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Ambiguity in the perception of moving stimuli is resolved in favour of the cardinal axes

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Abstract

The aim of this study was to determine whether there is a link between the statistical properties of natural scenes and our perception of moving surfaces. Accordingly, we devised an ambiguous moving stimulus that could be perceived as moving in one of three directions of motion. The stimulus was a circular patch containing three square-wave drifting gratings. One grating was always either horizontal or vertical; the other two had component directions of drift at 120° to the first (and to each other), producing four possible stimulus geometries. These were presented in a pseudorandom sequence. In brief presentations, subjects always perceived two of the gratings to cohere and move as a pattern in one direction, and the third grating to move independently in the opposite direction (its component direction). Although there were three equally plausible axes (one cardinal and two oblique) along which the coherent and independent motions could occur, subjects routinely saw motion along one of the cardinal axes. Thus, the visual system preferentially combines the two oblique gratings to form a pattern that drifts in the opposite direction to the cardinal grating. It was only when the contrast of one of the oblique gratings was changed that an oblique axis of motion was perceived. This perceptual anisotropy can be related to naturally occurring bias in the visual environment, notably the predominance of horizontal and vertical contours in our visual world. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Normal human observers detect and discriminate stimuli consisting of horizontal or vertical lines more easily than obliquely oriented ones (Appelle, 1972). This anisotropy is known as the oblique effect for orientation and has been related to environmental influences during development, notably the predominance of horizontal and vertical contours in the visual environment (Annis & Frost, 1973; Baddeley & Hancock, 1991; Coppola, Purves, McCoy, & Purves, 1998a). This bias in behaviour is reflected in a disproportionate allocation of neural circuitry related to the perception of horizontal and vertical lines — as determined by electrophysiological recording (Mansfield, 1974) and optical imaging (Chapman & Bonhoeffer, 1998; Coppola, White, Fitzpatrick, & Purves, 1998b). Consistent with

these reports are studies showing that animals reared in environments containing a single orientation have a commensurately greater number of neurons selective to that particular orientation (Blakemore & Cooper, 1970; Blakemore & Mitchell, 1973; Sengpiel, Stawinski, & Bonhoeffer, 1999). Thus, exposure of the visual system to an environment biased in such a way affects the development and hence the subsequent organisation of visual cortical areas (for review see Barlow, 1975).

Despite the wealth of knowledge on the processing of form by the visual system, there is no consensus as to whether the related aspect of vision — directional motion — shows a similar anisotropy. Using discrimination tasks at threshold to determine whether our sensitivity to moving objects varies as a function of direction, some studies have reported a bias for horizontal and vertical motion (Essock, 1982; Green, 1983; Heeley & Buchanan-Smith, 1992; Coletta, Segu, & Tiana, 1993; Gros, Blake, & Hiris, 1998; Matthews & Qian, 1999), but others have not (Ball & Sekuler, 1979; Ball and Sekuler, 1980; Nakayama, 1985). Indeed, even

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if an anisotropy is apparent, it has not been made clear how it might be related to a naturally occurring bias in the visual environment, given that objects appear to move equally in all directions. Here, we argue anisotropies in our perception of motion can result not from moving objects, but from a biased distribution of oriented contours in our environment.

To investigate whether there is an anisotropy for the perception of moving surfaces, which might correlate with exposure to naturally occurring bias in the environment, we used an ambiguous moving stimulus. The pattern was composed of three superimposed moving gratings. One grating was always horizontal or vertical; the other two had component directions of drift at 120° to the first (and to each other). We observed that two of the gratings invariably fused and moved as a plaid, in pattern motion, whereas the third moved in its component direction, exactly opposite to the direction of movement of the plaid. The approach used in this study differs from previous reports in that there were no correct–incorrect distinctions, but clearly defined perceptual interpretations that could easily be reported.

Clearly, the geometry of the three-grating stimulus is such that, theoretically, the axis along which motion is perceived (pattern in one direction, component in the other) could be either cardinal (horizontal or vertical) or oblique, depending on which of the three gratings adopts component motion. If the perceived axis-of-motion were to change on successive presentations, it would not be the stimulus that changes, but the observer's interpretation. As the three gratings in these stimuli are distributed symmetrically, there is no bias in the stimulus as to which two gratings should cohere to form a plaid. Our hypothesis, however, is that the visual system is biased toward perceiving motion along the cardinal axes.

2. Methods

Stimuli were circular patches (10° diameter) containing three square-wave gratings generated using a VSG graphics card (Cambridge Research Systems) and presented on a high-resolution, colour monitor (Vision Master 17, Iiyama), at a frame rate of 110 Hz. The display alternated between the three drifting gratings, which were presented on successive frames. Therefore, each grating was presented at a frame rate of about 37 Hz. Subjects viewed the stimulus through a circular aperture, smaller in angular size than the screen, using an adjustable chin rest and forehead bar at a distance of 0.57 m, and were surrounded by a black cloth to avoid any contextual bias from the surrounding room. All the five participants in this experiment had normal or corrected-to-normal vision and three of the subjects were naïve as to the purposes of the experiment.

2.1. Experiment 1

In the first experiment, we determined whether there was any bias in the perception of the ambiguous moving stimulus for a variety of stimulus parameters. One of the three gratings was always horizontal or vertical and the other two were oriented at 120° to the first (and to each other). There were therefore four possible stimulus geometries. By definition, the component directions of drift were taken to be orthogonal to the orientation of each grating (Fig. 1). In the first experiment, we examined whether there was any specific perceptual bias associated with the different stimulus configurations. The spatial frequency (0.5–2.0 cyc/deg), contrast (5–20%) (where contrast = $(\max \text{ lum} - \min \text{ lum}) / (\max \text{ lum} + \min \text{ lum}) \cdot 100$) and velocity (0.5–2.0 deg/s) of the component gratings were also systematically changed between presentations. The fixed values when parameters were not being manipulated parameters were a spatial frequency of 1.0 cyc/deg, contrast 10% and a velocity of 1.0 deg/s. During each presentation, the subject fixated a small black circle (0.2° diameter) in the centre of the screen while the stimulus was briefly presented (1.5 s) and indicated (by pressing a key) the direction of motion of the *component grating*. The different stimulus configurations were interleaved and subjects were asked to indicate the direction of motion of the component grating by pressing one of eight buttons on a keyboard. However, for each stimulus configuration, there are only three possible directions of component motion. Therefore, if no motion bias existed, we would expect that for each stimulus configuration each direction of motion would be perceived in 33% of trials. Occasionally, the perceived axis of motion changed during the presentation, but these trials (~2%) were always discarded. Hence all data came from presentations in which only one unequivocal axis of motion was perceived. Each subject performed five blocks of 80 trials. Additional trials were performed by two subjects at very short presentation times (109 ms) to preclude the involvement of eye movements (Robinson, 1965). The presentation time was chosen to ensure that each grating was shown for the same number of frames (i.e. four).

2.2. Experiment 2

To determine how performance varied with location in the visual field, grating patches (10° diameter, 1.0 cyc/deg spatial frequency, 1.0 deg/s velocity and 10% contrast) were presented in one of eight isoecentric positions (10° from fixation), along the cardinal and oblique axes. Each of the four stimulus configurations (see Fig. 2) were presented twice at each location in the visual field giving a total of 64 trials in each block. Each block was repeated five times.

2.3. Experiment 3

Next, we varied the contrast of one of the oblique gratings, to determine how this affects the perceived direction of motion. We used one stimulus configuration that comprised a horizontal and two oblique drifting square wave gratings (1.0 cyc/deg, spatial frequency and 1.0 deg/s velocity). The contrast of the horizontal grating and one of the oblique gratings were kept constant at either 3 or 10%, while the contrast of the odd oblique grating was varied. Subjects fixated a small circle in the centre of the 10° grating patch that was presented for 1 s. They then reported the perceived direction of motion as before. Each contrast increment was presented eight times in each block and each block was repeated ten times.

2.4. Experiment 4

In the final experiment, we compared the perceived contrasts of oblique and cardinal gratings. The stimulus comprised two circular grating patches (10° diameter, 1.0 cyc/deg spatial frequency, 1.0 deg/s velocity) that were located 0.5° to the right or left of a fixation spot. The orientation of one grating patch was horizontal or vertical while the orientation of the other grating was oblique. Therefore, both the cardinal and the oblique

grating patches had one of four possible directions of motion. Subjects fixated a spot while the grating patches were presented for 1 s. They then indicated whether the right or left patch had the higher perceived contrast. We showed all 16 possible pairs of grating patches four times in a block. Each block was repeated five times. The contrast of the cardinal grating was held constant at either 3 or 10% while the contrast of the oblique grating was varied. The oblique and cardinal grating patches appeared randomly on the right or left of the fixation spot. Both grating patches had the same mean luminance (25 cd/m²) as the background.

3. Results

3.1. Experiment 1

When subjects were briefly presented with the three grating stimuli, they invariably perceived two of the gratings to cohere and move as a pattern. The third grating moved independently in the opposite direction (i.e. its component direction), thus giving rise to the perception of a plaid and a single grating moving transparently over each other, in opposite directions along a single axis.

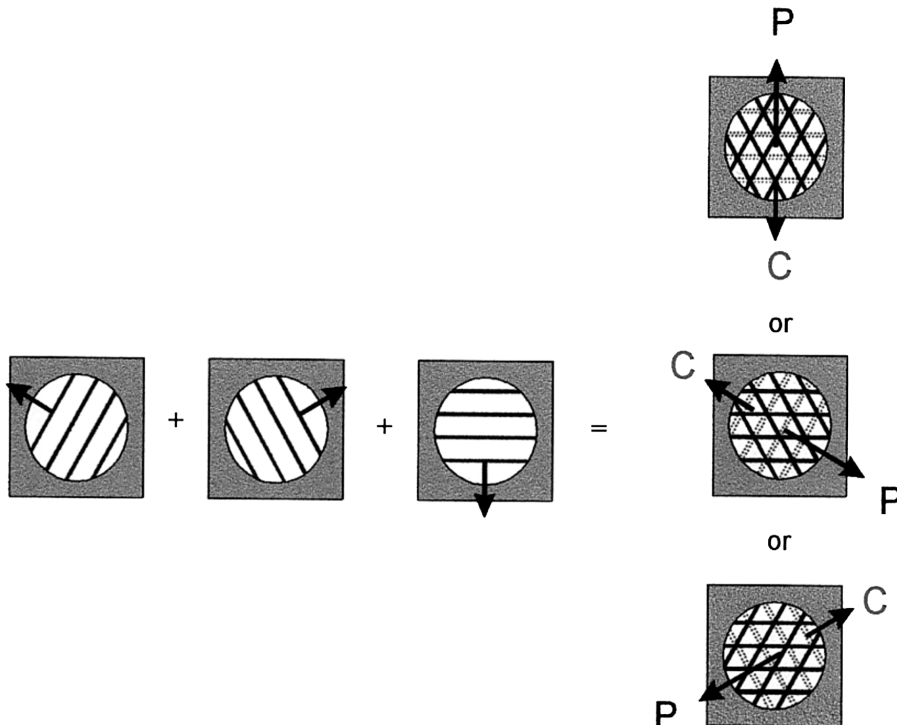


Fig. 1. This ambiguous motion stimulus consists of three, superimposed square-wave gratings drifting at an angle of 120° to each other. There is no unique solution in vector addition that will accommodate all three gratings, but invariably two of them appeared to combine as a plaid, drifting in the direction of pattern motion (P) and the third seemed to move transparently with component motion (C), along the same axis but in the opposite direction. As the angle between the moving gratings is equal, there are three, alternative, equally likely grating combinations of pattern and component motion.

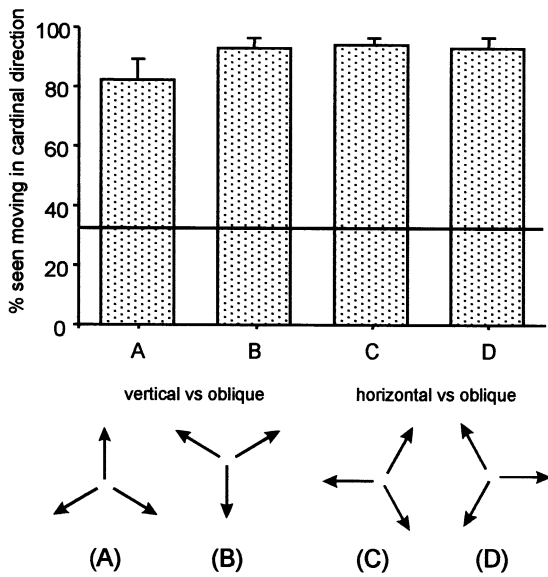


Fig. 2. Graph showing the effect of grating configuration on the proportion of presentations perceived to move along a cardinal (i.e. horizontal or vertical) axis. Because one grating was always horizontal or vertical and the other two had component directions of drift at 120° to the first (and to each other), there were four possible stimulus geometries (A–D). The component gratings had a spatial frequency of 1.0 cyc/deg, contrast 10% and a velocity 1.0 deg/s. The arrows indicate the component directions of motion of the three gratings in each of the four stimulus geometries. However, the averaged results from five subjects show, that for each stimulus configuration, motion was perceived predominantly along one of the cardinal axes. Error bars represent S.E.M. for five subjects.

Every stimulus was configured so that it could be perceived as moving in one of three axes (two oblique and one cardinal). If the visual system was isotropic, we would predict that each direction of motion would be perceived equally (i.e. motion in the cardinal axes would be perceived on 1/3 of all trials). Instead, subjects saw either horizontal or vertical motion on $92.0 \pm 4.7\%$ (mean \pm S.E.M.) of presentations. An analysis of variance (ANOVA) revealed that this bias did not vary with stimulus configuration ($P > 0.4$; Fig. 2), or with changes in velocity ($P > 0.9$), spatial frequency ($P > 0.36$) or contrast ($P > 0.9$) (Fig. 3).

To control eye movements, we repeated these experiments at brief stimulus intervals (109 ms). With brief presentations, the stimulus was always (100% of trials) perceived to decompose into a plaid and a single grating moving along a horizontal or vertical axis. Although subjects could identify a clear axis of motion, they had difficulty in discriminating the correct direction of motion of the component grating. Consequently, the correct direction of the component grating was only reported in $77.1 \pm 5.2\%$ of presentations (mean \pm S.E.M.); the direction of motion perceived in the remaining trials always being in the direction opposite to the correct component motion direction (i.e. in the direction of the plaid). The results, therefore, reflect

the difficulty in discriminating the direction of the component grating from the direction of the plaid in these very brief presentations, rather than a greater proportion of oblique motion.

3.2. Experiment 2

Next, we determined how this anisotropy in motion perception varied across the visual field. Each stimulus

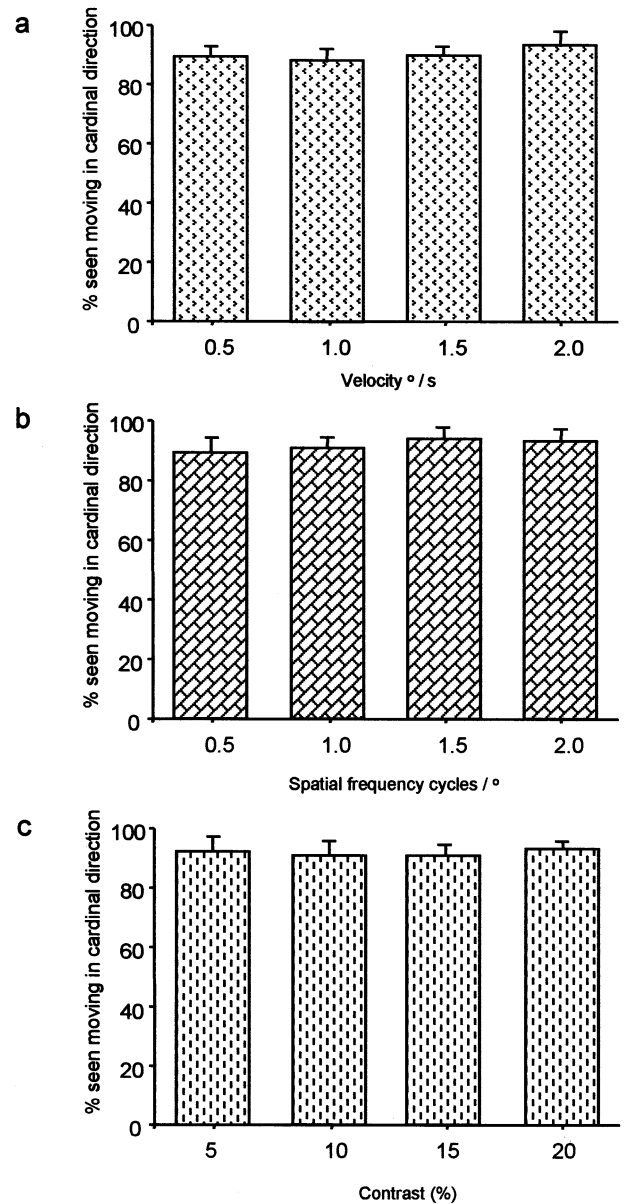


Fig. 3. Graphs showing the effect of varying the (a) velocity; (b) spatial frequency and (c) contrast of all the three gratings. The non-manipulated dimensions of the component gratings were fixed at a spatial frequency of 1.0 cyc/deg, contrast 10% and a velocity of 1.0 deg/s. The mean response from five observers shows that the bias toward perceiving motion in the cardinal axes did not vary with changes in these stimulus parameters. Error bars represent S.E.M. for five subjects.

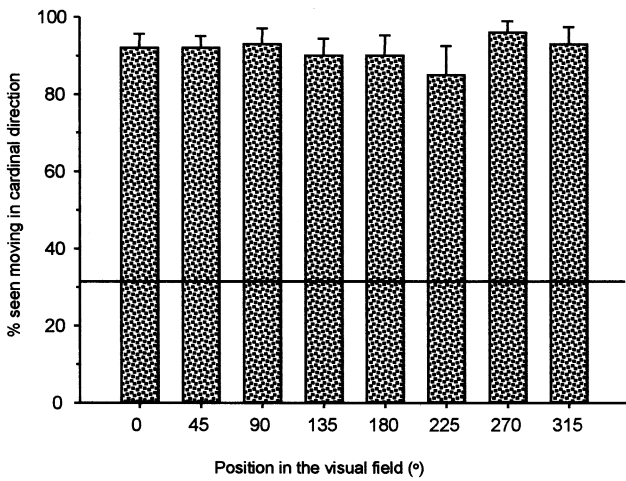


Fig. 4. Graph showing that an oblique effect for the perception of motion was also apparent at an eccentricity of 10° in the peripheral visual field (0°, right; 90°, up; 180°, left; 270°, down). Averaged responses from five observers show that the proportion of presentations perceived to move along the horizontal or vertical axes did not vary with position in the visual field. Error bars represent S.E.M. for five observers.

configuration was presented at eight isoeccentric locations that were 10° from the fixation spot. As in central vision, subjects perceived two of the gratings moving

coherently in one direction with the third grating moving in an opposite direction. Although there were three equally plausible directions of motion, triple gratings in the peripheral visual field were perceived to move predominantly along either the horizontal or vertical axis ($91.3 \pm 1.4\%$; mean \pm S.E.M.; Fig. 4). An ANOVA revealed that this bias did not vary with radial position around a particular isoeccentric circle ($P > 0.87$). That is, stimuli presented on the oblique meridians were perceived to have the same bias as stimuli presented on the cardinal meridians.

3.3. Experiment 3

We next determined whether variation in the contrast of one of the oblique gratings could bias motion perception towards the oblique axis of motion when the contrast of the other oblique grating and a horizontal grating were held constant at 10% (Fig. 5). When the odd oblique grating had a relatively low contrast (< 5%), the other oblique grating and the horizontal grating cohered as a plaid with an oblique axis of pattern motion. As the contrast of the odd oblique grating was progressively increased (> 5%), it cohered with the other oblique grating on an increasing fraction of pre-

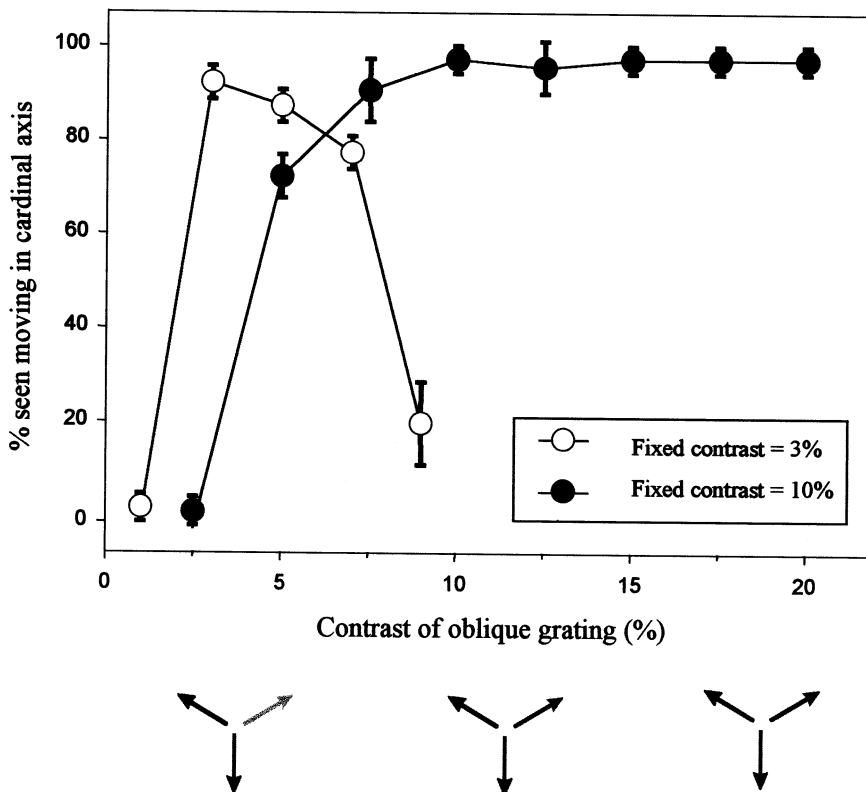


Fig. 5. A psychometric curve showing the proportion of presentations in which a three-grating stimulus was perceived to move in a vertical direction as the contrast of one of the oblique gratings was independently varied. The contrasts of the horizontal grating and other oblique grating were kept constant at either 3 or 10%. The arrows indicate the component directions of motion of the three gratings and the data represent the mean \pm S.E.M. for two observers.

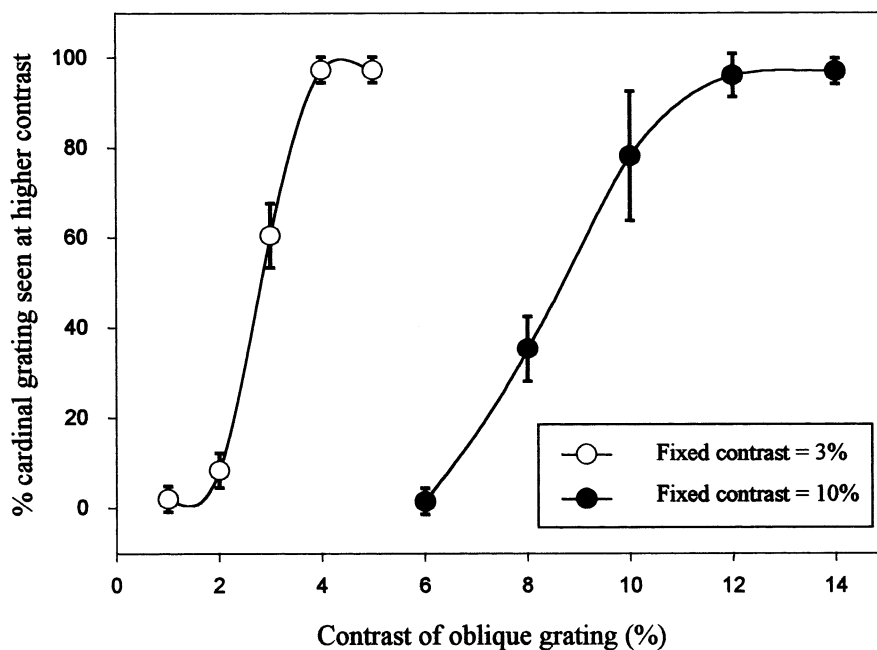


Fig. 6. A psychometric curve showing the proportion of presentations in which a cardinal moving grating was perceived to have a higher contrast than a simultaneously presented oblique grating whose contrast was independently varied. The contrast of the horizontal grating was kept constant at either 3 or 10%. The data represent the mean \pm S.E.M. for two observers.

sentations, to form a plaid that moved vertically. When all gratings had the same contrast (i.e. 10%), the oblique gratings cohered on over 90% of trials (see above). However, as the contrast of the odd oblique grating was increased still further ($> 10\%$), the other oblique grating and the horizontal grating did not increase their propensity to cohere. Rather, the two oblique gratings continued to form a pattern that moved vertically.

To test whether contrast saturation could explain these results, we reduced the contrast of the entire stimulus configuration (see Fig. 5). The contrast of the oblique and cardinal gratings was maintained at 3% while the contrast of the odd oblique grating was varied. In this instance, when the odd oblique grating had a relatively low contrast (1%), it moved in its oblique component motion direction while the other two gratings cohered to form pattern moving in the opposite direction. As the contrast of the odd oblique grating was progressively increased ($> 3\%$), it was generally perceived to cohere with the other oblique grating, to form a plaid that moved vertically. However, as the contrast of the odd oblique grating was increased still further ($> 7\%$), the other oblique grating and the horizontal grating increased their propensity to cohere. It would therefore appear that the motion system deems the contrast of an obliquely oriented grating to be lower than that of a cardinally oriented grating.

3.4. Experiment 4

In the final experiment, we determined whether this difference in use of contrast for coherence in moving gratings is reflected in differences in perceived contrast. Subjects were presented with a cardinal and an oblique moving grating patch on either side of a fixation spot and had to determine which patch was perceived to have a higher contrast. Despite the fact that the motion system treats cardinal gratings as having a higher contrast than oblique gratings, no similar difference was detected in perceived contrast. Thus, a cardinal grating at either 3 or 10% was matched with an oblique grating of approximately the same contrast (Fig. 6). This suggests that information about contrast is used differently in the perception of motion compared with the perception of brightness.

4. Discussion

When a grating drifts behind a circular aperture it is typically perceived as moving orthogonal to its orientation (Wallach, 1976). However, when two independently moving gratings of different orientation are superimposed they usually fuse into a plaid and drift along an axis midway between the two components (Wallach, 1976; Adelson & Movshon, 1982). Here, we studied the appearance of three, independently moving,

superimposed gratings. Invariably, two of the gratings were perceived to cohere to form a plaid moving in one direction, leaving the third grating moving independently in the opposite direction along a single axis. There were, therefore, three possible axes for such combinations of pattern and component motion. As one grating was always horizontal or vertical and the other two had component directions of drift at 120° to the first (and to each other), the stimulus could be perceived to move along either a cardinal or either of two roughly oblique directions. If the neural circuitry underlying motion perception were isotropic, an equal number of trials should be perceived for each direction of motion. Our results, however, show that the perceived direction of motion was predominantly along a cardinal axis (i.e. horizontal or vertical).

This bias for cardinal directions of motion shows similarities to anisotropies apparent in our perception of form. That is, normal human observers detect and discriminate stimuli consisting of horizontal and vertical contours more easily than obliquely oriented ones (Appelle, 1972). This phenomenon, known as the oblique effect, has been related to environmental influences during development, notably the predominance of horizontal and vertical contours in the visual environment (Coppola et al., 1998a)

Naturally occurring biases in the visual environment have also been implicated in our perception of motion. For example, an increase in sensitivity for centrifugal motion (i.e. away from the centre of gaze) (Scott, Lavender, McWhirt, & Powell, 1966; Georgeson & Harris, 1978; Ball & Sekuler, 1980) has been related to the patterns of motion that are generated during forward locomotion (Gibson, 1950; Koenderink, 1986). A corresponding physiological bias is apparent in the extrastriate visual area MT, where more neurons are selective for centrifugal motion (Albright, 1989). But why should a horizontal/vertical bias be apparent for the perception of moving gratings? We suggest that self-induced movement through a visual environment with a biased distribution of oriented contours underlies this anisotropy in our perception of motion.

In early stages of visual processing, direction-selective neurons are excited preferentially when contours with an orientation orthogonal to the preferred direction drift across their receptive field (Hubel & Wiesel, 1968; Schiller, Finlay, & Volman, 1976). Even when presented with two superimposed drifting gratings of different orientation, creating a 'plaid', which perceptually coheres and moves with 'pattern motion' in a single direction, such component motion selective cells respond preferentially when one or the other component grating lies at the orientation optimum for the cell. Although signals from these component-motion selective neurons are integrated by other neurons to reflect the actual movement of objects (Movshon, Adelson,

Gizzi & Newsome, 1985; Stoner & Albright, 1992), the fact remains that the signals generated in the initial stages of motion processing are constrained by orientation. It therefore, follows that self-induced movement through an environment containing a predominance of horizontal and vertical contours will result in the increased activity of component-motion selective neurons that respond to vertical and horizontal orientations.

The development of direction-selectivity in the visual cortex is known to be influenced by the early visual environment. For example, rearing animals in stroboscopic illumination (which deprives them of moving retinal images) leads to a reduced number of direction selective cells in visual cortex (Cynader, Berman, & Hein, 1973). Similarly, animals exposed to contours moving in one direction show a correspondingly asymmetrical distribution of direction-selective neurons (Tretter, Cynader, & Singer, 1975; Daw & Wyatt, 1976; Berman & Daw, 1977). It seems plausible, therefore, that exposure to this naturally occurring bias during the sensitive period of brain development will modify the underlying neural circuitry. Thus, when confronted with the ambiguous three-grating stimulus, the grating with a cardinal orientation (horizontal or vertical) generates relatively more activity at the level of component motion detection than the oblique gratings. Consequently, the pattern motion system assumes that the oblique gratings belong together, and the cardinal one is different (Adelson & Movshon, 1982; Stoner, Albright, & Ramachandran, 1990; Krauskopf & Farell, 1990; Thompson, Hill, Stone, & Stone, 1992).

To test this idea, we varied the contrast of one of the oblique gratings, but kept the contrasts of the other two gratings constant (10%). We found that when the contrast of one of the oblique gratings was sufficiently reduced, it did indeed appear to drift alone along its near oblique component direction, and the cardinal grating and the other oblique grating cohered to form a plaid drifting along the same axis. As the contrast of the odd oblique grating was progressively increased, there was a corresponding increase in the proportion of presentations in which it cohered with the other oblique grating. However, when the contrast of the odd oblique grating was increased still further, the two oblique gratings continued to show a preference to form a plaid. We had expected that, when the contrast of the odd oblique grating was sufficiently large, the other two gratings would again tend to move along an oblique axis of motion. One explanation for this is a saturation of contrast responses in the underlying direction selective neurons (Zeki, Watson, Lueck, Friston, Kennard, & Frakowiak, 1991; Tootell, Reppas, Kwong, Malack, Born, Brady, Rosen, & Belliveau, 1995; see also Derington & Goddard, 1989; Wright & Gurney, 1992). We tested this assumption by lowering the contrast of the non-manipulated gratings from 10 to 3%. In this instance, the data followed an inverted U-shaped func-

tion as we increased the contrast of the odd oblique grating (see Fig. 5). It would therefore, appear that the contrast of an oblique grating is treated as being lower than the contrast of a cardinal grating.

As a control, we compared the perceived contrast of oblique moving gratings with cardinal moving gratings in a 2AFC contrast-matching paradigm. We expected that the oblique gratings would have a lower perceived contrast than the cardinal grating. However, the results show that the perceived contrast of an oblique grating is almost identical to that of a cardinal grating. This suggests that the visual system's response to contrast is different for the perception of motion compared with the perception of brightness. Indeed, functional imaging studies in humans have shown that the contrast response functions of early visual areas such as V1, V2d, V3d and V3A are quite similar to psychophysical judgements of contrast discrimination (Boynton, Demb, Glover, & Heeger, 1999), whereas neurons in motion-sensitive areas such as V5/MT have high gain at low contrast, but demonstrate saturation at higher contrasts (Sclar, Maunsell, & Lennie, 1990; Zeki et al., 1991; Tootell et al., 1995). This differential use of contrast in the perception of motion and brightness is analogous with the use of orientation and chromatic signals in the visual system. Orientation information not only contributes to our perception of form, but also to the neural processing underlying stereoscopic depth perception (Barlow, Blakemore, & Pettigrew, 1967) and, as described above, motion perception (Movshon et al., 1985; see also Andrews & Blakemore, 1999). Similarly, chromatic signals are used differently in our perception of colour compared with our perception of motion (Dougherty, Press, & Wandell, 1999).

In conclusion, we have devised an ambiguous motion stimulus containing three square-wave gratings. Despite the fact that the axis along which motion is perceived could be either cardinal or oblique, motion was predominantly perceived in the cardinal direction. This perceptual bias, like others (Purves, 1999; Purves & Andrews, 1997; Purves, Shimpf, & Lotto, 1999), can be related to the statistical properties of natural scenes, in this case the predominance of horizontal and vertical contours in our environment.

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