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An independent effect of spatial frequency on motion integration reveals orientation resolution

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ABSTRACT

Problem: To investigate the independent role of spatial frequency on component motion integration.
Method: Two Type II plaids were presented at varying spatial frequencies. The velocity vectors of the underlying components were constructed so that predicted speed and direction from the components; the Intersection of Constraints; the vector average; and distortion products, remained constant for each of the two plaids across spatial frequency. Perceived direction was measured using a method of adjustment.
Results: Perceived direction changed as a function of spatial frequency, approaching the pattern direction only at spatial frequencies greater than 0.5 cpd.
Conclusions: Spatial frequency has an independent effect on the component integration stage that determines perceived pattern motion direction. The results appear to reflect the resolution of orientation for recombination of the components at low spatial frequencies. These results have implications for motion modelling and possible clinical applications.

1. Introduction

Spatio-temporal energy models of motion generally have a first stage where 2D pattern motion is decomposed into its constituent 1D components, and a later stage where these components are integrated to recover 2D pattern motion (Adelson & Movshon, 1982; Bowns, 2002; Movshon, Adelson, Gizzi, & Newsome, 1985; Simoncelli & Heeger, 1998; Wilson, Ferrara, & Yo, 1992).

The first stage decomposition results in the representation of 2D spatial components that vary in luminance in only 1D and have the properties of orientation, contrast, and velocity. This stage is consistent with both human and primate physiology. Evidence has shown that cells in layer 4B of area V1 in the visual cortex of primates respond specifically to such components (Hawken, Parker, & Lund, 1988; Livingstone & Hubel, 1988; Orban et al., 1986); similar properties are also found in area V5/MT of the visual cortex (Britten, Shadlen, Newsome, & Movshon, 1992; Dubner & Zeki, 1971). Further support comes from psychophysical research (Britten et al., 1992; Campbell & Robson, 1968; Movshon et al., 1985; Welch, 1989).

Visual cortical area MT/V5 appears to be specialised for the later integration stage. Single cell recordings in primates show that while cells in V1 are component-direction selective cells, cells in MT contain both component-direction selective neurons (approximately 40%) and pattern selective neurons (approximately 25%) (Movshon et al., 1985; Newsome & Pare, 1988; Newsome, Wurtz, Dursteler, & Mikami, 1985; Rodman & Albright, 1989). The receptive field size of cells in MT are approximately 10 times larger than those in V1 (Majaj, Carandini, & Movshon, 2007) and therefore make this area more suitable for encoding pattern motion. Also lesions in area MT of the macaque selectively disrupt the sensitivity to motion coherence (Newsome & Pare, 1988).

The two most ubiquitous methods for combining components at the second stage are the intersection of constraints (IOC) (Adelson & Movshon, 1982; Bowns, 2002); and the vector average (Wilson et al., 1992). The vector average solution is obtained by averaging the x- and y-components of each vector. The IOC rule requires velocity constraint lines to be drawn perpendicular to each of the vectors in velocity space, and it is their point of intersection that defines the IOC direction. Both methods make clear predictions regarding the perceived direction of moving patterns constructed from two components (plaids). When the IOC rule predicts perceived direction to fall to one side of both components these are referred to as 'Type II' plaids (Ferrera & Wilson, 1990). Type II plaids are interesting because they predict a different direction to that predicted by the vector average. Type I plaids are plaids where the IOC predicts perceived direction that falls between the components, and is similar to that predicted by the vector average. Predictions from the IOC rule have been tested and supported (Bowns, 1996, 2006; Burke & Wenderoth, 1993; Movshon et al., 1985; Stone, Watson, & Mulligan, 1990). However, when Type II plaids are used it is also clear that at short durations predictions favour the vector average (Bowns, 2006; Cropper, Badcock, & Hayes,

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1994; Yo & Wilson, 1992). However, Type II plaids can also be perceived in the IOC direction at short durations (Bowns, 1996; Bowns & Alais, 2006). In fact it appears that both solutions can be simultaneously present (Bowns & Alais, 2006).

There have been several explanations for why some Type II plaids move in the vector average at short durations. For example, the original explanation was that it revealed an early combination rule, i.e. the vector average rule (Yo & Wilson, 1992). However this cannot be the correct explanation because when the predicted difference increases, Type II plaids are not perceived in the vector average at short duration, and in fact shift towards the IOC direction; clearly showing that the result does not generalize (Bowns, 1996). A Bayesian explanation was also suggested (Weiss, Simoncelli, & Adelson, 2002), this involved the addition of noise to the velocity vectors. However, it has been argued that this is also an unsatisfactory explanation because there is over 50° difference for the two short duration plaids used here and yet they share the same components with just a small difference in speed (Bowns, 2002) – this paper in addition suggests an explanation based on a new underlying motion model (Component Level Feature Model), that has recently been further developed by Bowns (2009).

It is also known that plaid direction is influenced by second-order information, i.e. new components with different orientations and spatial frequencies that are introduced when two or more components are combined. These are distortion products (e.g. Castet & Morgan, 1996; Derrington, Badcock, & Holroyd, 1992). For a complete description of the IOC, Vector average, and distortion products together with the equations for computing predicted directions see Bowns (2006).

There have been a number of studies that have investigated the effects of spatial frequency on pattern motion. However, these mainly focus on the effects of relative spatial frequency of the components on perceived coherence (Kim & Wilson, 1993; Smith, 1992), or the effects of spatial frequency on speed (Aaen-Stockdale & Bowns, 2006; Cox & Derrington, 1994). There appears to be little or no research that measures perceived motion direction as a function of spatial frequency when the spatial frequency of both components is equal. One study used a motion-after-effect to reveal the effects of spatial frequency on pattern motion (Alais, Wenderoth, & Burke, 1994). They reported evidence for a feature/blob tracking mechanism, and showed that this mechanism was less visible to the motion system at low spatial frequencies, and suggested that there was some optimal feature size that would effect perceived motion. In this paper a set of experiments are carried out that measured perceived direction directly in plaids as a function of spatial frequency; and at the same time ensure that motion direction remained constant from all known possible sources, i.e. the components, IOC, vector average, and distortion products. In addition each of these sources had different directions to facilitate interpretation of the results.

2. Experiment 1

2.1. Method

The stimuli were presented randomly with a similar number of presentations. Perceived direction was measured using a method of adjustment. Observers had normal or corrected vision and all except the authors were naïve with respect to the hypothesis.

2.2. Apparatus and stimuli

All stimuli were generated on an Apple Macintosh computer with a 20″ monitor with a screen resolution of 1024 × 768 pixels running at a frame rate of 99 Hz. The screen subtended 31° of visual angle when viewed from 57 cm, therefore each pixel subtended 1.8 arcmin. The experiment was programmed and run in Matlab version 5. The screen background was maintained at a constant level corresponding to the mean luminance of the stimuli.

2.3. The stimulus

Two plaids were constructed using two components in cosine phase in the first frame that moved within a circular aperture with a diameter of 8 cm, giving a viewing angle of 8°. The orientation of the components in the stimuli was always 202° for the first component and 225° for the second component. Orientation was specified with respect to the horizontal and increased in an anticlockwise direction (polar definition of orientation). The phase of the components was updated on every second frame to create motion. The frame rate was linked to the vertical blanking of the screen, and there were 16 frames. Therefore at 99 Hz the duration was 161 ms. The phase of the component with orientation 225 was either 0.45 (speed = 0.754 cm/s) or 0.75 (speed = 1.257 cm/s) of the phase of the component with orientation 202 (speed = 1.676 cm/s), thus creating the two Type II plaids. The speed of the gratings was kept constant as a function of spatial frequency. The plaid was computed using the following equations:

$$\text{Plaid} = 1/2(c_1\cos(p_1 + \lambda_1(2\pi y\cos\theta_1 + 2\pi x\sin\theta_1)) + c_2\cos(p_1 + \lambda_2(2\pi y\cos\theta_2 + 2\pi x\sin\theta_2))$$

where c = contrast, p = phase, λ = spatial frequency, θ = orientation.

The plaid was then squared and the following equations were used to extract the two most salient distortion products:

$$f_1 \text{ spatial frequency} = \sqrt{\lambda_1^2 + \lambda_2^2 + 2\lambda_1\lambda_2\cos\theta_1 - \theta_2}$$

$$f_2 \text{ spatial frequency} = \sqrt{\lambda_1^2 + \lambda_2^2 - 2\lambda_1\lambda_2\cos\theta_1 - \theta_2}$$

$$f_1 \text{ Orientation} = \frac{180\arctan\left(\tan\frac{\theta_1+\theta_2}{2}\right)}{\pi}$$

$$f_2 \text{ Orientation} = -\frac{180\arctan\left(\cot\frac{\theta_1+\theta_2}{2}\right)}{\pi}$$

The vector average and the IOC were computed using:

$$x = (s_1\cos\theta_1) + (s_2\cos\theta_2)$$
$$y = (s_1\sin\theta_1) + (s_2\sin\theta_2)$$
$$VA = \arctan(y/x)$$

$$x = \csc(\theta_1 - \theta_2)(s_2\sin\theta_1 - s_1\sin\theta_2)$$
$$y = -(s_2\cos\theta_1 - s_1\cos\theta_2)\csc(\theta_1 - \theta_2)$$
$$\text{IOC} = \arctan(y/x)$$

where θ = direction, s = speed.

The predicted directions for each of the sources of possible motion was:

Plaid with speed ratio 1.0:0.45: IOC = 61.710°; vector average = 121.840°.

Plaid with speed ratio 1.0:0.75: IOC = 88.430°; vector average = 119.09°.

The predicted direction for the distortion products is the same for both types of plaid because it is measured at 0 phase angle. The predicted direction for the high frequency distortion product (spatial frequency = 7.8394) was 123.5°; and for the low frequency distortion product (spatial frequency = 1.59494) predicted direction was 33.5°.

2.4. Procedure

Observers viewed the stimulus in a dimly lit room. A chin and head-rest was used to ensure correct viewing distance. The experiment began with a 700 ms. fixation point in the center of the screen. Observers were asked to fixate on the point throughout each trial. The fixation was replaced by the stimulus. The stimuli were randomly presented in blocks of 40 trials. Within each block there were eight different stimuli, two Type II plaids each of which could have 1 of 4 different spatial frequencies ranging from 0.125 cpd to 1 cpd. When the stimulus disappeared an adjustable indicator line was generated at the center of the screen with length equal to the diameter of the stimulus. Observers were asked to rotate the line to indicate the direction of their perceived motion for each stimulus, and then click the mouse when they were satisfied with their judgment. This initiated the next trial. Observers were informed that all judgments would be in the upper quadrant. Each observer responded to four blocks giving 20 observations per unique stimulus.

2.5. Results for experiment 1

Fig. 1 shows the individual results for three observers. The perceived direction is plotted against the spatial frequency of the components. The error bars indicate the standard *error* of the mean. The black lines on the graphs represent the predicted directions for the components, the IOC, vector average, and the two most salient distortion components (DP described as high or low to distinguish them). Fig. 1a shows the data for the Type II plaid with speed ratio 1.0:0.45, the results have been fitted to a power function. Observers show a gradual shift from just below the 225 components towards the IOC pattern direction. A similar result is shown in Fig. 1b. This time the pattern direction is the vector average. The difference between component and pattern direction is larger in Fig. 1a and therefore the slope is greater. It is important to remember that both of the Type II plaids are observed at short durations. It is known that observers perceive the Type II plaid with speed ratio 1.0:0.75 in the vector average direction at short durations, (Bowns, 1996, 2006; Bowns & Alais, 2006; Yo & Wilson, 1992).

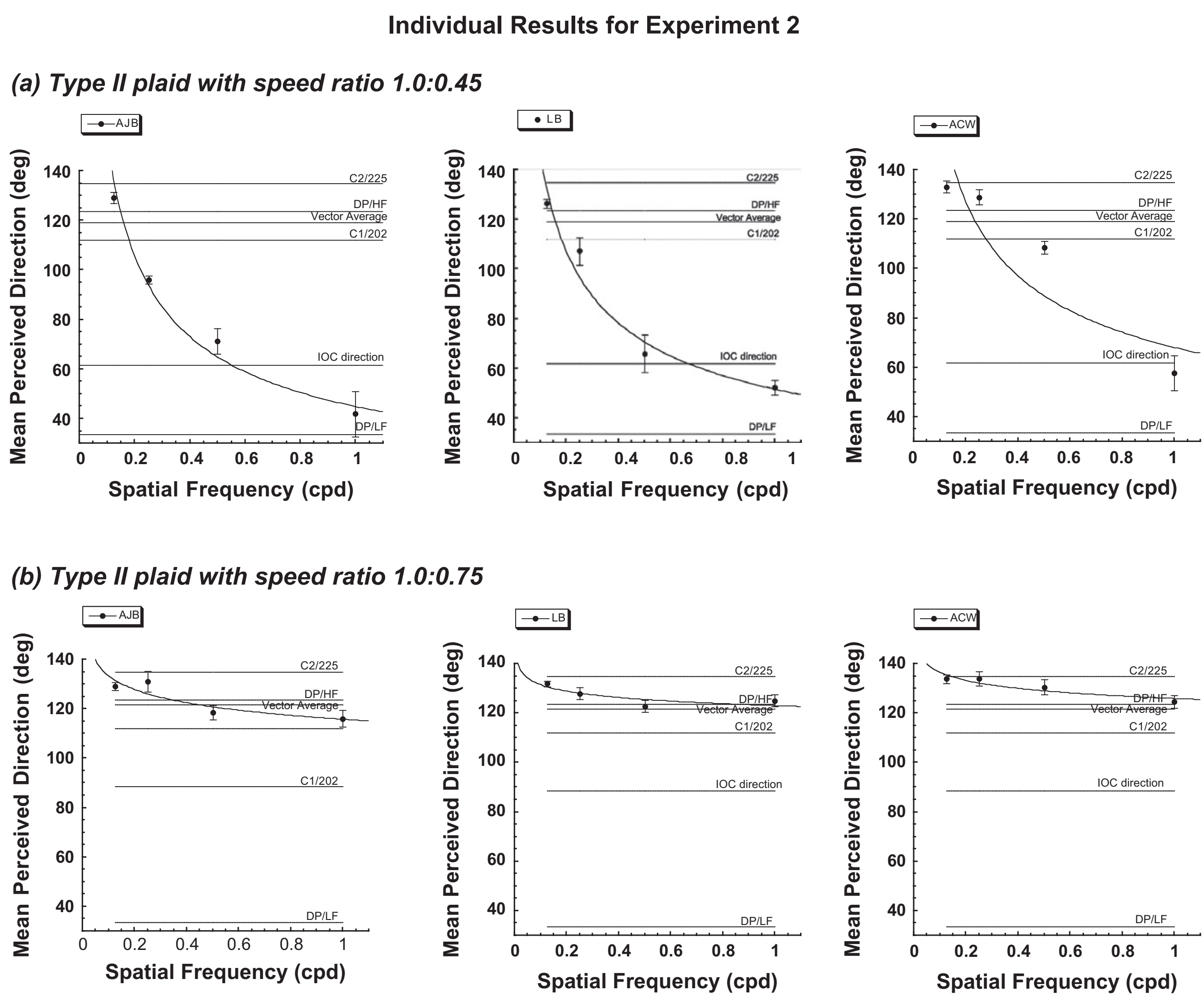

Fig. 1. The results for three individual observers for experiment 1. The data have been fitted to a power function and show that at low frequencies observers perceived direction close to one of the components (orientation 225) and shift perceived direction towards the pattern direction as a function of spatial frequency. This is true for the Type II plaid with speed ratio 1.0:0.45: (a) and also for the Type II plaid with speed ratio 1.0:0.75; (b) even though the predicted differences between the components and the pattern is much less.

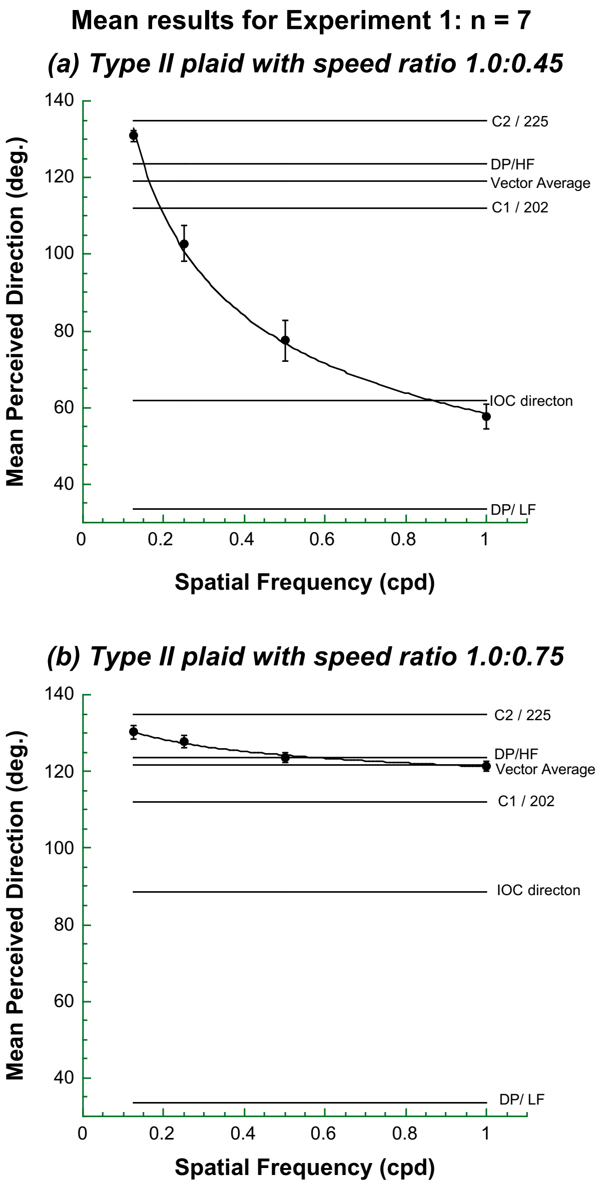

Fig. 2. The mean results for experiment 1 for 7 observers.

The Type II plaid with speed ratio 1.0:0.45 is perceived in the IOC direction at short durations (Bowns, 1996, 2006; Bowns & Alais, 2006). Fig. 2 shows the mean results for 7 observers.

3. Experiment 2

Experiment 2 addressed a possible cause for the shift in perceived direction. It is assumed that the most obvious cause of the shift from component to pattern direction in the above experiments is that the outputs of oriented filters do not resolve orientation of the two components well at low spatial frequencies. Experiment 2 tests this hypothesis by comparing results where the orientation difference is increased in steps of 10°. It was predicted that observers would be more likely to perceive the pattern direction at lower spatial frequencies as the difference between the orientations of the components increased.

The method was identical to that used in experiment 1 with the exception that the orientation difference instead of being 23° was increased to 53° in steps of 10°. Therefore the orientation of the first component was changed from 202° to 172° in steps of 10°. This changed the predicted pattern directions.

3.1. Results for experiment 2

The results for three individual observers are shown in Fig. 3a. Mean perceived direction is plotted against spatial frequency for each angle separation. Only the results for the Type II plaid with speed ratio 1:0.45 are shown because this plaid has the steeper function. The pattern direction is the IOC direction but this is different for each pair of components. For all observers, as the size of the angle difference between components increases the function becomes flatter across the spatial frequencies as predicted. Fig. 3b shows the difference between the perceived direction and the predicted IOC direction for each pair of components for our three observers. At the lowest spatial frequencies the bias is positive (closer to the component direction), it then decreases or becomes negative (closer to pattern direction) for all plaids at the higher spatial frequencies. As the angle increases the decrease or negative bias also occurs at lower spatial frequencies. The difference between the bias and the two most salient distortion products is also shown. At first glance the two sets of bias appear to vary slightly with spatial frequency, however, this reflects the similar directions of the distortion products to the direction of the components (high spatial frequency distortion

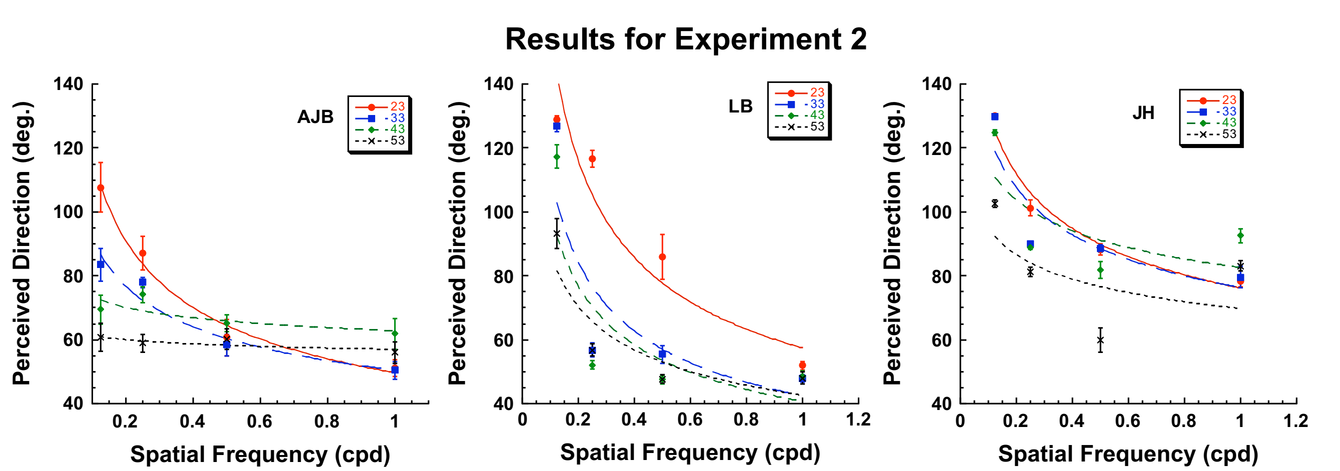

Fig. 3a. The results for three individual observers for experiment 2. Perceived direction is plotted against spatial frequency for each of the four component orientation differences. Perceived direction shifts closer to the pattern direction as a function of the size of the component orientation difference.

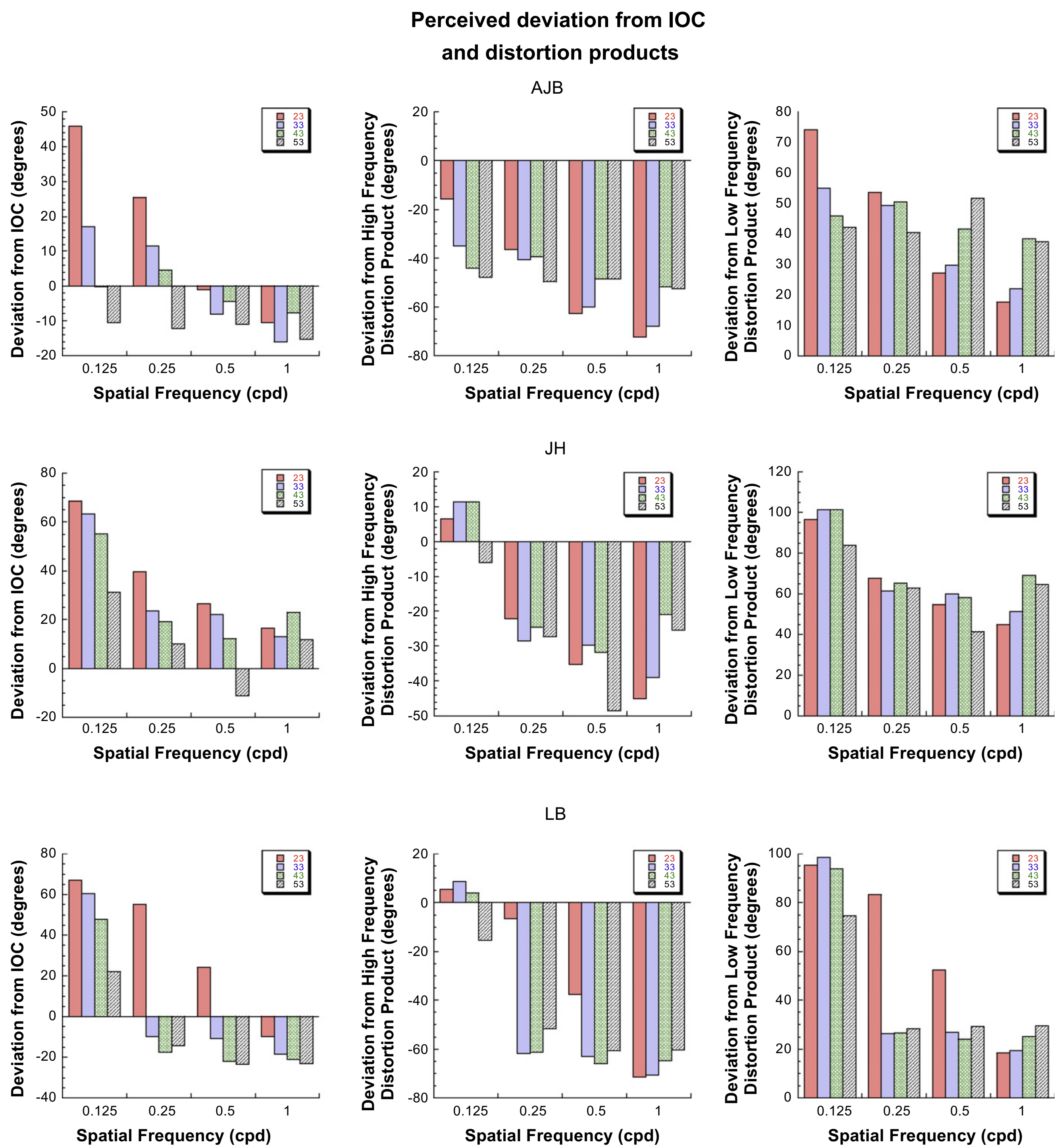

Fig. 3b. The first column shows the perceived deviation from the IOC for thee observers. The IOC is represented by a line at 0. All three observers show a strong positive bias at low spatial frequencies, with increasingly lower or negative bias as a function of spatial frequency. The positive bias also decreases or becomes negative as a function of component angle difference. The second and third columns show the bias for the high and low frequency distortion product respectively in a similar way. The bias appears to vary with spatial frequency, however the bias reflects the similar directions of the distortion products to the direction of the components (high frequency dp) and pattern (low frequency dp) frequency, and not because it predicts responses.

products) and the pattern (low frequency distortion products). It might be argued that the shift is in fact between the high frequency and low frequency distortion products. However, the data do not support this, There may be some influence from the distortion products, for example, observers AJB and LB overshoot the IOC direction towards the low spatial frequency distortion product, however the average results for $n = 7$ in Fig. 2 are much closer to the IOC direction. In addition, this would not explain the shift for plaid with speed ratio 1.0:0.75.

4. Experiment 3

Experiments 1 and 2 used a constant sized aperture envelope. This means that the ratio between the aperture envelope and the

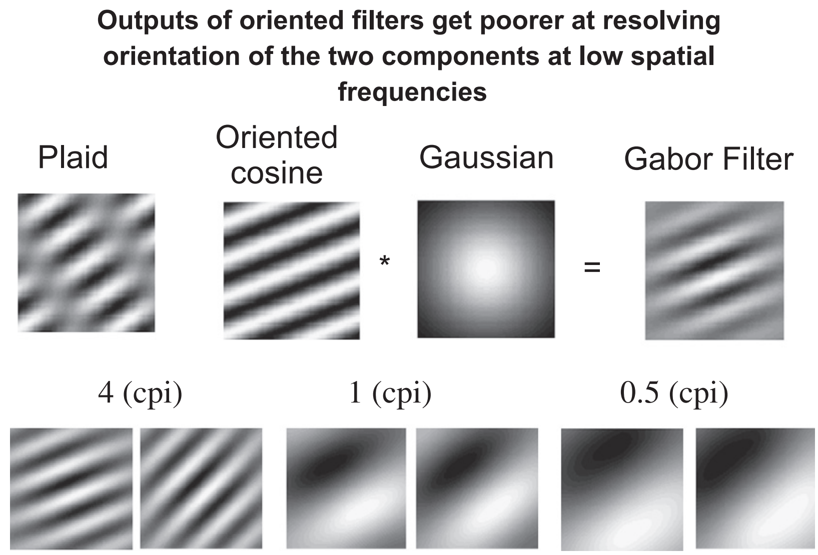

Fig. 4. Illustrates a possible explanation for the results. A plaid made up of two components used in our experiment is convolved with orientated Gabor filters. The output of the convolution of matched filters is shown for the two components at different cycles per image. As the spatial frequency gets lower the orientation differences become less distinct.

carrier of the stimulus was not held constant. It is known that the spatial-frequency bandwidth is approximately proportional to the reciprocal of the spatial extent (the stimulus envelope) perpendicular to the bars (Daugman, 1985). Experiment 3 measured any influence of this on our main result by holding this ratio constant.

The method was identical to that used in experiment 1 with the exception that the size of the aperture varied as a function of spatial frequency. The viewing distance was changed to 28.5 cm. There were two cycles per image, and the image subtended 16° for the 0.125 cpd stimulus, 8° for the 0.25 cpd stimulus, 4° for the 0.5 cpd stimulus, and 2° for the 1 cpd stimulus.

4.1. Results for experiment 3

The results for experiment 3 are shown in Fig. 5 for two observers. The graph compares the pattern of results from experiment 1 with those from experiment 3. The mean perceived direction is plotted against spatial frequency. Maintaining the ratio of the aperture envelope to that of the carrier frequency has reduced the main effect however the bias remains at the lowest spatial frequencies. The perceived direction is shifted towards the components at the lower spatial frequencies.

5. Discussion

The results from experiment 1 show how spatial frequency changed the perceived direction of a plaid. At low spatial frequencies the observers perceived the direction close to the component with orientation 225, and then shifted their perceived direction towards the IOC pattern direction as a power function of the spatial frequency. In the case of the plaid with speed ratio 1.0:0.45 the pattern direction is predicted by the IOC, and for the plaid with speed ratio 1.0:0.75 the pattern direction is predicted by the vector average direction. The slope of the curves is very different in the two cases with the former being more steep ($y = 58.438 ^* x^{-0.39491}$) than the latter ($y = 121.24 ^* x^{-0.035166}$) reflecting the differences in the two different pattern directions. This illustrates that even when the pattern direction varies, the shift follows a similar function. The results are consistent with the (Alais et al., 1994) study and support the concept of an "optimal spatial frequency" for pattern motion direction to be perceived. By control-

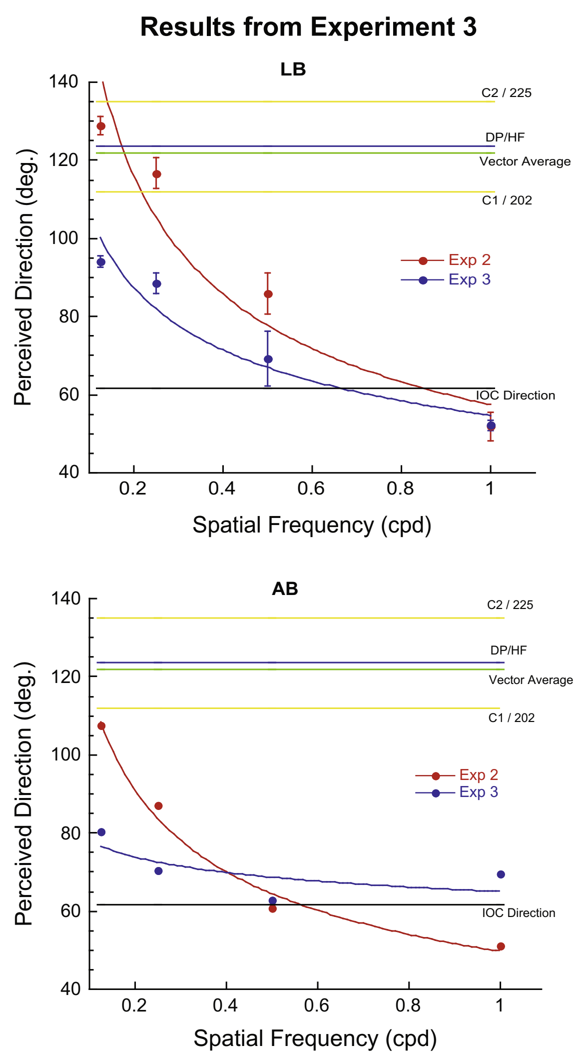

Fig. 5. Compares the results from experiments 1 and 2 for two subjects. The results show a reduced effect when the ratio of the aperture to the spatial frequency is held constant.

ling for all known possible pattern directions, a function relating spatial frequency to perceived direction has been shown that can determine this optimal spatial frequency.

Experiment 2 tested the hypothesis that pattern direction detection was impaired at low spatial frequencies because outputs from oriented filters cannot resolve orientation of the two components at low spatial frequencies. The results supported this by showing that perceived direction was shifted closer to the pattern direction and further away from the components as the difference between the component orientations increased. Fig. 4 illustrates this idea. A plaid made up of two components used in our experiment is convolved with appropriate orientated Gabor filters. The output of the convolution of matched filters is shown for the two components at different cycles per image. As the spatial frequency gets lower the orientation differences become less distinct. A necessary requirement for computing the intersection of constraints (or for that matter any pattern direction) is that there are at least two components with sufficiently different orientations. If the orientations converge at low spatial frequencies it would be as if there were only a single component in the stimuli and that alone would determine the perceived direction. Our experiments support this explanation. In our final experiment we examine the possible effect of varying the ratio of the aperture envelope and the spatial frequency. Spatial frequency continues to have an affect on perceived direction at the lowest spatial frequencies although maintaining the ratio of the aperture envelope to spatial frequency has had a marked reduction on the effect. This is particularly interesting because it shows that when the spatial frequency tuning is broader at the lower spatial frequencies, a broader range of directional tuned sensors would be stimulated and thereby increase the orientation bandwidth. The independent affect of spatial frequency appears to be similarly increasing the orientation bandwidth.

If our explanation is correct it has very important implications for measuring individual responses to spatial frequencies extracted from patterns. By ensuring that the predictions are different for all sources of veridical motion, the pattern direction perceived by an individual or group of individuals can be determined, along with the function relating perceived direction to spatial frequency. Separating the different predicted directions is important because the perceived pattern direction may vary depending on both the stimulus and the observer. The method provides an accurate measurement of an individual's ability to resolve orientation as a function of spatial frequency; therefore facilitating access to the neural orientation resolution as a function of spatial frequency in humans. Inter-subject variation on this task would be reflected by the parameters of the power function that relates the perceived direction and spatial frequency. This would provide an explicit description of any individual differences. We cannot at this point explain why this variation occurs, but it may correlate with other areas of performance. For example, we currently have preliminary results showing that dyslexic observers do not perceive pattern direction in the range we have investigated. We are currently investigating this effect using a much larger sample. This method would be very useful for understanding variation across individuals, either in the normal population or in other clinical population. Type II plaids can facilitate this by allowing a much greater difference between the components and the pattern direction. The method is simple and would be very accessible for use with untrained observers or patients.

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