse than performance for the components. For this prediction it is critical that the task actually requires the observer to combine the information from both components. If only obliquely oriented components were used and the observer had to indicate whether the plaid moved upward or downward, one would expect direction thresholds for the plaids to be lower than for the components, since in that case detection of either component is sufficient for a correct answer (Derrington, Badcock & Holroyd, 1992).

There are models that predict plaid thresholds to be lower than component thresholds. If the motion of local contrast differences was used to identify the motion of the plaids, then thresholds for the identification of the direction of motion of plaids would be expected to be half as high as the component thresholds, given our specification of plaid contrast as the contrast of either components, since the actual peak-to-trough contrast of the plaid is actually at twice the level of the components. This is clearly not the case for any of our data.

Comparison with suprathreshold experiments

Earlier experiments on the relationship of 2-D plaid motion to the motion of the 1-D components have almost exclusively used suprathreshold stimuli. Of these, the experiments described by Cox and Derrington (1994) are most closely related to the experiments described here. They measured minimum motion thresholds for stimuli 0.5 and 1.5 log units above detection threshold. In their experiments, a probability summation model failed to account for performance for plaid patterns. Performance for plaids was reliably better than the predictions based on the components for the high contrast stimuli. Owing to the nature of their experiments—they determined the lowest temporal frequency where motion could be seen—all stimuli had extremely low temporal frequencies (<0.5 Hz). Our results also indicate a departure from probability summation at such low speeds, but in our case performance for slowly moving luminance plaids was slightly worse than predicted. Interestingly, at low contrasts their data were much closer to probability summation. It seems that mechanisms at contrast threshold act according to probability summation and that other mechanisms come into play at higher contrasts.

Mechanisms for motion and color

The difference in the behavior of slowly moving and fast-moving isoluminant plaids agrees remarkably well with the hypothesis of dual pathways for color and motion (for a review, see Gegenfurtner & Hawken, 1996). According to this proposal, there are not two separate pathways for color and motion, as suggested by Livingstone and Hubel (1988) and Zeki (1978), but two pathways which both convey information about motion and color. In these pathways, the emphasis is on different aspects of the stimulus, depending on the specific task the information is used for. One pathway, termed fast because of its tuning to fast-moving stimuli, has a high

sensitivity to luminance defined stimuli and codes stimulus velocity invariant with respect to different cues such as contrast or color. The neural substrate of the mechanism is likely to be magnocellularly dominated and includes area MT. The slow pathway has a high sensitivity to chromatic contrast and is able to code the direction of motion of isoluminant patterns but not their velocity. It has been shown for a whole variety of tasks that above the critical temporal frequency of about 2–4 Hz there are no differences between the processing of luminance and isoluminant stimuli. Below 2–4 Hz such differences are observed, as in our plaid experiments. Apparently, the motion of the slowly moving components is detected outside of area MT and the information is not available in MT.

Neural mechanisms for plaid perception

For luminance plaids the results agree with the expectations based on what is known about the underlying physiology. The components are most likely detected by mechanisms selective to orientation and direction of motion. Amongst the most sensitive of these mechanisms are neurons in area MT (Sclar, Maunsell & Lennie, 1990), an area which mostly receives input from the magnocellular pathway (Maunsell, Nealey & DePriest, 1990). There is a sizeable proportion of neurons in area MT which can code the direction of motion of plaids (Movshon *et al.*, 1985). It seems plausible to assume that the sensitivity of the inputs to the cells responding to plaids is not different from the sensitivity of the inputs to other MT cells. If that were the case, cells in area MT responding to plaids should be able to signal the direction of motion of a plaid whenever both component inputs specify a signal. Our data support such a model for the detection of motion of plaids.

MT cells are known to respond poorly to color (Zeki, 1978; Saito, Tanaka, Isono, Yasuda & Mikami, 1989; Dobkins & Albright, 1994; Gegenfurtner *et al.*, 1994). Specifically, it has been shown that the sensitivity of MT cells to slowly moving isoluminant gratings is rather poor (Gegenfurtner *et al.*, 1994) and that MT cells are not the neural substrate for identifying the direction of motion of these stimuli. However, there is a residual sensitivity of MT cells to isoluminant gratings, and for fast-moving gratings this residual sensitivity can account for psychophysical motion thresholds. Is it possible then that the grating stimuli in our experiments are detected by highly sensitive color mechanisms outside area MT, whereas the plaid stimuli rely on the mechanisms within area MT which are less sensitive to color?

If this were indeed the case, then the threshold level isoluminant plaids should behave just like threshold level luminance plaids. The residual sensitivity of MT cells to isoluminant gratings is due to variations of the weighting factors for L- and M-cones in individual MT neurons (Gegenfurtner *et al.*, 1994). These neurons signal chromatic contrast in the same way as a low luminance contrast. Therefore, the slopes of the psychometric functions for luminance and isoluminance plaids should be identical. Figure 2(B and D) indicates that this is not the case. The slopes are much shallower for the isoluminant plaids.

A mechanism for plaid perception outside of area MT seems plausible. The complex chromatic properties of suprathreshold plaid perception also make it more likely that the underlying neural substrate would not be area MT (Krauskopf & Farell, 1990; Krauskopf, Wu & Farell, 1996; Cropper, Mullen & Badcock, 1996). Whatever the neural substrate for this mechanism is, the tuning curves in Fig. 5(B) show that it has a poor contrast sensitivity, and an orientation bandwidth much wider than the mechanisms underlying the detection of gratings. Since earlier experiments have shown that the perception of suprathreshold plaids cannot always be accounted for by the perception of the components (see, for example, Gorea & Lorenceau, 1991; Derrington *et al.*, 1992; Wenderoth, Alais, Burke & van der Zwan, 1994), it could very well be that such a less sensitive mechanism contributed to performance in these tasks.

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