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Directional Acuity for Drifting Plaids

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Orientation discrimination thresholds were estimated for symmetrical "plaids", constructed by the super-imposition of two, independent drifting sine-wave gratings of 2.5 c/deg. Experiments were conducted when the apparent direction of drift was on the two principal meridians (vertical and horizontal), and when the apparent direction of drift was at the two oblique orientations (45 and 135 deg). Acuity for the direction of drift for these stimuli is of the same order of precision as orientation acuity for static or drifting gratings, and exhibits a meridional anisotropy that favours the principal meridians. This anisotropy follows a pattern that is determined by the apparent direction of drift, and not *the orientation of the underlying elements. Acuity for orientation is lowest for oblique drift directions, even though both of the elements are oriented on the principal meridians. This finding was confirmed when the orientation of the underlying elements was subject to a random variation. The results are not easily accommodated by models that propose that the individual elements of the plaid are analysed separately. Second, the data are incompatible with models of the oblique effect of orientation discrimination that are based on an axis dependent, differential sampling of the retinal image.*

Orientation acuity Meridional anisotropy

INTRODUCTION

The orientation of features or components of the retinal image must form a crucial part of the neural representation of that image. Visual object recognition would not be possible without an accurate code for orientation. It is clear that orientation perception is remarkably acute, and that observers can discriminate and recognise changes in orientation that are <2.0 deg. Orientation discrimination falls, in the majority of cases, within the range of precision that corresponds to "hyperacuity" (Westheimer, 1979). This level of precision has been obtained by many authors, using a diverse range of stimuli and psychophysical techniques (e.g. Buchanan-Smith & Heeley, 1992; Caelli, Brettel, Rentschler & Hilz, 1983; Heeley & Buchanan-Smith, 1990, 1992; Heeley & Timney, 1988; Matin & Drivas, 1979; Matin, Rubsamen & Vannata, 1987; Orban, Vandenbussche & Vogels, 1984a, b; Paradiso & Carney, 1988; Regan & Beverley, 1985; Regan & Price, 1986; Scobey, 1982). Whilst there is considerable agreement concerning the overall levels of precision of orientation acuity, there is less consensus over the manner in which the code for image orientation is derived.

One major class of models of orientation perception has a basis in the known physiology of the mammalian visual system. These models presuppose that the retinal image undergoes an initial stage of processing by a range of orientation selective, band-pass spatial filters. It is then hypothesised that the outputs of the individual filters are combined in such a manner as to yield a signal that varies with image orientation. Different models propose different combinatorial rules, but all have the same implicit assumption that the filters or "channels" carry unique labels for orientation (Watson & Robson, 1981; Thomas & Gille, 1979; Thomas, Gille & Barker, 1982). All reject the hypothesis that orientation is encoded by changes in the output level within individual units (cf. Bradley, Skottun, Ohzawa, Sclar & Freeman, 1987; Hawken & Parker, 1990).

Three major types of combinatorial rule may be identified. Regan and co-workers (Regan & Beverley, 1985; Regan & Price, 1986) have suggested that orientation is encoded as the ratio of the outputs of adjacent channels by an opponent process. Orientation discrimination is then limited by the magnitude of the change in this ratio, rather than that of the response of an individual filter. They have demonstrated that this model can explain their finding that orientation acuity is enhanced by contrast adaptation.

Alternatively, a model of hyperacuity performance has been proposed by Wilson and his colleagues that could be applied to the case of orientation discrimination (Wilson, 1986; Wilson & Gelb, 1984). Their model is a form of line-element computation where discrimination is based on the pooling in a Euclidean space of the change in filter responses to the two discriminanda. This model implies that the visual system must accurately store the individual filter outputs in temporal forced

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choice experiments so that the change in response of the individual filters can be computed prior to combination.

Finally, Thomas has developed a model of orientation perception that is based on the computation of a vector in a multi-dimensional space (Thomas & Gille, 1979; Thomas, Gille & Barker, 1982). He proposes that the orientation of a stimulus is encoded as a vector sum of the outputs of individual, orientation specific filters. The representation is not exact, but is disturbed by noise. Orientation discrimination within this model reduces to a discrimination between two noisy signal distributions within this vector space and can be treated within the analytical framework of Signal Detection theory. There is, at present, little or no empirical evidence that clearly favours one, rather than another of the above hypotheses.

A characterising feature of orientation acuity, and one that is not treated explicitly by any of the above models, is that discrimination thresholds exhibit a marked meridional anisotropy. Thresholds are lower on the principal meridians than on either of the two obliques and are unaffected by the exact luminance distribution used for the stimulus (Heeley & Buchanan-Smith, 1990, 1992; Heeley & Timney, 1988). Meridional anisotropies are not found for all spatial discriminations, which casts doubt on a structural origin of the phenomenon (Heeley & Timney, 1988, 1989). The anisotropy of orientation acuity would be compatible with any of the above combinatorial models if there were differences in the sampling of the orientation domain between the obliques and vertical and horizontal (Orban *et al.*, 1984a, b), differences in the orientation band-widths (Thomas & Gille, 1979; cf. Heeley, Timney & Thompson, 1988), changes in intrinsic noise, or even differences in the efficiency of the combinatorial process. However, recent experiments have demonstrated that the meridional anisotropy is a multi-component effect that involves storage processes and the use of information that does not arise directly from the retinal image (Buchanan-Smith & Heeley, 1992; Heeley & Buchanan-Smith, 1990, 1992). Even when these factors are taken into account an anisotropy remains that must be presumed to be a reflection of meridional variation in cortical architecture or physiological properties. Whether these variations exist at the level of the striate cortex is a matter of conjecture.

The present experiments exploited the meridional anisotropy of orientation discrimination as a test of channel or filter based combinatorial models. The stimuli used were drifting "plaids" originally devised by Adelson and Movshon (1982) in their studies of motion perception. Ferrera and Wilson (1990) identify two major classes of "plaid", of which their Type I are used here. The "plaids" are constructed by super-imposing two independent drifting sine-wave gratings. The Type I "plaids" that we used in our experiments had (with the exception of drift direction), identical spatio-temporal parameters for the two elements. As a consequence, the perceived direction of drift of the overall pattern is in a direction that is intermediate between that of the two symmetrical elements.

An established experimental finding is that orientation acuity is lower for oblique gratings than for either vertical or horizontal gratings. The question arises as to whether or not there is a meridional anisotropy of orientation acuity for the direction of drift of "plaids". On the presumption that the anisotropy reflects structural properties of the visual system (Mansfield, 1974; Mansfield & Ronner, 1978), all three filter or channel based models above would predict (i) that there should be a meridional anisotropy for "plaids" and specifically (ii) that the anisotropy should be determined by the orientation of the underlying elements, and *not* the direction of drift.

METHODS

Apparatus and stimuli

The stimuli were combinations of sine-wave grating modulations of luminance that were produced by a "Picasso" image generator. They were displayed by conventional means on the face of a Tektronix 606A monitor. The monitor had a P31 phosphor with a mean luminance of 31 cd/m^2 and was calibrated with a Tektronix J16 digital photometer.

The linearity of the screen response to the brightness modulating signal was measured by a UDT PIN photodiode, mounted on a travelling microscope. The microscope was fitted with an adjustable spectrometer slit in the image plane. The screen brightness was found to be linear within 2% over the range used for the experiments.

An opaque screen was fixed to the face of the monitor to reveal a free area of 4 deg dia at the viewing distance of 114 cm. A small opaque spot was placed in the centre of the screen to aid fixation and accommodation. Mild head restraint was used in the form of a chin rest, forehead bar and temple pads. Viewing was binocular through natural pupils.

The image generator was interfaced to a laboratory computer that provided independent control of the contrast, spatial frequency and orientation of the two components of the "plaid". The "plaid" was formed by frame alternation of the two components at a rate of 200 Hz. The computer controlled the progress of the experiment and accumulated the observers' responses. The stimuli were presented with a Gaussian temporal envelope of contrast with a dispersion coefficient of 250 msec, truncated at $\pm$750 msec and a peak Michelson contrast of 0.7. All stimulus presentations were preceded by a warning tone.

In all cases the spatial frequency of the gratings was set at 2.5 c/deg with a temporal frequency of 8 Hz.

Procedure

Orientation discrimination thresholds for drift direction were estimated by a modified method of constant stimulus differences, combined with a two-interval temporal forced-choice. A set of five possible orientations of drift direction were computed in advance of the experiment. They were evenly and symmetrically disposed around the reference or "standard" direction. The width of the set was determined from pilot studies to cover the range from the 5 to 95% frequency of seeing points approximately.

An experimental trial comprised two stimulus intervals, defined by the Gaussian envelope of contrast. Each interval was preceded by a warning tone. One interval contained the "standard" stimulus and the other contained the "test" stimulus, drawn at random from the set of five possible values. The order of "test" and "standard" was varied randomly from trial to trial. The task of the observer was to decide, on each trial, which of the two intervals contained the stimulus that was tilted most in a clockwise direction. This decision was communicated to the computer by pressing one of two buttons on a hand-held response box. A third button press initiated the next trial. The experiment was self-placed and no feedback was given. Each of the five possible pairings of "test" and "standard" were repeated in random order 25 times, making a total of 125 observations for each condition.

In order to prevent the possibility that the observer may mediate the task by recognition, as distinct from discrimination mechanisms (Heeley & Buchanan-Smith, 1990), an identical random offset of orientation was added to both the "test" and "standard" stimuli on each trial. The offset was changed from trial to trial, and was drawn from a uniform probability density distribution with a width of 5 deg.

A cumulative normal error function was fitted to the forced choice responses by an iterative, maximum likelihood technique based on the Probit method on completion of testing (Finney, 1971). The iterative cycle was terminated when the estimate of the slope parameter had converged to within 0.5% of the value derived on the preceding cycle of calculation. Thresholds were defined as the reciprocal of the slope of normalised probability against test orientation. This definition corresponds to the difference between the 84 and 50% frequency of seeing points.

Observers

Four observers were used. They were two volunteers, paid for their participation, and the two authors. The volunteers were naive to the purposes of the study. S.M. and G.H. had no prior experience and were given approx. 1 hr training trials before the commencement of testing. All observers were refracted professionally and were found to be emmetropic, with no astigmatism greater than 0.25 D.

Experiments

We adopt the terminology "elements" to refer to the two sinusoids that were summed to form the "plaid". The number of observers is shown, in each case, in parentheses. The conditions that were tested were:

Experiment 1, single drifting grating at 0, 45, 90 and 135 deg ($N = 4$).

Experiment 2, static plaid with 90 deg between elements, orientation of elements of 0 combined with 90 deg, and 45 combined with 135 deg ($N = 2$).

Experiment 3, drifting plaid with 90 deg between elements, drift direction of 0, 45, 90 and 135 deg ($N = 2$).

Experiment 4, drifting plaid with random variation of the inter-element orientation ($N = 4$). For this condition, the orientation difference between the two elements was altered randomly from presentation to presentation. Specifically, the relative orientation between the two elements of the "plaid" was fixed throughout the duration of any presentation ("test" or "standard"), but was then altered prior to the presentation of the comparison stimulus ("standard" or "test"). The spatial frequency of the two sine-wave grating elements was always identical to maintain the symmetrical nature of the "plaid", but was co-varied with the alteration in relative orientation between presentations. The manipulation of spatial frequency maintained a constant perceived drift rate in the desired direction.* The Picasso image generator produced a stimulus of constant temporal frequency. Given that the velocity is inversely related to the spatial frequency, the spatial frequency of the plaid elements was adjusted such that:

$$f \times \cos(\Theta) = \text{constant} \qquad (1)$$

where: f = spatial frequency, and Θ = the angular subtense between the sine-wave and the desired direction of perceived drift of the plaid.

The random variation of orientation was drawn from a uniform probability density distribution with a width of 40 deg, centred on a 90 deg orientation between the elements. In all experiments that employed "plaids", whether the inter-element orientation was fixed or varied randomly, we emphasise that the stimuli always appeared to be rigid and drifting coherently.

RESULTS

The results from Exp. 1 (thresholds for single, drifting sine-wave gratings) are illustrated in Fig. 1. The data for different observers are indicated by different bar styles for the four orientations tested.

The results are conventional in every way, and serve as a reference point for the later results using "plaids" (see below). The thresholds overall are of very much the same level of precision as those reported previously for orientation recognition and orientation discrimination thresholds using static stimuli (Heeley & Timney, 1988; Heeley & Buchanan-Smith, 1990). In particular, they are closely comparable with the results from our previous experiments that have employed a random offset of the

*Pilot studies revealed that unless spatial frequency was co-varied with inter-element orientation to maintain a constant drift velocity, there were many instances when the "plaid" appeared to be either virtually stationary, or drifting so rapidly that the pattern could only just be resolved. In these cases the judgement of drift direction could not be made.

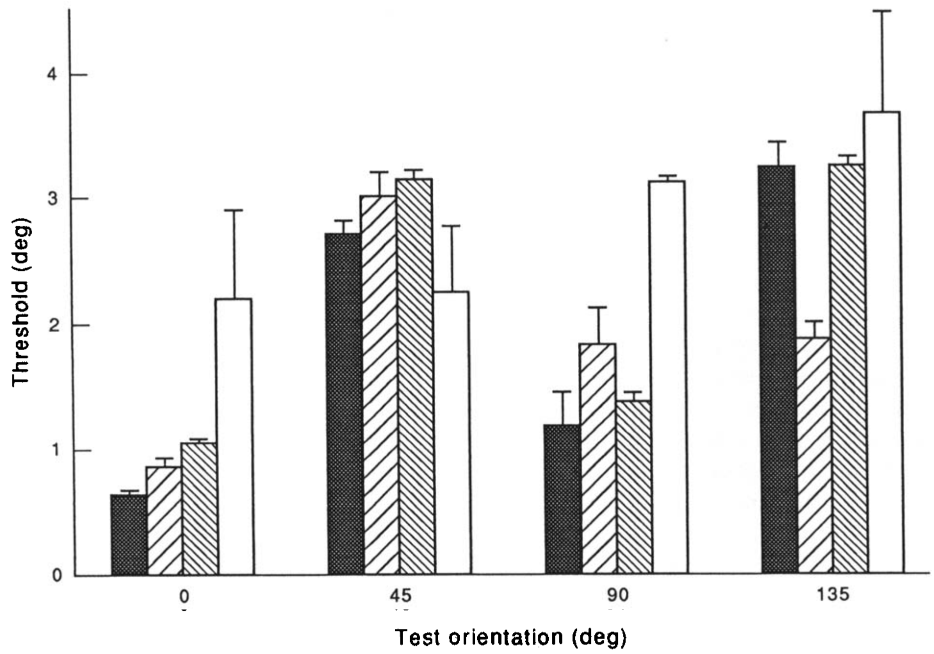

FIGURE 1. Orientation discrimination thresholds as a function of test orientation for single, drifting sine-wave gratings of 2.5 c/deg. The differing styles of bar are data from different observers.

orientation of the "test" and "standard" in a temporal, two-alternative forced-choice.

Figure 1 illustrates that orientation acuity for drifting stimuli is slightly in excess of 1 deg on the principal meridians, and exhibits a pronounced meridional anisotropy. Testing at obliques yields thresholds that are nearly a factor of 2 greater than those obtained for vertical or horizontal stimuli. It is notable that acuity on the principal meridians is remarkably fine. A liminal rotation of the target of 1.3 deg implies that the maximum displacement of the outermost edge of the grating traverses a distance of only five cone photoreceptor diameters at most. We note that the meridional anisotropy for drift direction that we report here contrasts sharply with the lack of an oblique effect that is found for many of the other parameters associated with the perception of motion stimuli, such as the motion after-effect and contrast thresholds (reviewed by Nakayama, 1985).

The thresholds that were obtained with static "plaids" with 90 deg between the gratings are shown in Fig. 2. The different styles of bar indicate the data from different observers. It should be noted that the abscissa *does not* indicate the orientation of the individual elements. The abscissa is the orientation that is half way between that of the individual gratings, and corresponds to the direction in which the "plaids" would be seen as moving if the gratings were temporally modulated.

Two possible drift directions for the overall "plaid" can be achieved that depend on the exact direction of drift of the individual components. As a consequence, a stimulus that is indicated as either "0 deg" or "90 deg" has elements at 45 and 135 deg. Similarly, a stimulus that is indicated as "45 deg" or "135 deg" has elements at 0 and 90 deg.

The data are again clear, with close agreement between the two observers that were tested with this condition, and are comparable with those from Exp. 1. Discrimination thresholds show a meridional anisotropy with the lowest acuity when the structural elements are oriented at obliques. In the present case this is for the

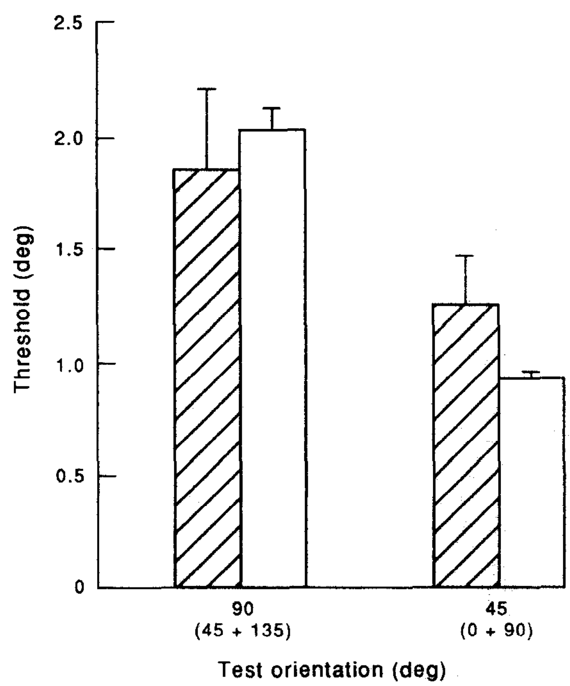

FIGURE 2. As for Fig. 1 with static "plaid". The orientation between the two elements of the stimulus was fixed at 90 deg. The abscissa indicates the direction that the plaid would be seen to drift in if the gratings had been temporally modulated. The orientation of the individual elements are at ±45 deg with respect to the abscissa values (see text).

"90 deg" "plaids". Acuity is a factor of 2 lower compared to stimuli with the two elements on the principal meridians ("45 deg").

The pattern of the meridional anisotropy changes radically when the "plaids" are drifting. This is emphasised by the data illustrated in Fig. 3. The format of the figure is similar to that of Fig. 2. The same two observers were used and the orientation between the two elements was fixed at 90 deg. Thresholds overall are of a similar level of precision as those reported for the other experimental conditions.

There are, however, three aspects of these results, taken in combination with those of Exp. 2 (Fig. 2) that can be noted. First, there is once more a marked meridional anisotropy in orientation acuity. Second, and of greater theoretical importance, is the fact that the anisotropy *follows the direction of perceived motion* and not that of the orientation of the underlying structural elements. Figure 3 shows that the greatest acuity (and lowest thresholds) are found for the vertical and horizontal directions of drift. Thresholds drop by 23% on average for "plaids" on the principal meridians when the "plaids" are drifting rather than stationary. The change in threshold that accompanies the transition from static to moving is even more marked in the case of the oblique "plaids". In this case thresholds *rise* by 72% on average.

Finally, an important aspect of these results derives from the rise in threshold with oblique "plaids". As was shown in Exp. 1 (Fig. 1), the individual thresholds for the two elements that comprise the drifting oblique "plaids" are both lower than the overall threshold obtained when the two are combined into a "plaid". The mean threshold for drifting gratings on the principal meridians is 1.21 deg. This contrasts sharply with the mean threshold of 2.91 deg for "plaids" drifting in an oblique direction.

This result is not compatible with simple statistical considerations. It might have been supposed that the two elements of the "plaid" were processed by separate filtering mechanisms with orthogonal preferred orientations, each disturbed by stochastically independent noise. The simplest prediction is therefore that thresholds should fall by a factor of $2^{0.5}$ when the two elements are combined. The rise in threshold strongly implies that the visual system does not have access to the outputs of the early stages of visual filtering.

The results of the final experiment (Exp. 4) are illustrated in Fig. 4. The orientation discrimination thresholds are shown as a function of the perceived direction of drift for the two principal, and the two oblique meridians. The different styles of bar correspond to the data for the four observers. The data for the different observers are in close agreement. There is a marked meridional anisotropy in thresholds that follows the direction of drift, and thresholds are again closely comparable with those found for other stimuli with radically different spatio-temporal properties.

The random variation in the orientation of the underlying elements in this experiment has abolished the possibility of channel uncertainty effects (Nachmias & Kocher, 1970) that could have contaminated the results obtained with fixed inter-element orientations (Exp. 3, Fig. 3). The fact that spatial frequency co-varied with the random alteration in orientation means that an observer can only solve the experimental challenge by comparing the apparent directions of the two stimuli.

It follows that any filter or channel based model of the general form outlined above would predict that this discrimination would be impossible. There is a random variation in the absolute level of response of individual orientation selective units between the two intervals that define the discriminanda. Any combinatorial process or algorithm that is based ultimately on response level in linear filters cannot yield a reliable signal for orientation in this task.

DISCUSSION

A synopsis of the results is provided in Fig. 5 to emphasise the findings. The different styles of bar illustrate the different test orientations. The figure clearly shows that all test conditions yield a meridional an-

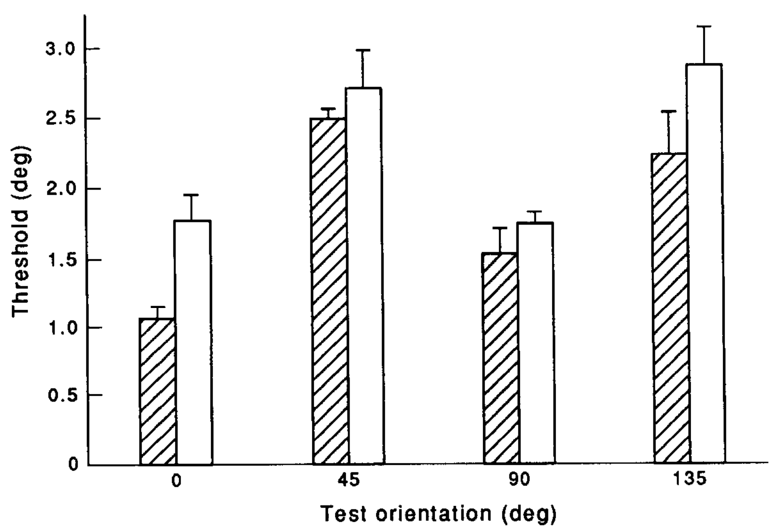

FIGURE 3. As for Fig. 2 with drifting plaids. The abscissa indicates the perceived direction of drift.

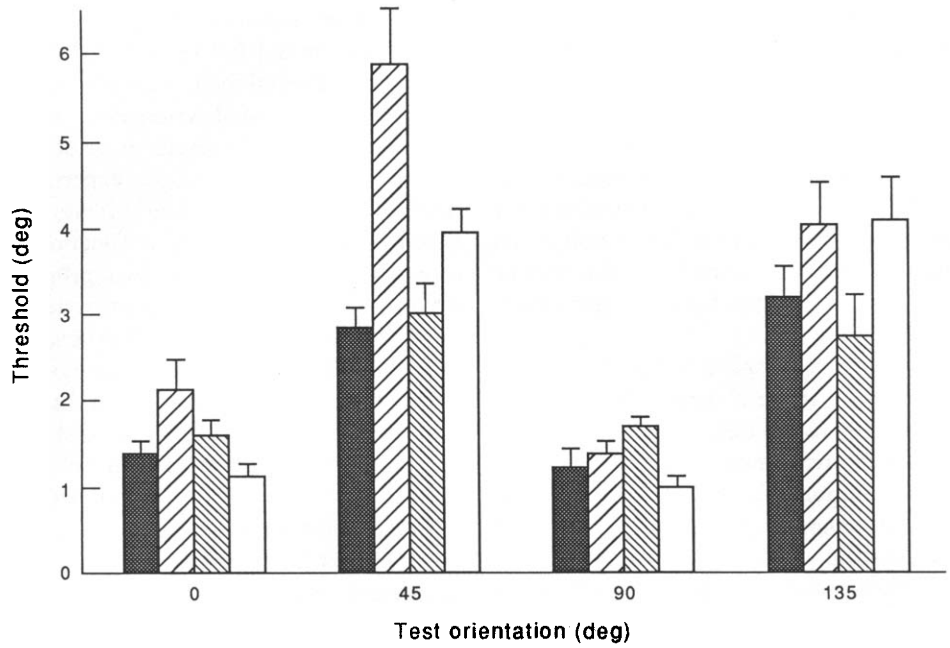

FIGURE 4. As for Fig. 3 with plaids that had a random variation of the relative orientation between the two elements. The spatial frequency of the gratings was co-varied with the random alteration of orientation in order to maintain a constant perceived velocity (see text).

isotropy. The overall pattern of results appears to be different for the "static plaid" condition, but as was outlined above this is due to the fact that for these stimuli, the orientation of the underlying gratings was at 45 deg to the axis of orientation shown. The figure highlights the important comparison between test orientations that interacts with temporal modulation. The axis of the meridional anisotropy in orientation discrimination thresholds rotates through 45 deg when a static plaid is subjected to motion, even though all other spatial parameters are kept constant.

The results also illustrate the fact that orientation acuity on the principal meridians with "random plaids" is as high as with any other stimulus. It should be born in mind that this performance level was obtained with stimuli that were subjected to a random orientation jitter of the underlying elements over a range of 40 deg. The only constant factor in these stimuli was the direction and velocity of drift. The data cast doubt on the adequacy of filter or channel based models of orientation perception.

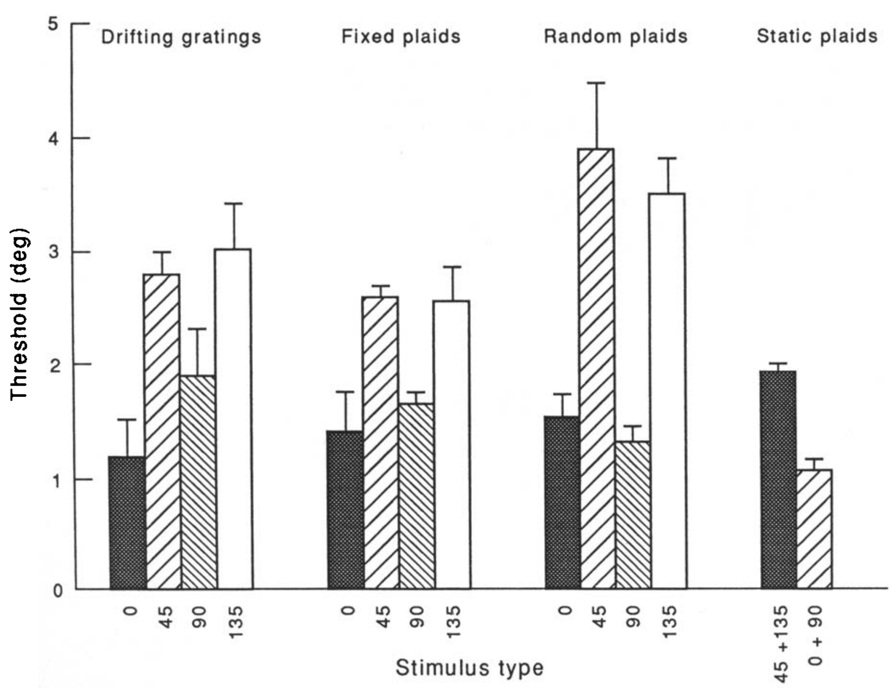

FIGURE 5. Synopsis of experimental results. Mean thresholds for the four axes tested are shown for the different stimulus conditions.

It has been suggested recently by Bowne (1990) that the general class of error propagation models are an inappropriate description for orientation discrimination. He compared the shapes of the contrast functions for contrast increment and orientation thresholds at low contrasts. Contrast increments depend strongly on the absolute contrast level, whereas orientation thresholds do not. Error propagation models explicitly place the main limiting factor in discrimination as occurring at the early stages of filtering, and would predict a contrast dependence for all spatial tasks. Additive noise at the early levels creates an error distribution to the response that is then carried through to higher level processes. The present data support Bowne's rejection of error propagation theories. Thresholds with random plaids are no higher at vertical and horizontal test orientations than those obtained with single drifting gratings. The introduction of the random variation would be equivalent to a very substantial increase in noise at the early stages of filtering. Error propagation models would predict that orientation discrimination should be extremely difficult, if not impossible, with these stimuli.

We may form three main conclusions. First, that the main limiting factors in orientation acuity are at a relatively high level in the hierarchy of visual processing. This level is clearly beyond the point at which the underlying structural elements (or Fourier components) have been independently extracted and the outputs of this operation have been combined. Second, the observer does not have direct access to orientation information that arises at the early levels of processing, presumably in striate cortex (Bradley *et al.*, 1987; DeValois, Yund & Helper, 1982; Hawken & Parker, 1990; Paradiso, Carney & Freeman, 1989; Parker & Hawken, 1985). If the observer did have access to low level orientation information, then orientation discrimination thresholds should always be limited by the precision with which changes in the orientation of the underlying elements can be detected. Our data in Fig. 5 clearly show that this is not the case, because "plaids" that are drifting in an oblique direction have higher thresholds than either of the two elements from which they are constructed when these elements are presented in isolation. This conclusion is similar to that of Welch (1989) who showed that observers do not have access to information regarding the speed of the underlying elements that form a "plaid", but only have access to pattern information that arises at a second stage where component information is combined. Welch's finding differs from ours in that she showed that the limiting factor in velocity discrimination lay at the lower level, rather than at some point beyond that at which pattern structure is computed.

Finally, the present results lead to a rejection of theories of the origin of the meridional anisotropy in spatial vision that are based on architectural properties of the striate cortex (Mansfield, 1974; Mansfield & Ronner, 1978; Orban *et al.*, 1984a, b). They provide additional support for this conclusion that we have previously drawn from comparisons of the meridional variation in human visual performance on contrast detection, spatial fequency and orientation discrimination (Heeley & Timney, 1988, 1989).

A more appropriate theoretical characterisation of early visual processes than response level filter based models, is needed in the particular case of orientation perception. Formal computational models that are based on the extraction of a primitive symbolic representation have been proposed that differ in a fundamental way from models that operate in the Fourier domain (Marr & Hildreth, 1980; Watt & Morgan, 1985). A common feature of these models is that the outputs of low level filters are inextricably combined prior to analysis, and that all analysis proceeds on a spatially mapped symbolic description of the image. Investigations of the statistical efficiency of spatial frequency acuity are well described by models of this general class (Heeley, 1985, 1987, 1990; Heeley & Thompson, 1989).

A concept of "central" or "task dependent" noise as the main limiting factor in visual acuities is easily accommodated within these theories. However, adoption of this general approach implies a change of emphasis regarding the status of feature orientation as a component of the visual image code. It has been traditionally assumed that orientation is part of an orthogonal basis set that defines the neural representation. The present results would support the alternative view, that orientation is a *derived* quality that had been computed from a low level symbolic description. Within this scheme, the exact origin of the meridional anisotropy remains to be made explicit.

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