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Investigation of a Patient with Severely Impaired Direction Discrimination: Evidence Against the Intersection-of-Constraints Model

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A man with presumed posterior cortical atrophy had a markedly elevated threshold for orientation discrimination (approx. 25 deg) and selective impairment of "pop-out" tasks based on orientation. Direction discrimination for moving plaids was superior to direction discrimination for their component gratings. The superior performance for plaids disappeared when the spatial frequencies of the component gratings were altered to eliminate coherence. This finding implies that extraction of plaid motion is not dependent on pre-processing within narrow spatial frequency bands. It is inconsistent with simulations based on the "intersection of constraints" model, which predict that the error rate for plaids would be larger than the error rate for gratings, particularly for the plaids composed of gratings moving at nearly opposing angles. It is consistent with models such as the Heeger [(1987) *Journal of the Optical Society of America A, 4,* 1455–1471] model, which extract direction from the pattern of activity across broadly-tuned spatiotemporal filters.

Intersection of constraints   Orientation tuning   Plaids   Posterior cortical atrophy

INTRODUCTION

Under ordinary circumstances, the visual system readily extracts a unique direction of motion from the pattern of neural activity elicited by moving objects. However, the computations used by the visual system for this purpose are at present unknown.

Any visual pattern, no matter how complex, may be decomposed into a sum of drifting gratings. Since the behavior of neurons in primary visual cortex is often considered to be well-approximated by the behavior of linear spatiotemporal filters (De Valois & De Valois, 1988), attention has been focused on how the motion of the component gratings is related to the perceived motion of the composite pattern. Plaid patterns, consisting of a superposition of two drifting gratings, provide perhaps the simplest way to explore this combination law (Adelson & Movshon, 1982). The direction of motion of a single grating is intrinsically ambiguous, in that translation parallel to the bars of the grating is invisible. But for a rigid moving object whose Fourier decomposition includes two or more non-parallel drifting gratings (such as a plaid), there is a unique velocity which is consistent with the possible velocities of all of the grating components. This unique velocity is known as the "intersection of constraints" (IOC) velocity (Adelson & Movshon, 1982; Movshon, Adelson, Gizzi & Newsome, 1985).

Since the intersection of constraints velocity is usually similar to the perceived velocity, it is natural to wonder whether the extraction of motion of complex patterns is indeed based on an IOC calculation. Here we distinguish between a neural two-stage IOC calculation and a distinct neural calculation which may provide a similar answer.

Broadly speaking, there are two kinds of models for the calculation of the direction of motion of a moving plaid. One class of models, which includes the two-stage IOC model itself, has as its essence an initial stage in which component (grating) motion is analyzed, and a second stage in which these components are combined. Psychophysical studies (Welch, 1989) showing that velocity discrimination of plaids is related to the velocity discrimination of their components lends support to this model, as does the behavior of some neurons in MT (Movshon *et al.*, 1985). Derrington and coworkers (Derrington & Badcock, 1992; Derrington, Badcock & Holroyd, 1992) elaborated on the basic IOC model to include an initial stage of processing which extracted non-Fourier motion as well. This class of models also includes the model of Wilson, Ferrera and Yo (1992),

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which is a two-stage model in which the combination of component signals differs from that of the IOC rule. This model accounts for IOC velocity perception in most circumstances, and also accounts for certain deviations of perceived velocities from the IOC velocity (Yo & Wilson, 1992).

A fundamentally different kind of model is typified by that of Heeger (1987). In this model, the visual stimulus is considered to set up a pattern of activity in an array of oriented spatiotemporal filters, and the pattern of activity in these filters is analyzed to determine the local motion. This analysis procedure does not rely on the extraction of grating components, and does not depend on whether the pattern in question is a grating or a more complex one.

Since the IOC velocity is the veridical velocity, any neural calculation which approximates the veridical velocity will necessarily approximate the IOC velocity. For this reason, it is not easy to find a psychophysical task which robustly distinguishes between the predictions of the two-stage IOC model and alternatives (but, see Yo & Wilson, 1992). However, one approach to making this distinction is that models predict not only the perceived speed and direction, but also how the uncertainty in the speed and direction judgments for a plaid is related to the uncertainty in the speed and direction judgments for its components (Welch, 1989; Stone, 1990; Heeley & Buchanan-Smith, 1992). Indeed, Welch (1989) found that speed discrimination for a plaid was determined by speed discrimination for its components, and used this result to support the two-stage IOC model. This logic can also be applied to the analysis of direction discrimination for plaids. Since precision of direction judgments is usually very high, this approach is likely to be very tedious when applied to normal observers.

We had the opportunity to study a patient whose precision at direction and orientation judgments was profoundly abnormal (threshold for orientation discrimination was approx. 25 deg). For such profound impairment, two-stage models predict that direction judgments for moving plaids composed of nearly opposing gratings will be inferior to direction judgments for the components. This is because inaccuracies in the judgment of the direction of motion of the component gratings will be compounded by the calculation stage. In contrast, models based on the pattern of activity in an array of oriented spatiotemporal filters predict that performance for plaids will be superior to performance for gratings, since more information is available in the neural response to the more complex stimuli. These alternative predictions motivated the present study. Our findings imply that the extraction of plaid motion is not dependent on an initial stage of extraction of component motion.

CASE SUMMARY

Neurological summary

The patient CS, in excellent general health, began to notice difficulty with driving at age 64, with reading and writing at age 66, and with calculations, dressing, and facial recognition at age 68. A left inferior quadrantanopsia was noted, as well as simultagnosia. Head CT and EEG were normal. Around this period, CS remarked that he had difficulty identifying the characters in a dot-matrix LED display (such as the one above the clinic elevator) unless he was sufficiently far from the display that he could not resolve the individual LEDs. Neurologic evaluation at age 70 revealed reading impairment due to character recognition rather than language difficulty *per se*, left–right confusion, finger agnosia, left-sided neglect in visual and somatosensory domains, a new right inferior field defect, mild left-sided motor signs (flattened nasolabial fold and pronator drift), and bilateral extensor plantars. General intellectual function was well-preserved, as evidenced by the patient's successful authorship of two books by dictation during this period. An MRI at age 70 showed generalized atrophy with occipital accentuation. Based on the patient's clinical course and imaging studies, the diagnosis of posterior cortical atrophy (Benson, Davis & Snyder, 1988) was made. Goldmann perimetry confirmed a left inferior quadrantanopsia at age 70, approx. 5 months prior to the study of motion discrimination. Perimetry was exceedingly time-consuming because the patient had difficulty maintaining fixation, and was therefore limited to study of the right eye. Over the next 2 yr, symptoms progressed to include poor short-term memory and impaired word-finding.

Visual disturbances

In addition to the testing of direction discrimination for moving targets described in the body of this report, extensive visual testing in other submodalities was performed at age 68 and at age 71. Contrast sensitivity (Fig. 1) as determined by a two-alternative forced-choice staircase procedure was normal for age at age 68, and was within a factor of two of normal at age 71. Routine Snellen acuity was 20/30 at age 68 and worse than 20/800 at age 71. However, the patient's difficulty identifying letters confounds the interpretation of this measure, as is evident from the near-normal contrast sensitivity even

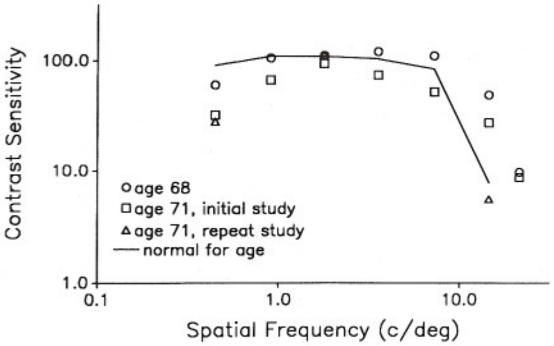

FIGURE 1. Contrast sensitivity for patient CS at age 68 and 71. The measurements (□) were obtained 6 months before the direction-discrimination measurements reported here; the measurements (△) were obtained 6 months later, just prior to these measurements. The solid line is average normal contrast sensitivity, as estimated from Owsley, Sekuler and Siemsen (1983).

at high spatial frequencies. Critical flicker fusion was above 60 Hz for full-field (Grass photostimulator) and approx. 32 Hz for a 2-deg central spot (Conrac 7351, 59 cd/m^2) at age 71.

Analysis of the patient's color vision was limited by his cognitive deficits (CS was unable to read or trace lines on any of the Ishihara luminance control plates), and complicated by a probable congenital color vision deficit (CS was excluded from military aviation training on the basis of a color deficit). A Farnsworth D15, administered at age 68 and requiring 15 min to complete, contained three transpositions [(4, 5), (10, 8, 9), (13, 14, 12)] not indicative of any specific dichromacy. The patient was unable to perform the D15 at age 71 because of difficulty keeping track of the locations of the caps. Flicker photometry at age 71 on a Conrac 7351 (central 2 deg field, 16 Hz, 59 cd/m^2) revealed a green/red balance ratio of 0.41 ± 0.03 (SEM), suggestive of deuteranomaly or deuteranopia (normal green/red balance ratio for these conditions is 0.28–0.32).

At age 68, the patient had a stereoacuity of 140 sec-arc on a vectorgraph test (Stereo Optical Co., Chicago, Ill.), and could identify the depth percept in random-dot stereograms (Julesz, 1971) with 80% correlation, but could not identify the cyclopean figure. At age 71, no stereoptic depth perception was demonstrable on either test.

Parallel search (Treisman, 1982) was assessed by asking the patient to identify a target stimulus from an array of distractors positioned in a 40-element array on test cards, as described in Victor, Maiese, Shapley, Sidtis and Gazzaniga (1989). This task, which requires that the subject point at the oddball, requires <1.6 sec/card in normals. At age 68, the patient's search rate for a blue token amidst yellow distractors (or vice versa) was nearly normal (2.0 sec/card), and the search rate for red tokens among green distractors was moderately abnormal (6.9 sec/card), most likely owing to the patient's color vision deficit. During this testing session, the search rate based on orientation (vertical tokens amidst horizontal distractors, or vice versa) was markedly abnormal, at 20.0 sec/card. The patient remarked that for the blue/yellow test cards, the unique target "jumped out", but that he had to make an explicit search when confronted with the horizontal/vertical cards. At age 71, the search rates for blue/yellow cards (1.6 sec) and red/green cards (8.0 sec) were essentially unchanged, but the patient was unable to perform the task for the horizontal/vertical cards. The patient's threshold for detecting a deviation of two lines from parallel (5-deg lines separated by 5 deg) was 18 deg at age 68, and 25 deg at age 71.

Simultaneous contrast effects and assimilation effects were qualitatively present [stimuli of Shapley (1986)] at ages 68 and 71. At age 71, the patient was unable to sort even, odd, or random isodipole textures (Victor & Conte, 1989).

At age 68, checkerboard visual evoked potentials (20 cd/m^2, 100% contrast) were mildly abnormal for $\frac{1}{2}$-deg checks (P100 latencies: 119 msec OS, 118 msec OD; 2 SD above normal: 112 msec) and borderline for $\frac{1}{4}$-deg checks (P100 latencies: 120 msec OS, 119 msec OD; 2 SD above normal: 119 msec). Results at age 71 were similar for both stimuli ($\frac{1}{2}$-deg checks: 111 msec OS, 116 msec OD; $\frac{1}{4}$-deg checks: 121 msec OS, 126 msec OD). VEP's elicited by isodipole interchange (age 68) revealed symmetric response components, but not antisymmetric response components (Victor & Zemon, 1985).

METHODS

Motion stimuli

Stimuli were presented on a Tektronix 608 monitor. The display, a 256 × 256 pixel raster at 270.3 Hz, subtended 8.8 deg at a distance of 57 cm and had a mean luminance of 140 cd/m^2. The contrast $[(L_{\max} - L_{\min})/(L_{\max} + L_{\min})]$ of the grating stimuli was 0.5. Plaid stimuli were created by interleaving two gratings at a contrast of 1.0, resulting in an effective contrast of 0.5 for the component gratings. Control signals required to produce these stimuli (raster X, raster Y, blanking and Z drive compensated for nonlinear voltage/intensity characteristics of the display) were generated by specialized digital hardware (Milkman, Schick, Rossetto, Ratliff, Shapley & Victor, 1980) interfaced to a DEC 11/73. All stimuli were viewed binocularly through a circular aperture placed on the face of the CRT.

Psychophysical methods

At the patient's cue, one experimenter triggered a 2-sec presentation of a stimulus. The stimulus moved in one of eight directions (four cardinal directions and four diagonal directions) with equal probability. The patient was asked to communicate the direction of perceived motion by word and gesture to the second experimenter, who was positioned to observe the patient but not the stimulus. The second experimenter communicated with the patient until both were satisfied that the patient's perception was understood. The second experimenter's impression of the subject's response was then recorded. This rather elaborate approach was necessary to minimize the confounding effects of the patient's left/right confusion. Blocks consisted of 30–40 trials of each stimulus (in randomized directions), with short breaks every 10 trials, and four or five blocks per weekly testing session. Data presented here represents performance averaged across two to four blocks of each condition on separate testing days.

RESULTS

Direction judgments for moving gratings and plaids

We examined direction judgments for 2 c/deg gratings moving at four velocities (0.58, 1.15, 3.0 and 7.8 deg/sec), and for three moving plaids composed of 2 c/deg gratings: 135-deg plaids with components at 1.15 and 3.0 deg/sec, and a 157.5-deg plaid with components at 0.58 deg/sec. For gratings, the patient's direction judgments ranged from 16% correct [not significantly different from chance (12.5%)] at 0.58 deg/sec to 69% correct at 7.8 deg/sec (Fig. 2). For all three plaids, performance was superior to grating performance for all but the fastest grating. The fraction of correct judgments for plaids ranged from 66 to 71% correct.

It is useful to compare performance for gratings and plaids on the basis of the velocity of the individual component gratings and the velocity of the pattern itself (Welch, 1989). For a plaid composed of two gratings of equal velocity moving at a relative angle θ, pattern and component velocities are related by $v_{\text{pattern}} = v_{\text{component}}/\cos(\theta/2)$.

Figure 2(a) compares performance for plaids to performance for gratings whose velocities match those of the components of the plaid. In all cases, performance was substantially better for the plaids (66–71% correct) than for their components (16–52% correct). χ^2 statistics for the three comparisons were: (1) $v_{\text{component}} = 0.58$ deg/sec, $v_{\text{pattern}} = 3.0$ deg/sec, $\theta = 157.5$ deg: $P < 0.0001$; (2) $v_{\text{component}} = 1.15$ deg/sec, $v_{\text{pattern}} = 3.0$ deg/sec, $\theta = 135$ deg: $P < 0.0002$; (3) $v_{\text{component}} = 3.0$ deg/sec, $v_{\text{pattern}} = 7.8$ deg/sec, $\theta = 135$ deg: $P < 0.02$. Thus, by this test, performance for plaids was substantially superior to performance for their component gratings.

We also compared performance for plaids to performance for gratings whose velocities match the pattern velocity of the plaid [Fig. 2(b)]. Performance for plaids moving at 3 deg/sec ($\theta = 135$ deg with $v_{\text{component}} =$ 1.15 deg/sec and $\theta = 157.5$ deg with $v_{\text{component}} = 0.58$ deg/sec) was superior to that for gratings moving at the pattern velocity ($P < 0.005$ and $P < 0.03$ by χ^2). Performance for the plaid moving at 7.8 c/deg ($\theta = 135$ deg with $v_{\text{component}} = 3$ deg/sec) was similar to that for a grating at the pattern velocity ($P = 0.8$ by χ^2).

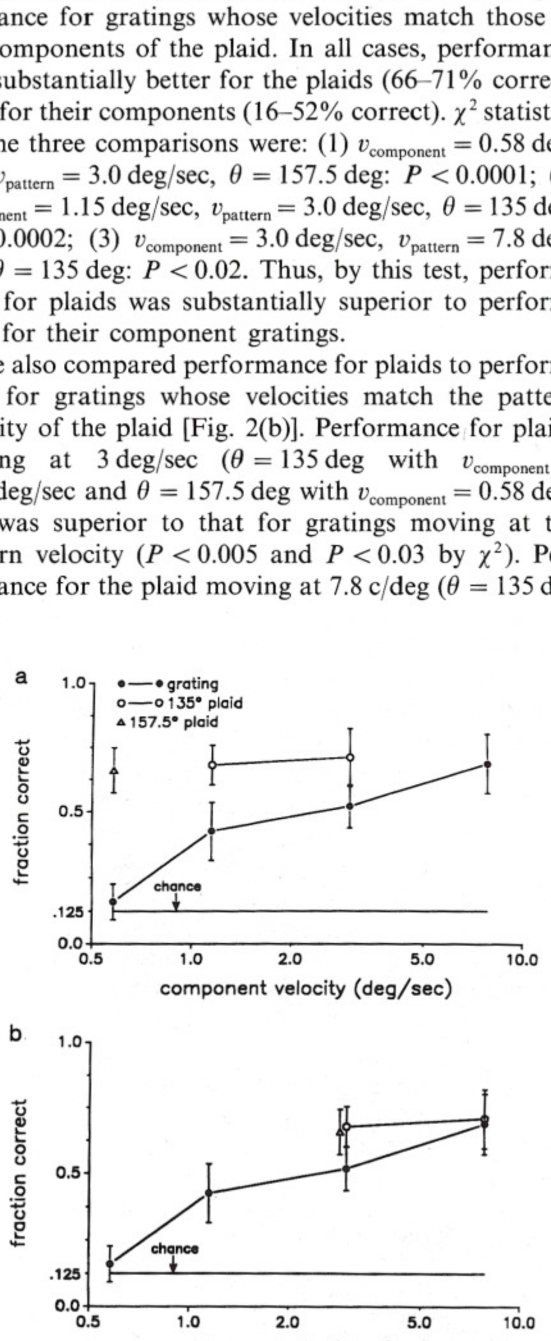

FIGURE 2. Direction discrimination performance for gratings and plaids compared on the basis of component velocity of the plaids (a) and pattern velocity of the plaids (b). Error bars are 95% confidence limits calculated by binomial statistics.

To extract a parametric measure of direction judgment from our eight-alternative forced-choice task, we examined CS's error pattern in more detail. We estimated an r.m.s. error by assigning a 45-deg error to each response that was one removed from the correct response, a 90-deg error to each response that was two removed from the correct response, etc. r.m.s. errors in direction judgments for gratings decreased monotonically with velocity, from 82 deg at 0.58 deg/sec to 32 deg at 7.8 deg/sec. r.m.s. errors in direction judgments for plaids were essentially independent of velocity, and ranged from 33 to 38 deg. For the high-velocity comparison (7.8 deg/sec plaid and grating), performance was similar both as measured by percent correct (71 vs 69%) and root-mean-squared error (35 vs 32 deg). The disappearance of the plaid vs grating difference at high pattern velocities may represent a ceiling in the patient's ability to make direction or orientation judgments of any kind.

The details of CS's performance for one of the 3 deg/sec plaids ($\theta = 157.5$ deg with $v_{\text{component}} = 0.58$ deg/sec) are analyzed in Fig. 3. As is seen from the histograms, even though direction judgment for the plaids was correct 66% of the time, direction judgments for the components were in error by 90 deg or more nearly half of the time [Fig. 3(b)]. The estimated r.m.s. error for the plaid was 33 deg [Fig. 3(a)]. The estimated r.m.s. error for its components was 82 deg [Fig. 3(b)], and the estimated r.m.s. error for a grating at the pattern velocity was 49 deg [Fig. 3(c)].

Dependence of performance on direction of motion

For gratings, there was no significant difference in the patient's judgments for leftward vs rightward motions (30 vs 38% correct across all velocities, $P = 0.17$ by χ^2). There was a suggestion of superior performance for cardinal over diagonal directions of motion (46 vs 36% correct across all velocities, $P = 0.047$), but performance for diagonal directions was superior at 1.14 deg/sec. For plaids, there was no significant difference in performance for leftward vs rightward motions (55 vs 61% correct, $P = 0.41$) or for cardinal vs diagonal motions (70 vs 65% correct, $P = 0.32$).

There was, however, a difference in performance for vertical and horizontal directions of motion. For gratings, performance was 29% correct for horizontal motions and 53% correct for vertical motions ($P < 0.001$). For plaids, performance was 46% for horizontal motions and 84% correct for vertical motions ($P < 0.001$). Of note, because of the large plaid angles, plaid trials with horizontal motions contained component gratings moving nearly vertically, and plaid trials with vertical motions contained component gratings moving horizontally. Thus, the vertical vs horizontal difference reflects a difference in performance based on pattern motion, not motion of the grating components.

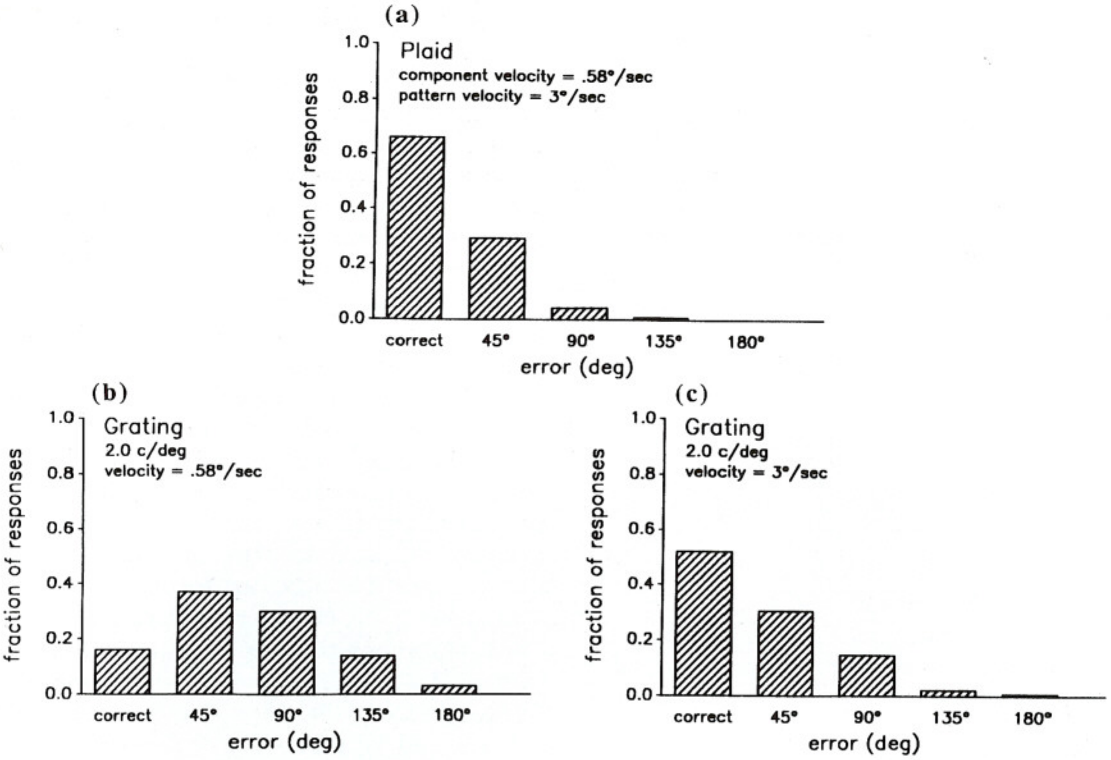

FIGURE 3. Details of the subject's performance for one of the 3 deg/sec plaids [(a) $\theta = 157.5$ deg with $v_{\text{component}} = 0.58$ deg/sec], and for single gratings moving at the component velocity (b) and the pattern velocity (c).

Plaids composed of gratings of unequal spatial frequency

In normal subjects, plaids composed of gratings of equal spatial frequencies are more likely to be perceived as coherent than plaids composed of gratings of unequal spatial frequency (Adelson & Movshon, 1982). We therefore altered the relative spatial frequency (but not the velocity, contrast, geometric mean spatial frequency, or relative direction) of the two gratings which comprised one of the 3 deg/sec plaids ($\theta = 157.5$ deg with $v_{\text{component}} = 0.58$ deg/sec). As seen in Fig. 4, direction-discrimination performance fell from its baseline value of 66% correct for component spatial frequencies in the ratio 1:1 to near-chance with component spatial frequencies in the ratio 1:8.

In normal subjects, the stimulus with a spatial frequency ratio of 1:1 (2 c/deg) produces a percept of nearly pure coherence, and the stimulus with a spatial frequency ratio of 8:1 (spatial frequencies of 5.6 and 0.7 c/deg) produces a percept of nearly pure transparency. Subjectively, CS perceived the 1:1 stimulus as coherent (he described it as a "waffle"), and was unable to provide a clear verbal description of the 8:1 stimulus, although he did indicate that he saw motion. Thus, it appears that the patient's superior performance for plaids disappeared when the spatial frequencies of the component gratings were altered to eliminate coherence.

Simulations based on the IOC calculation

We compared CS's performance with that predicted by the IOC model (Adelson & Movshon, 1982) for the extraction of plaid motion. The geometry of this model (Fig. 5) implies a specific relation between the errors in estimation of component directions and the errors in the estimation of the plaid direction. Stone (1990) has provided analytic expressions for this relationship which are asymptotically correct for small errors. However, CS's performance for gratings was not in the "small-error" range—as is seen in Fig. 3(b), errors of 90 deg or more were common. With errors as large as these, the IOC geometry would predict frequent miscalculations of the direction of plaid motion by 180 deg. Since this regime is difficult to analyze by the method of Stone (1990), we resorted to Monte Carlo simulations.

We considered two possibilities for the nature of the uncertainty of the component velocities: errors in direction alone, and errors in direction and speed. To simulate errors in direction alone, the veridical velocity vectors of the components were perturbed by rotation

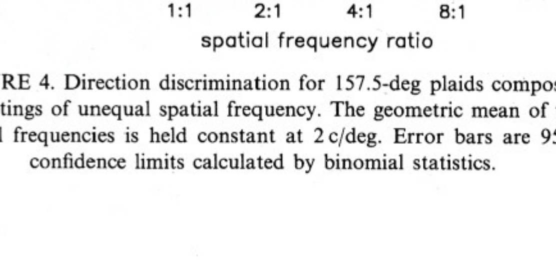

FIGURE 4. Direction discrimination for 157.5-deg plaids composed of gratings of unequal spatial frequency. The geometric mean of the spatial frequencies is held constant at 2 c/deg. Error bars are 95% confidence limits calculated by binomial statistics.

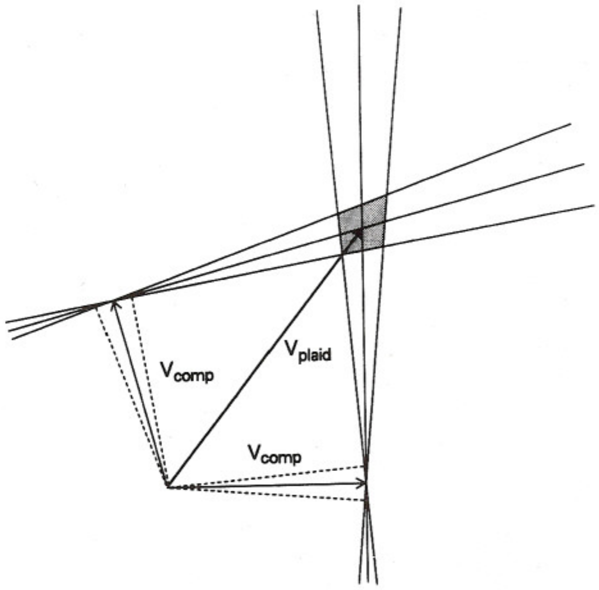

FIGURE 5. A diagram of the intersection-of-constraints model. Errors in the determination of the direction of component motion determine the errors in the determination of the direction of the plaid motion.

through an angle which was chosen from a Gaussian distribution. To simulate errors in direction and speed, the veridical velocity vectors of the components were perturbed by addition of a random vector, chosen from a two-dimensional (circular) Gaussian. Then, the plaid velocity was calculated by the IOC geometry from these perturbed velocity vectors. This calculation was carried out for 10,000 examples of plaids, with 20 levels of error (r.m.s. error ranged from 0.05 radians to 1.0 radians in steps of 0.05) and seven plaid angles, ranging from 22.5 to 157.5 deg.

The ratio of the r.m.s. error in plaid direction to the r.m.s. error in the component direction is shown in Fig. 6. For errors in direction only [Fig. 6(a)], plaid error is less than component error, provided that component error of the plaid angle θ is small. For shallow plaid angles and small errors, the IOC calculation essentially averages the directions of the components, and in this regime, the plaid error/component error ratio approaches $2^{-1/2}$. However, for larger plaid angles, the effects of component errors are magnified. For example, with plaid angles of 157.5 deg and component errors of 0.7 rad (similar to the range of error in patient CS), plaid errors would be expected to be two or three times as large as component errors. This behavior is qualitatively

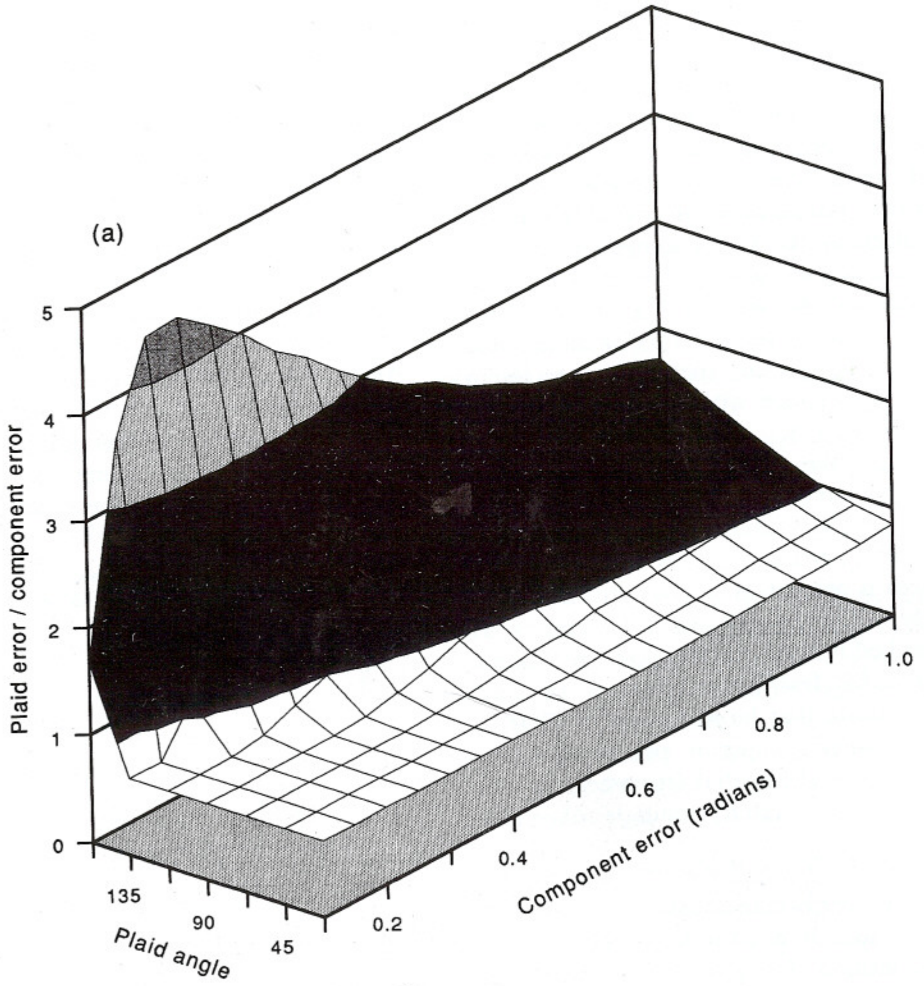

FIGURE 6(a). *Caption opposite.*

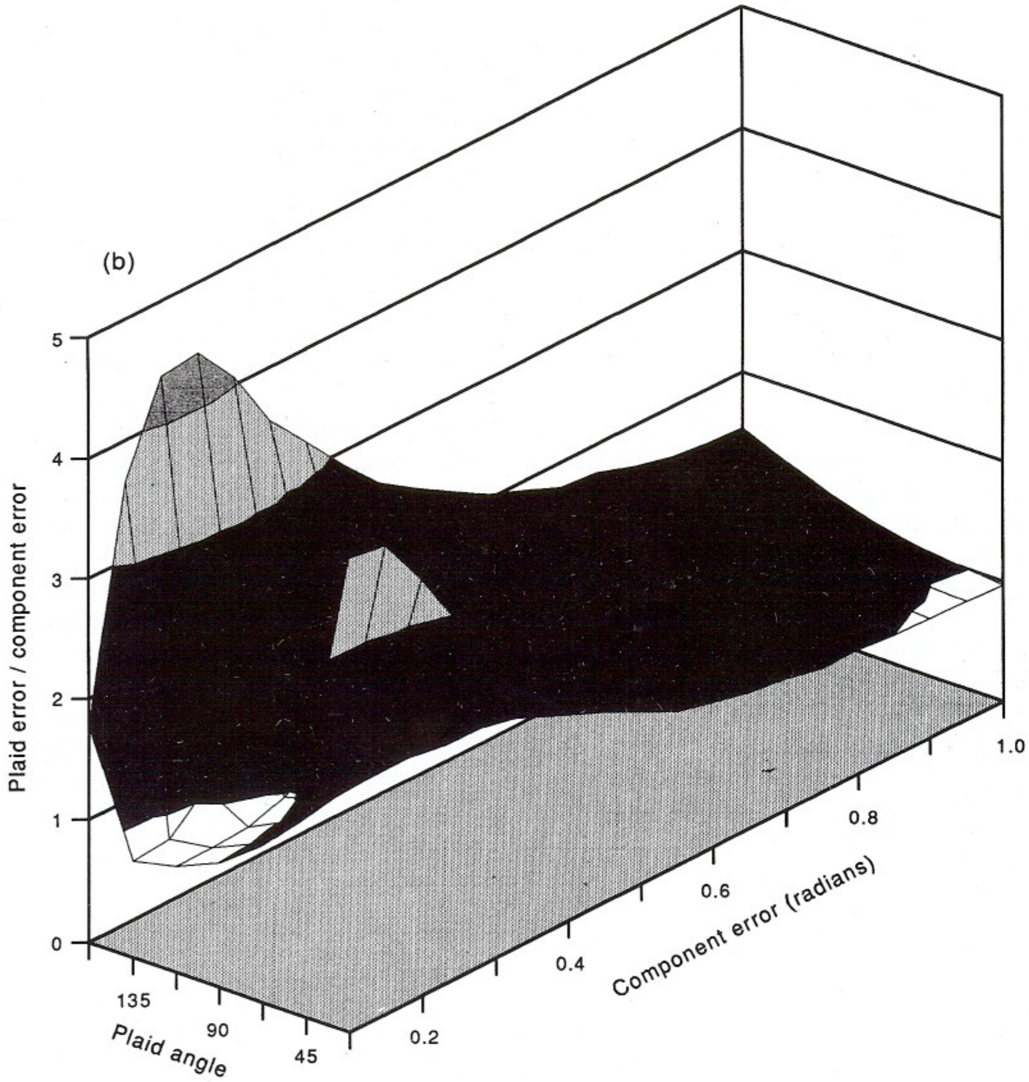

FIGURE 6. Simulations of the relationship of errors in the determination of the direction of a plaid to errors in the determination of the direction of its grating components, as predicted by the intersection-of-constraints computation. Errors are r.m.s. angular deviations. (a) Errors in direction only. (b) Errors in direction and speed.

inconsistent with what we have observed: at low velocities, CS performed better for plaids than for gratings, even for large plaid angles.

For errors in speed and direction, behavior of the IOC model was similar for large component errors or large plaid angles, and thus also fails to account for what we have observed. The main effect of introducing errors in component speed estimation into the IOC models is in the regime of small plaid angles and small component errors. In this regime, the speed-and-direction error only model predicts that directions of plaid motion will be estimated with several times greater error than the directions of their components [front corner of Fig. 6(b)]; the reverse is true if the only direction errors are made in the estimation of component velocities [front corner of Fig. 6(a)]. The sensitivity of the IOC calculation to small velocity errors for nearly parallel components is a consequence of the geometry of Type II plaids (Ferrera & Wilson, 1990).

Simulations based on vector averaging

We next considered the behavior of another model for the neural combination of component directions: that of vector averaging. We used a similar Monte Carlo method to simulate the effects of errors in direction alone, and errors in direction and speed. As seen in Fig. 7, vector averaging (for either kind of error) behaves in a similar fashion to the IOC calculation for errors in direction only. For large plaid angles and large errors, vector averaging predicts that errors in plaid judgments will exceed errors in component judgments by a factor of two or more.

Simulations based on the model of Heeger (1987)

We next compared the patient's performance with that predicted by a very different kind of model, in which the determination of the direction of plaid motion does not depend on a prior determination of the direction of motion of the component gratings. The core of this model (Heeger, 1987; Heeger & Simoncelli, 1992) is that the pattern of activity elicited by the visual stimulus in an array of relatively broad-band filters is compared with the pattern of activity elicited by rigidly-moving broadband noise. The speed and direction extracted by the model is given by the speed and direction of the moving broadband noise whose pattern of activity most closely matches that of the stimulus itself.

To simulate the behavior of a particular example of this kind of model, we used a set of idealized Gabor-function linear filters, each with aspect ratios of 2:1 and two oscillations per receptive-field width. Filters were constructed with best spatial frequencies spanning the range 1–8 c/deg in half-octave steps, best temporal frequencies spanning the range 1–8 Hz in half-octave steps, and in 12 equally-spaced orientations. Following Heeger (1987), we constructed a goodness-of-fit function which compares the normalized pattern of activity in these filters elicited by a moving broadband noise to the pattern of activity in these filters elicited by the stimulus. The location of the maximum of the goodness-of-fit function (as a function of the velocity of the moving noise) provides the extracted velocity. Uncertainty in velocity estimation corresponds to a particular region of tolerance around the maximum. Uncertainty in the extraction of velocity is thus proportional to the sharpness of this maximum. Consequently, to a first approximation, the ratio of expected errors for plaids and gratings is independent of the assumed level of uncertainty for gratings: it depends only on the relative sharpness of the maxima.

In effect, this notion of uncertainty amounts to the addition of noise to a pattern-matching calculation. Because this pattern-matching is based on the output of Gabor detectors, addition of independent noise to the outputs of these detectors themselves (or to their inputs) would have a similar effect, and is not separately considered. Another way in which uncertainty could be added to this model would be to jitter the "labels" which tag each Gabor filter with its spatial frequency, orientation, or temporal frequency. This might seem most closely analogous to the addition of uncertainty to component directions in the IOC model. However, in the Heeger model, the extraction of direction does not depend on these labels, but only on comparisons of the overall pattern of activity with that elicited by a standard stimulus as seen by the same detector array. Thus, jittering of the labels would have no effect on the performance of the Heeger model.

Results of the simulation are shown in Fig. 8. For all plaid angles above 45 deg, the uncertainty for plaids is *less* than the uncertainty for gratings. Similar behavior was found for other choices of the parameters for the

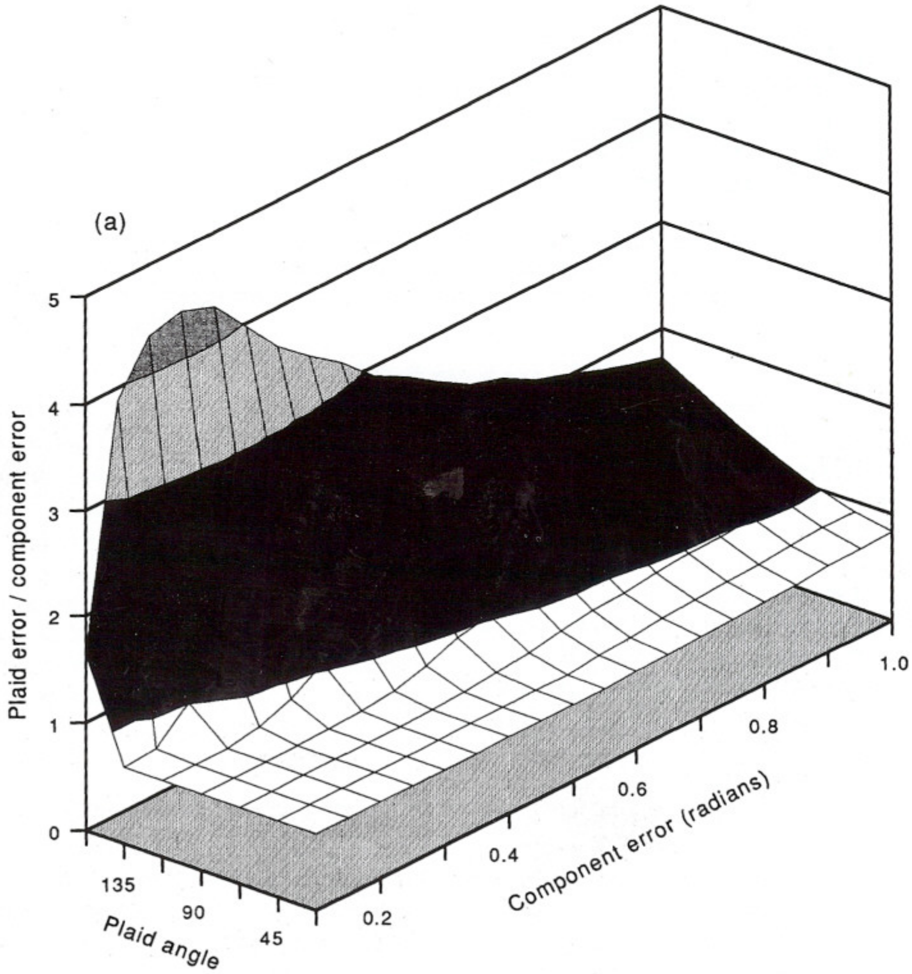

FIGURE 7(a). *Caption opposite.*

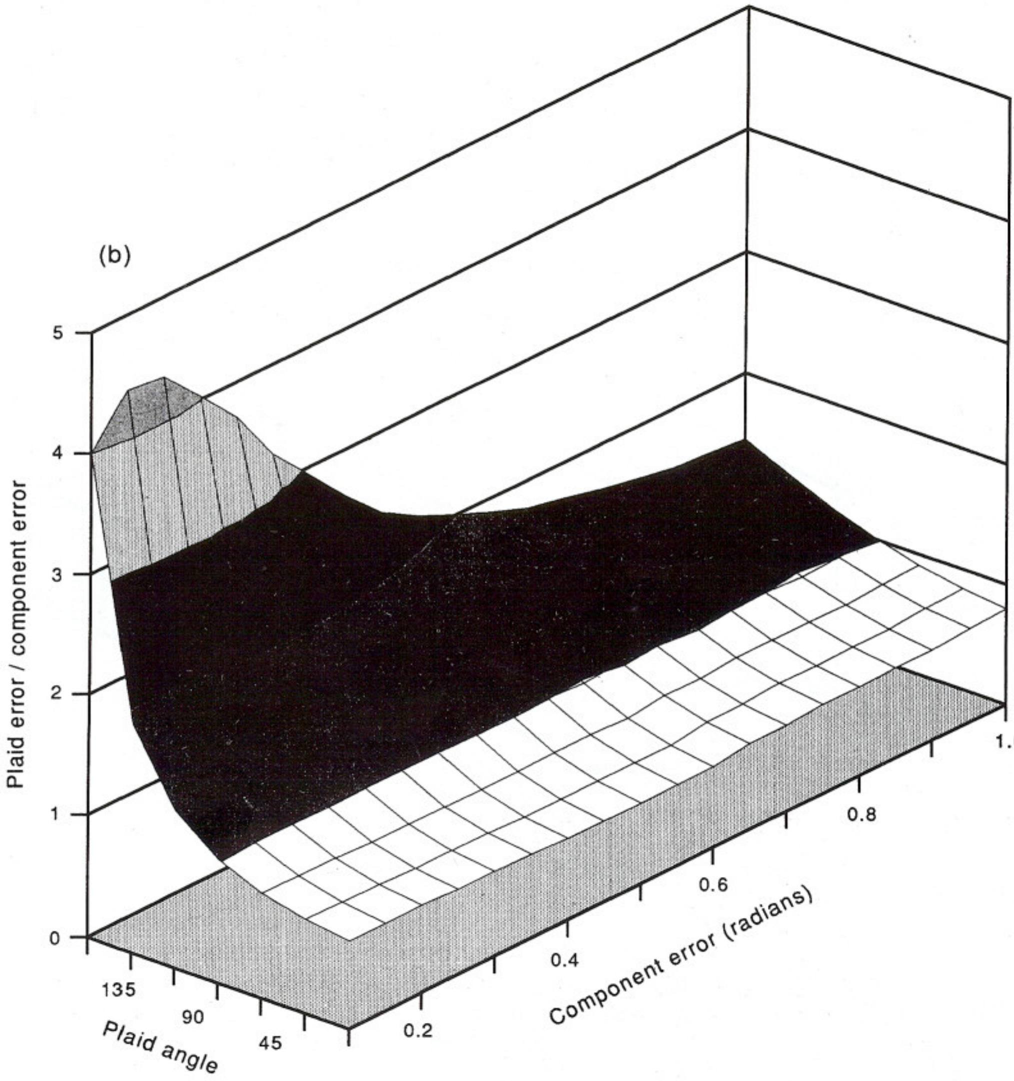

FIGURE 7. Simulations of the relationship of errors in the determination of the direction of a plaid to errors in the determination of the direction of its grating components, as predicted by vector averaging. Errors are r.m.s. angular deviations. (a) Errors in direction only. (b) Errors in direction and speed.

Gabor filters. The reason for this behavior is as follows. A given drifting grating will appear in the Fourier decomposition of a drifting noise stimulus whenever the component of the grating's velocity along the direction of motion of the noise stimulus equals the velocity of the noise. Therefore, the Fourier decomposition of a drifting noise stimulus contains drifting gratings of a multiplicity of speeds and directions. Conversely, a drifting grating will have Fourier components in common with drifting noises of a multiplicity of speeds and directions. As a consequence, the neighborhood of the maximum of the goodness-of-fit function [viewed as a function of the vector velocity of the drifting noise (Heeger, 1987)] for a grating will look more like an elongated ridge than a peak: all drifting noises which contain the grating as a Fourier component provides similarly good fits. For a plaid, the situation is different. A drifting noise which contains one of the grating components provides a partial fit, but the unique drifting noise which contains both grating components (the IOC velocity) provides a superior fit. Therefore, the neighborhood of the maximum of the goodness-of-fit function for a plaid will be a sharp peak, positioned at the intersection of the two ridges corresponding to each of the component gratings.

DISCUSSION

We have presented a patient CS with gradually progressive loss of visual function associated with MRI evidence of occipital atrophy. This patient had a markedly elevated threshold for orientation discrimination (25 deg), despite grating contrast sensitivity and visual acuity which were normal for age. Performance on "pop-out" tasks based on orientation differences was selectively impaired. The markedly elevated threshold for orientation differences allowed us to determine the relationship of errors in direction judgments for moving plaids to errors in direction judgments for their grating components. In all cases, the patient was able to judge the direction of motion of plaids with greater accuracy

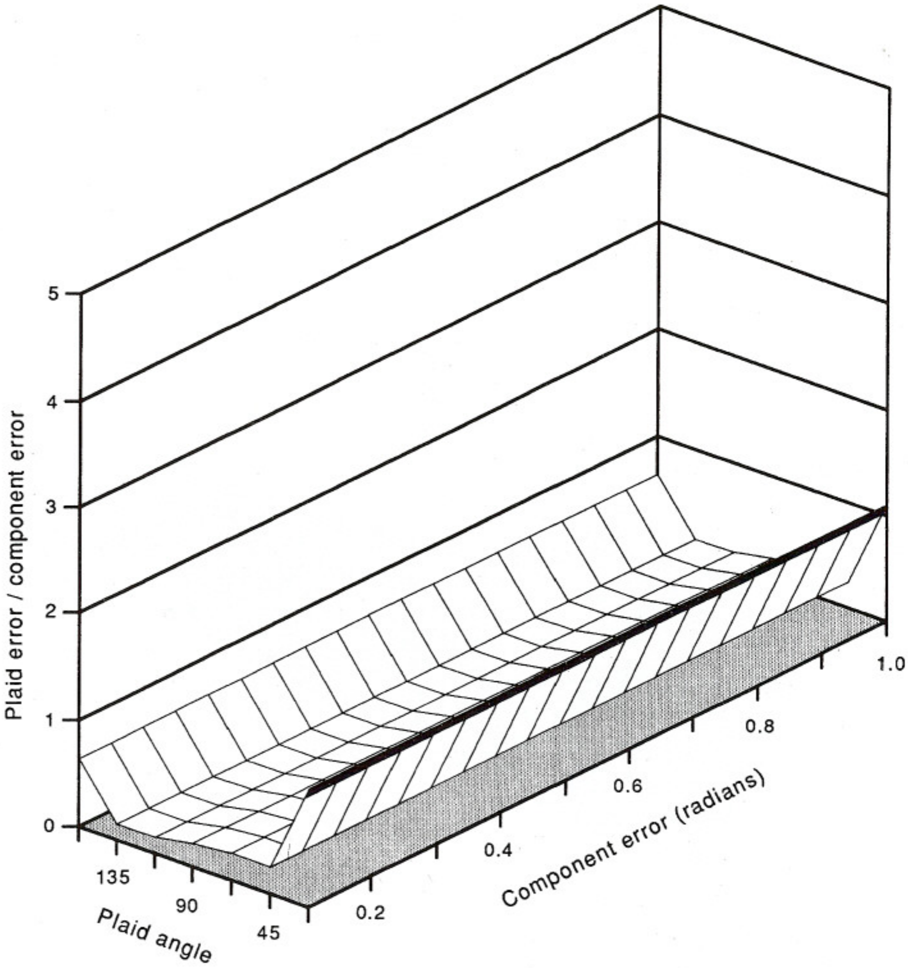

FIGURE 8. Simulations of the relationship of errors in the determination of the direction of a plaid to errors in the determination of the direction of its grating components, as predicted by a model based on that of Heeger (1987). Errors are r.m.s. angular deviations.

than he could judge the direction of motion of the component gratings, or of gratings moving at the plaid velocity.

While it is clear that this patient had many associated abnormalities (reading and memory impairment, left-right confusion, motor impairments), we believe it is unlikely that these abnormalities contributed to the above finding. As shown by the patient's precise and reproducible null points in heterochromatic flicker photometry, the patient retained the ability to make precise psychophysical judgments based on visual information. Any general impairment in making or communicating direction judgments would not have resulted in a selective impairment of judgments for gratings vs plaids. Our findings cannot be explained by a selective impairment for direction judgments for stimuli of a particular speed, since plaid performance was superior when compared to performance of gratings which matched the plaid either in component velocity [Fig. 2(a)] or pattern velocity [Fig. 2(b)]. Finally, although left–right confusion may well have contributed to the poorer performance for horizontal vs vertical motions, left–right confusion cannot account for our findings. Even within vertical motion trials, direction judgment was superior for plaids (84% for plaids, 53% for gratings). Note that since our plaids were constructed with large angles (135 or 157.5 deg), vertically-moving plaids consisted of component gratings whose motion was nearly horizontal.

An *exact* IOC calculation based on inaccurate component directions results in performance which (for the plaid angles used) is substantially worse than performance for gratings (Fig. 6). Thus, in order to account for the superior performance for plaids compared to gratings, it is necessary to postulate that the process of extraction of direction of moving plaids has access to more information than merely the result of the process of extraction of direction of moving gratings. (Otherwise, one would be forced to hypothesize that the patient had a deficit in the ability to report direction of motion which was specific to gratings, an idea which is formally consistent with our data, but defies understanding in terms of known physiology or psychophysics.) Thus, two-stage models, in which component motion is first extracted and then this information is the input to plaid motion extraction, cannot explain our data.

The alternative view is that the pattern of activity in motion-sensitive units is available for the extraction of motion of complex stimuli, such as plaids, without first generating component-velocity signals. We have shown (Fig. 8) that our findings are consistent with one proposed model of this form (Heeger, 1987). It is unclear whether our data are consistent with the model of Wilson *et al.* (1992). This model contains an initial stage of motion-sensitive elements followed by a combination rule which resembles vector averaging, and thus deviates from the IOC computation. Vector averaging as such fails to explain our data (Fig. 7), but a full test of this model would require alteration of its parameters to match the very poor direction tuning shown by our data. Given the substantial number of parameters of this model, it may be possible to do so in a way which retains the essential features of our data. It is also possible that a two-stage computation of pattern motion occurs in parallel with a Heeger-like process. In the patient studied here, the two-stage arm would yield very little direction information (since grating direction information was highly degraded), and thus performance would be dominated by a Heeger-like computation.

A moving grating is an ambiguous stimulus—it is consistent with motion in a continuum of directions and velocities. However, plaids, provided that they are perceived as coherent, are unambiguous. Viewed in this fashion, it is no surprise that computations which extract motion from a pattern of activity in motion-sensitive units operate more precisely for plaids than for gratings. But, if processing of plaid motion depended only on the output of a stage of grating motion analysis, extraction of direction of motion for plaids (for large-angle plaids) could not be more accurate than extraction of direction of motion for gratings. Our finding that extraction of direction of motion for plaids may be substantially more accurate than the extraction of direction of motion for its components implies that motion processing is not adequately modelled as a two-stage process dependent on an initial stage of extraction of motion of grating components.

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