



# 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.

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## 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 vi-

sual 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,  $\lambda$  = spatial frequency,  $\theta$  = orientation.

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

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

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

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

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

The vector average and the IOC were computed using:

$$x = (s_1 \cos \theta_1) + (s_2 \cos \theta_2)$$

$$y = (s_1 \sin \theta_1) + (s_2 \sin \theta_2)$$

$$VA = \arctan(y/x)$$

$$x = \csc(\theta_1 - \theta_2)(s_2 \sin \theta_1 - s_1 \sin \theta_2)$$

$$y = -(s_2 \cos \theta_1 - s_1 \cos \theta_2) \csc(\theta_1 - \theta_2)$$

$$IOC = \arctan(y/x)$$

where  $\theta$  = 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°.

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