Integration of motion information during binocular rivalry

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Abstract

When two moving gratings are superimposed in normal viewing they often combine to form a pattern that moves with a single direction of motion. Here, we investigated whether the same mechanism underlies pattern motion when drifting gratings are presented independently to the two eyes. We report that, with relatively large circular grating patches (4 deg), there are periods of monocular dominance in which one eye's orientation alone is perceived, usually moving orthogonal to the contours (component motion). But, during the transitions from one monocular view to the other, a fluid mosaic is perceived, consisting of contiguous patches, each containing contours of only one of the gratings. This entire mosaic often appears to move in a single direction (pattern motion), just as when two gratings are literally superimposed. Although this implies that motion signals from the perceptually suppressed grating continue to influence the perception of motion, an alternative possibility is that it reflects a strategy that involves integrating directional information from the contiguous single-grating patches. To test between these possibilities, we performed a second experiment with very small grating stimuli that were about the same size as the contiguous single-grating patches in the mosaic (1-deg diameter). Despite the fact that the form of only one grating was perceived, we report that pattern motion was still perceived on about one third of trials. Moreover, a decrease in the occurrence of pattern motion was apparent when the contrast and spatial frequency of the gratings were made more different from each other. This phenomenon clearly demonstrates an independent binocular interaction for form and motion. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Pattern motion; Form; Perceptual awareness; Parallel processing; Binding

1. Introduction

A moving surface covered with stripes of a single orientation, viewed through a circular aperture, is usually seen as drifting in a direction orthogonal to the grating's orientation, whatever the actual direction of surface movement (Wallach, 1976). The ambiguity of a moving grating is resolved, however, if other features are added to the surface. A simple demonstration of such 'pattern' motion is provided by the superimposition of two drifting gratings, orthogonal to each other. While each grating presented alone would appear to move in its own 'component' direction, orthogonal to its contours, the two fuse together, forming a 'plaid' that drifts along an axis that usually corresponds to the vector sum of the two components (Adelson & Movs-

hon, 1982). Thus both gratings contribute to the direction of pattern motion, as well as to the perceived form of the stimulus.

In primates, information about direction of motion originates in the M-type retinal ganglion cells, whose signals are relayed through the magnocellular layers of the lateral geniculate nucleus to layer 4Cα in primary visual cortex (V1), and then to layers 4b and 6. From there serial and parallel projections pass to the thick cytochrome-oxidase stripes of V2, V3, area MT (V5) and other extrastriate motion areas (Albright & Stoner, 1995). In the early stages of the visual cortex, even those neurons that respond more strongly to one direction of motion (Hubel & Wiesel, 1968) appear to be fundamentally orientation-selective. In response to moving plaids, they fire only when one of the two gratings has an orientation close to optimal for the cell (Movshon, Adelson, Gizzi, & Newsome, 1985). However, in MT, where most neurons are direction-selective (Dubner & Zeki, 1971), a sizeable fraction seem to signal the true, perceived direction of surface motion, rather than

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the component motion of individual contours. When confronted with a drifting plaid, such pattern-motion neurons respond best when the shared vector of motion of the two gratings corresponds to the preferred direction of the cell, as determined with single gratings (Movshon et al., 1985; Stoner & Albright, 1992). Such cells appear to combine component motion signals to produce a signal that generates, or at least reflects, the perceived motion of the object.

In a previous experiment, we reported that the system responsible for the awareness of movement could combine component motion signals even if they were delivered separately to the two eyes (Andrews & Blakemore, 1999). It is unclear, however, whether this interocular combination of motion signals employs the same mechanism as when moving signals are combined in normal binocular vision. Support for this possibility has come from studies that have shown the prevalence and direction of dichoptic pattern motion varies with the degree of similarity between the two gratings (Banton, Durgin, & Bertenthal, 1994; Cobo-Lewis, Gilroy, & Smallwood, 2000; Saint-Amour, Lepore, & Guillemot, 2000), much as it does during non-dichoptic viewing (Adelson & Movshon, 1982; Stoner, Albright, & Ramachandran, 1990; Krauskopf & Farell, 1990). However, in previous studies of dichoptic pattern motion, elements of both gratings were visible in the display. It is possible, therefore, that the visual system combines directional information from the connected grating patches, rather than through processing motion from a suppressed grating. For example, closely adjacent patches of drifting gratings, of two different orientations, all viewed normally, can cohere to give a single shared direction of perceived motion (Alais, van der Smagt, van den Berg, & van de Grind, 1998).

In the present study, we asked whether the characteristics of dichoptic pattern motion were similar to pattern motion during normal binocular viewing when only one grating was perceptually dominant. Small grating patches were used so that on a significant proportion of the dichoptic trials only one grating dominated perception. We then determined whether relative changes in the spatial frequency and contrast of the component gratings have similar effects on the occurrence of perceived pattern motion in dichoptic and normal binocular viewing.

2. Methods

Stimuli were circular patches of sinusoidally modulated grating generated using a VSG graphics card (CRS, Rochester, England) linked to a high-resolution, colour monitor (Vision Master 17, IIyama) at 110 Hz. Subjects viewed the monitor from an adjustable chin rest and forehead bar, at a distance of 0.57 m through Ferro-

Electric Shutter Goggles (CRS, Rochester, England) that alternately occluded the two eyes at the same frequency as the frame rate of the monitor (110 Hz). The display alternated on successive frames between two gratings, one tilted clockwise, the other anticlockwise, so that each was seen by only one eye with no perceptible flicker at this high alternation rate. Cross-talk was minimised by the 3-log unit contrast ratio of the shutter goggles and by using low contrast gratings for fast phosphor decay. All four participants in this experiment (one author and three naïve subjects) had normal or corrected-to-normal vision and good stereopsis.

2.1. Experiment 1

First, we determined the conditions that might elicit pattern motion when relatively large patches of grating were presented independently to the two eyes. The stimuli were 4-deg diameter circular patches of grating, of two different orientations, presented dichoptically, on corresponding points in the two eyes for 60 s. The 'standard' grating presented to one eye was a red, sinusoidally modulated grating of 0.3 contrast, with a velocity of 1 deg/s and a spatial frequency of 1 c/deg. The hue, spatial frequency, contrast and velocity of the grating presented to the other eye varied randomly between trials. The orientations of the two gratings were symmetrical about vertical (±45 deg from vertical— except when the angle between components was varied). Subjects were informed that the predicted direction of pattern motion was always upward except when there were differences in velocity, in which case the pattern motion direction was slightly off vertical. The average luminance of the gratings in the colour trials was equalised photometrically.

Subjects fixated a small dark square in the centre of the stimulus and pressed one of three keys to indicate whether perceived motion corresponded to the component motion of one grating or the other, or to the predicted pattern motion direction (upward). They were instructed to switch as quickly as possible from one key to another to indicate changes in perceived direction. No subject ever reported motion in a direction other than one of these three choices.

2.2. Experiment 2

Next, we examined the circumstances that might evoke pattern motion when relatively small grating patches (1-deg diameter) were presented independently to the two eyes, so that only one grating dominated perception on successive trials. For this experiment, grating patches were presented for brief periods of time (2 s). Previous studies have shown that with small gratings one orientation can dominate over the entire patch and for the whole duration (Blake, O'Shea, &

Mueller, 1992). On successive trials, the standard grating, had a sinusoidal luminance profile with a spatial frequency of 4 c/deg; contrast, 0.16; temporal frequency of drift, 0.5 Hz, whereas the contrast and spatial frequency of the other non-standard grating was varied. The two gratings were always of oblique orientation (±45 deg from vertical) and could move in either direction giving rise to four directions of component motion. The component direction of motion of gratings presented to the two eyes was randomised between trials producing four possible directions of pattern motion. At the end of each trial, the subject chose the perceived direction of grating motion from eight possible directions that were spaced at intervals of 45 deg. Subjects were only asked to report the perceived direction of motion when one orientation was perceptually dominant for the whole trial. Trials in which the two gratings appeared fused or a perceptual switch occurred during the trial were ignored.

We then used identical stimuli and a similar task to determine the conditions that elicit pattern motion during normal binocular viewing. On non-dichoptic trials, both gratings were presented to the each eye: the shutters still operated, but the same grating was displayed on successive frames. When a coherent direction of pattern motion was perceived, subjects were instructed to indicate the direction of both gratings. On occasions when pattern motion was not perceived, subjects were instructed to report the direction of one of the component gratings. Each subject performed 10 dichoptic and 10 non-dichoptic sessions in which the contrast of the non-standard gratings was varied, and the same number of sessions in which the spatial frequency of the non-standard grating was varied. Each session comprised 80 trials.

3. Results

3.1. Experiment 1

We started by examining the nature of rivalry for orthogonally oriented gratings of a relatively large area (4-deg diameter) viewed dichoptically. Even when the two gratings were identical in colour, spatial and temporal frequency, they never fused to form a plaid, as they do when viewed through both eyes simultaneously. For periods of a few seconds at a time, totalling about half the entire one-minute viewing period, one or other of the two monocular gratings appeared to fill the entire field. During these epochs of apparently pure monocular perception, the grating almost always appeared to drift orthogonal to its orientation, just as it would if the other grating were not present at all. Rarely, with these large fields, did direct and complete transitions occur between one eye's view and the other's. But usually, after a few

seconds of apparently monocular perception, the grating broke up into a fluid 'mosaic' consisting of contiguous patches of grating of the two different orientations, the boundaries of which could shift slowly. Eventually the patchy mosaic was replaced for a few seconds by the other completely monocular view (Fig. 1).

In the fluid mosaic, which was seen for about half the entire viewing period, the individual patches were typically about one-third of the diameter of the entire patch (i.e. about 1 deg or more across). Again, only one orientation was ever seen within each individual patch. Nevertheless, the entire mosaic usually appeared to move coherently, as if on a single surface, in the *pattern-motion* direction, appropriate to the combination of velocities of the two monocular gratings. Hence, during these periods, the motion but not the orientation of the two gratings appeared to combine binocularly. It is important to note that, during the trials, subjects were only asked to report the direction of motion of the patch. The correlation between the state of rivalry and
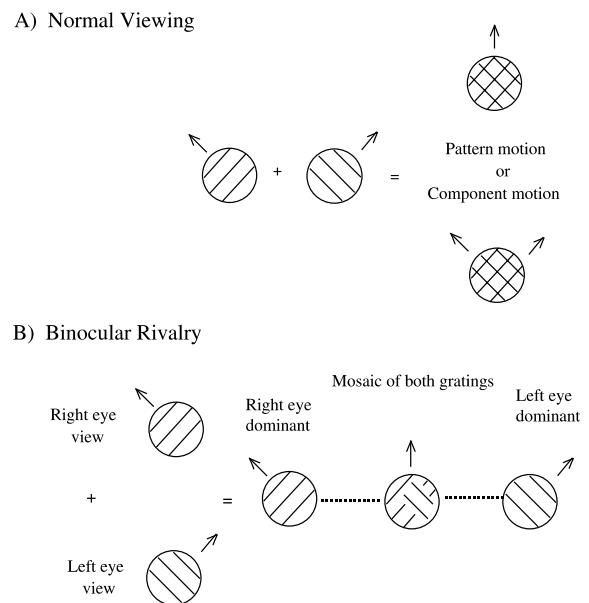

Fig. 1. (A) When two moving gratings, identical except for their orientation, are superimposed in normal binocular viewing they usually cohere and appear to move unambiguously in a single direction and velocity, equivalent to the shared vector of motion of the two (pattern motion). However, if the two gratings are substantially different from each other in colour, contrast, velocity, etc, they do not fuse, but slide transparently across each other, each moving orthogonal to its orientation (component motion). (B) Here, we show that when differently oriented moving gratings are presented separately to the two eyes, their contours compete for perceptual dominance such that wherever in the field one is visible, the other is suppressed. Even with quite large fields (4-deg diameter), one grating or the other dominates the whole area, each for about a quarter of the viewing time. During the transitions between exclusive dominance of one grating to dominance by the other, a fluid mosaic of contiguous patches of the two gratings is often seen (for about half the exposure duration, altogether). The grating patches within this mosaic are usually seen to move together, in the direction of pattern motion. Thus, the motion signals in the two eyes are combined, while orientation signals continued to rival.

the perceived direction of motion of the patch was based on the subject's informal observations.

We found that, as the stimulus parameters of the two large grating patches became more different, there was an increased tendency for each of them to move independently in its component motion direction. Relative velocity, for instance, strongly affected the probability of dichoptic pattern motion. Thus, as the velocity of the non-standard grating was increased, there was a progressive decrease in the probability of
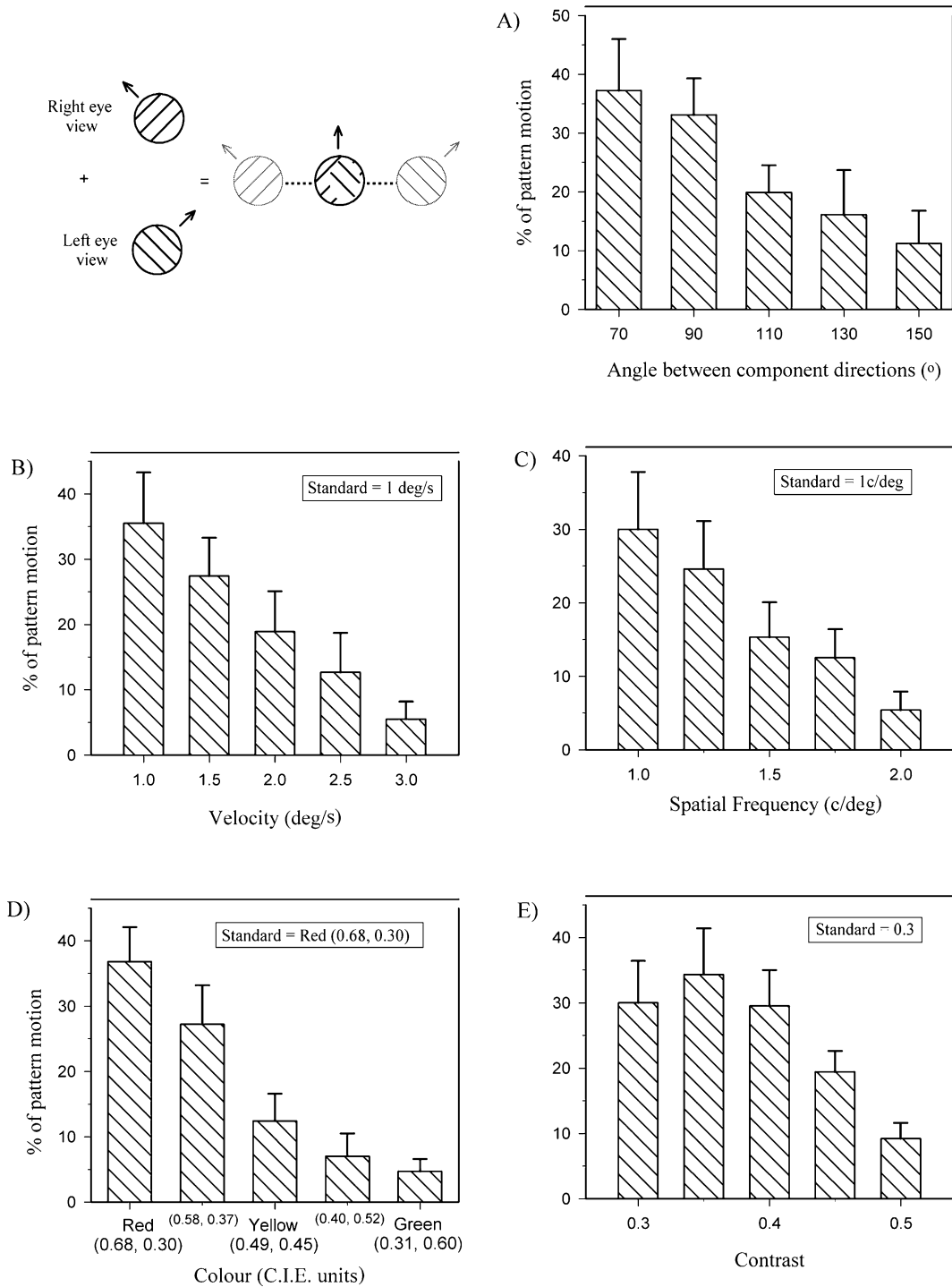

Fig. 2. The proportion of dichoptic pattern motion decreased as the gratings were made more different from each other in direction of drift (A), velocity (B), spatial frequency (C), colour (D), or contrast (E). For each column, an observer's mean value was calculated from 10 one minute trials. The columns and error bars on the graphs represent the mean and SEM respectively of four observers.

pattern motion being perceived (Fig. 2B). This fell from about 35% of the total viewing time when both gratings moved at the same velocity (1 deg/s) to about 5% when the velocity of gratings presented to the two eyes differed by a factor of three (1 and 3 deg/s). The perceived direction of motion when two gratings had different velocities was slightly off vertical. It is possible, therefore, that the decrease in the proportion of pattern motion reported resulted from subjects confusing off-vertical pattern motion with the component direction of one of the gratings (±45 deg from vertical); the predicted direction of pattern motion ranged from 0 to 26.5 deg off vertical in the velocity trials. Although it is not possible to rule this out entirely, we think it unlikely for two reasons: (1) subjects were informed to indicate component motion only if the perceived direction was 45 deg from vertical, and (2) Cobo-Lewis et al. (2000) recently demonstrated that subjects are quite able to discriminate fine direction differences when viewing dichoptic plaids.

The predicted direction of pattern motion for the spatial frequency, contrast, direction of motion and colour trials was always upward. In these trials, increasing the difference between the component similarly reduced the coherence of motion signals (Fig. 2A–E). A (within subject) repeated measures ANOVA was performed to quantify these trends. Significant F-values were apparent for each condition (velocity, $F = 11.7$, $p < 0.0005$; spatial frequency, $F = 7.9$, $p < 0.005$, contrast, $F = 7.6$, $p < 0.005$; direction, $F = 6.5$, $p < 0.005$, colour, $F = 14.3$, $p < 0.0005$).

As the stimulus properties of the gratings presented to the two eyes were made more different, there was a complementary increase in the amount of time that one grating or the other dominated perception over the whole patch (Fig. 3). For example, there was an increase in the periods of exclusive dominance from about 50% of the viewing time when both gratings had the same colour (both red) to about 80% when one of the grating was red and one was green (Fig. 3D). Similar trends were apparent for the other conditions (velocity, $F = 6.7$, $p < 0.0005$; spatial frequency, $F = 3.65$, $p < 0.05$; contrast, $F = 6.35$, $p < 0.01$; direction, $F = 4.0$, $p < 0.05$, colour, $F = 14.4$, $p < 0.0005$).

The total period of time during which either complete perceptual dominance or pattern motion was perceived (sum of blocks in histograms of Figs. 2 and 3) accounts for about 80–90% of the total duration. The remaining time reflects the periods between responses and when the mosaic of the two gratings was perceived not to move in the direction of pattern motion.

3.2. Experiment 2

Next we directly compared pattern motion in dichoptic and normal binocular viewing to determine whether they are similar in their characteristics (and perhaps underlying circuitry). Specifically, we assessed the effect of changing the spatial frequency and contrast of the gratings. The grating stimuli used during dichoptic presentations were identical to those used in normal binocular presentations. The size of the grating patches (1 deg) was based on the approximate size of the connected patches that form the fluid mosaic when larger grating stimuli were viewed (see Fig. 1), so that, on a large proportion of the dichoptic trials, one orientation dominated completely over the whole area and for the whole period of exposure. Indeed, trials in which the two gratings appeared fused or a perceptual switch occurred during the trial were ignored.

For the dichoptic presentations, when the standard and non-standard gratings had the same contrast and spatial frequency, the predicted direction of pattern motion was perceived on about one third of trials; on the remaining trials, the grating that dominated perception appeared to move in its component direction (Fig. 4). As the spatial frequency and contrast of the non-standard grating were made more different from the standard grating, the prevalence of dichoptic pattern motion decreased markedly and the dominant grating was more often perceived moving in a direction orthogonal to its orientation (its component direction). For example, when the contrast of the two gratings was the same, pattern motion was perceived on about 30% of trials (mean ± sem, S1, $35 \pm 6\%$, S2, $24 \pm 7\%$), whereas when the contrasts of the two gratings differed markedly (0.16 and 0.02) pattern motion was rarely reported (mean ± sem, S1, $1 \pm 2\%$, S2, $0 \pm 0\%$). Similarly, when both gratings had the same spatial frequency they cohered in about 20–30% of trials (mean ± sem, S1, $31 \pm 2\%$, S2, $22 \pm 4\%$), but, when the spatial frequency of the standard grating was 4 c/deg and the non-standard grating had a spatial frequency of 0.5 c/deg, pattern motion was perceived on only a few trials (mean ± sem, S1, $6 \pm 2\%$, S2, $0 \pm 0\%$).

We then measured the incidence of pattern motion when identical stimuli were viewed during normal binocular presentations when both gratings were visible. When the two gratings had different directions of component motion, but similar spatial frequency and contrast, they cohered and moved together in a single direction on the majority of trials (mean ± sem, Contrast: S1, $100 \pm 0\%$, S2, $95 \pm 3\%$; Spatial frequency: S1, $100 \pm 0\%$, S2, $100 \pm 0\%$). However, as the contrast and spatial frequency of two superimposed gratings become more different, there was an increased tendency for the gratings to move independently in their component motion direction, giving rise to the impression of two gratings sliding over each other (see Fig. 4).
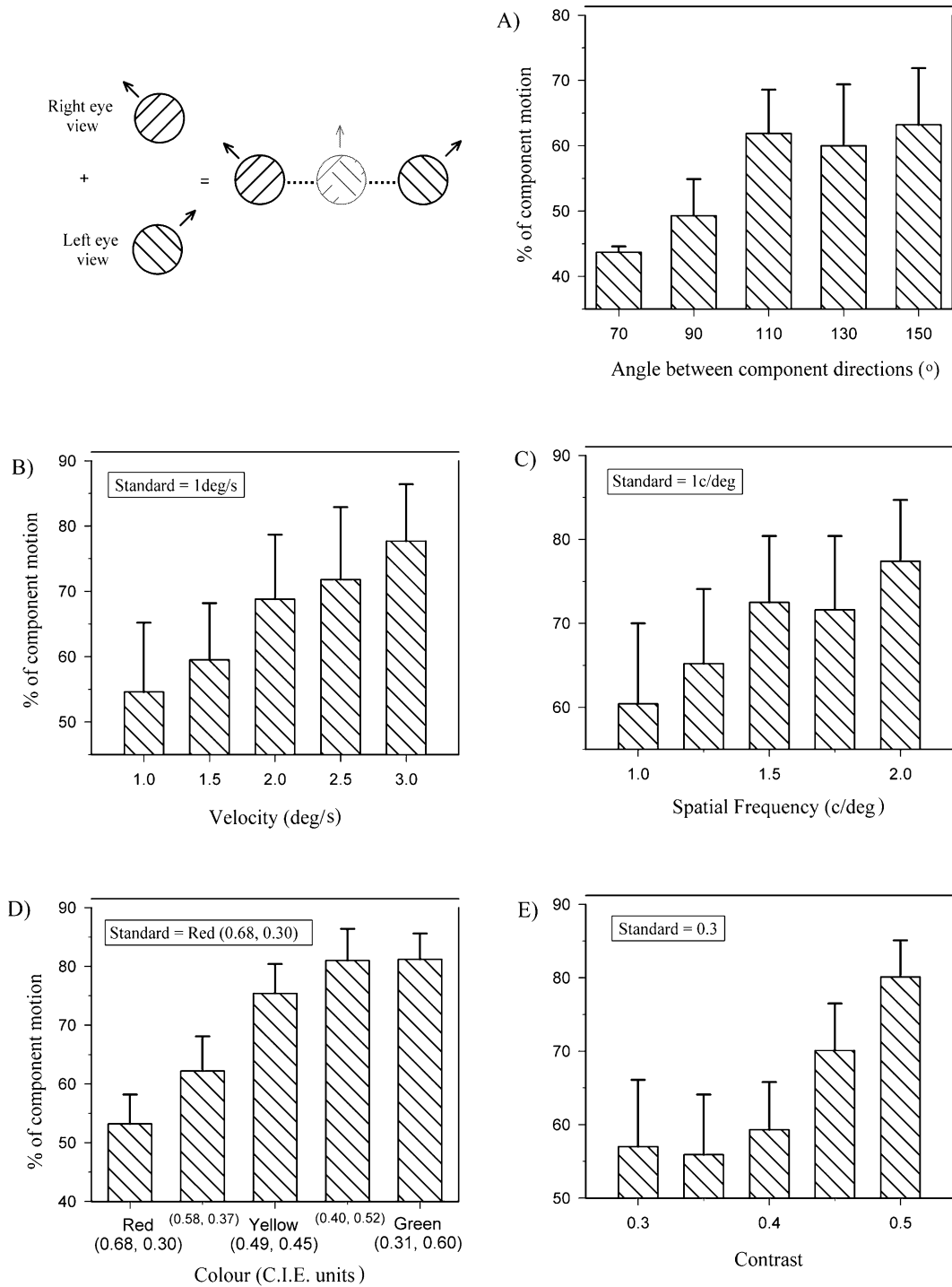
Fig. 3. The periods of exclusive perceptual dominance during the rivalrous viewing of differently drifting gratings increase in duration as the stimulus characteristics of the two gratings are made more dissimilar. The data are taken from the experiment described in Fig. 2, but now the graphs plot the fraction of each exposure for which one of the two gratings totally dominated perception. This was typically about half the exposure when the two gratings were identical (except for their orientation), but it progressively increased as the gratings were made more different in direction of drift (A), velocity (B), spatial frequency (C), colour (D), or contrast (E). The columns and error bars on the graphs represent the mean and SEM respectively of all four observers.

4. Discussion

When two large patches of moving grating were superimposed dichoptically, the pattern perceived alternated between the right eye view, the left eye view, and, in between, a mosaic of patches of the two differently oriented gratings. When a single grating dominated, the perceived direction of motion seemed to be orthogonal
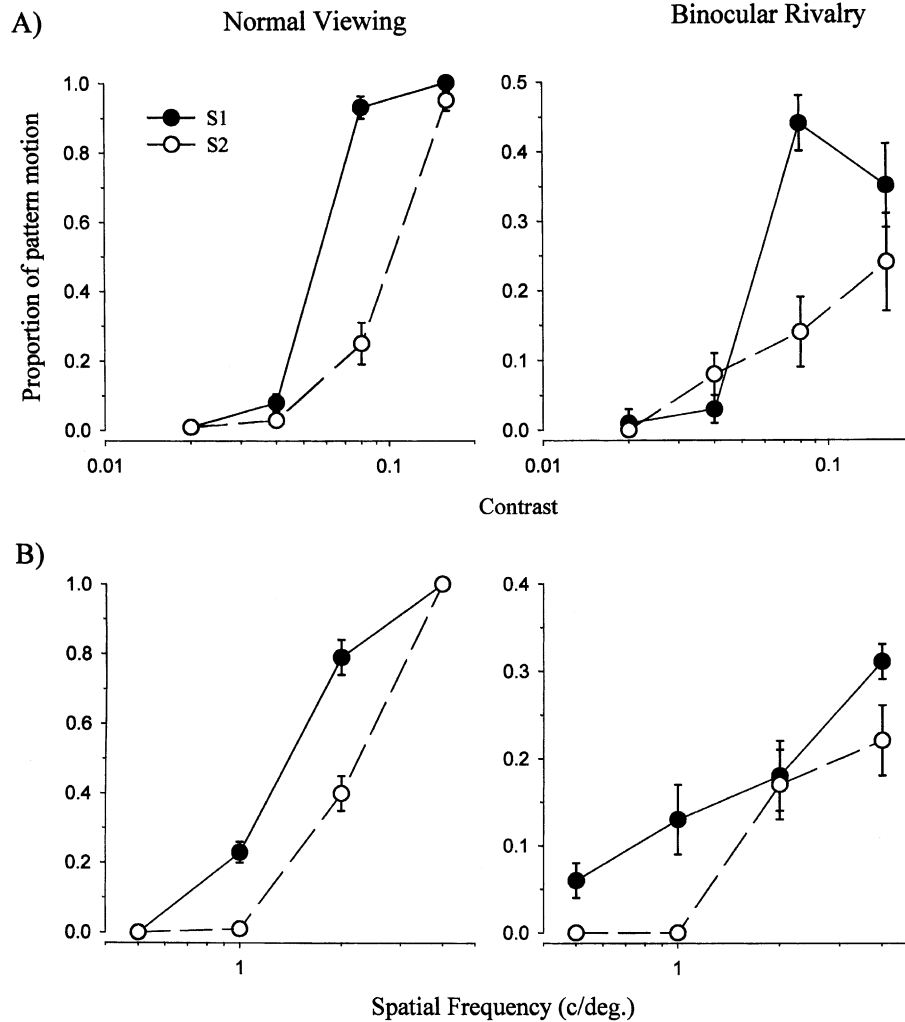
Fig. 4. Conditions favouring pattern motion during normal and binocularly rivalrous viewing. One grating had a spatial frequency of 4 c/deg, and a contrast of 0.16, whereas the contrast and spatial frequency of the other grating was varied. For the rivalrous trials, subjects were only asked to report the perceived direction of motion when one orientation was perceptually dominant for the whole trial. The graphs show the proportion of trials in which pattern motion was perceived. This proportion of pattern motion perceived decreased as the gratings became more different from each other in spatial frequency or contrast. The mean value for every point on the graphs is based on an average of 80 trials taken over 10 sessions. The error bars represent the SEM.

to the grating's orientation (just as if viewing the single grating alone). However, the direction of motion within all the different patches of the mosaic was most often a vector combination of the two grating component directions and velocities (pattern motion). In other words the patches appeared to belong to a single surface, moving in the pattern motion direction.

Evidence that the same mechanism underlies pattern motion in dichoptic and normal binocular viewing was apparent when the component gratings were made progressively more different from each other. In agreement with studies of pattern motion in normal viewing (Adelson & Movshon, 1982; Stoner et al., 1990; Krauskopf & Farell, 1990), subjects reported a decrease in the incidence of pattern motion when the difference in colour, direction of motion, contrast, velocity or spatial frequency between gratings was increased (see also

Banton et al., 1994; Cobo-Lewis et al., 2000; Saint-Amour et al., 2000). However, in this and previous studies, elements of both gratings were perceived at different spatial locations within the stimulus. Now, Alais et al. (1998) have reported that closely adjacent patches of drifting gratings, of two different orientations, all viewed normally, can cohere to give a single shared direction of perceived motion. Therefore, one might imagine that, when the mosaic is seen during dichoptic viewing, the perceived direction is simply determined by integration of directional information from the contiguous single-grating patches, rather than through the integration of motion information from a grating whose orientation information is suppressed from perception.

To further compare pattern motion in normal and dichoptic viewing, we briefly presented moving gratings

that were approximately the same size as the connected single-grating patches in the mosaic (1-deg diameter). This was done deliberately so that, on a significant proportion of trials, one orientation dominated completely over the whole area and for the whole period of exposure. On about one third of these trials, subjects reported that the dominant grating was perceived to move in the direction of pattern motion, just as if the two gratings were superimposed (see also Andrews & Blakemore, 1999). This clearly shows that a visual stimulus whose form is rendered literally invisible through binocular rivalry can nevertheless contribute to the perception of movement. In addition, changes to the stimulus characteristics of the gratings demonstrated that the interocular combination of moving gratings occurred in a similar manner to that observed in normal binocular vision.

The implication of these results is that the normal mechanism for generating pattern motion involves an initial analysis of the component motions followed by an integration of these signals to realise the perceived direction of movement for the object. There has previously been some debate about the possibility that the motion of true plaids is simply due to the tracking of the singularities provided by the intersection points of the superimposed gratings (Adelson & Movshon, 1982; Ferrera & Wilson, 1987; Welch, 1989; Rubin & Hochstein, 1993). With dichoptic pattern motion of one grating, there is no physical summation of the stimuli and only one orientation is seen at a time. Thus, there are no such singularities, yet pattern motion still occurs. This shows that in this situation, rather than monitoring unambiguous moving elements in the scene, the visual system analyses the component motions of its constituent contours and then integrates these to generate the perceived object motion.

The influence of an unseen grating on perceived direction of motion is consistent with other findings that show stimuli rendered invisible during binocular rivalry can nevertheless contribute either to the perception of apparent motion (Wiesenfelder & Blake, 1991), or to the motion after-effect (Lehmkuhle & Fox, 1975). Similarities are also evident with reports showing that when stimuli of different colour are presented to the two eyes, chromatic rivalry occurs independently of binocular interaction for shape, movement and depth (Creed, 1935; Carney, Shadlen, & Switkes, 1987; Treisman, 1962). Taken together with other illusory conjunctions of form, colour and motion (Treisman & Schmidt, 1982; Moutoussis & Zeki, 1997a,b; Zeki & Bartels, 1998), these findings suggest that the unity of perception is illusory and that different attributes of vision can independently access perceptual awareness.

Can we draw any conclusions about where the neural correlates of dichoptic pattern motion might exist? Most neurons in primary visual cortex (V1) of monkey re-

spond selectively to bars and gratings at particular orientations (Hubel & Wiesel, 1968). During contour rivalry, these neurons exhibit significant interocular suppression (Sengpiel, Blakemore, & Harrad, 1995). However, it has been reported that only a small proportion of neurons in V1 and early extrastriate areas show changes in activity that co-vary with the ongoing alternations in perceptual dominance (Leopold & Logothetis, 1996) and it is only in later stages of visual processing, particularly within the temporal lobe, that neurons respond to the perceived rather than the retinal stimulus (Sheinberg & Logothetis, 1997; Tong, Nakayama, Vaughan, & Kanwisher, 1998). These results have recently been challenged recently by two functional imaging studies showing that activity in V1 can co-vary with the ongoing changes in form perception during contour rivalry (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). It is possible, therefore, that simple orientation perception could depend on the activity of neurons at an earlier stage of visual processing than was previously thought.

Direction-selective responses are also apparent in the activity of neurons in V1 (Hubel & Wiesel, 1968). However, these neurons only respond to component motion. When shown plaids moving in various directions, they fire only when one of the components has an orientation close to the optimum for the receptive field, as if they are blind to the other grating. Clearly such activity cannot account for pattern motion perception. Direction-selective neurons in V1 send signals, directly and indirectly, to the extrastriate area MT. A significant fraction of cells in MT are selective for pattern motion: they have the same preferred direction for drifting plaids as they do for single gratings. Such cells, which presumably combine component motion signals from earlier stages of analysis, appear to encode the perceived direction of motion. Indeed, the activity of neurons in MT has been shown to co-vary with the changes in perceived direction of motion during binocular rivalry (Logothetis & Schall, 1989).

Finally, dichoptic pattern motion was perceived on only a fraction of trials when only one grating was dominant. One explanation for this might be that, under these experimental conditions, the visual system undergoes different types of rivalrous competition (see Andrews, 2001). For example, visual information could be suppressed by inhibitory interactions that occur early in the visual pathway prior to the stage of monocular convergence (e.g. the lateral geniculate nucleus or layer IV of primary visual cortex). This type of suppression would lead to the complete dominance of one or other monocular image. Alternatively, competition could occur between different stimulus representations at later stages of visual processing. It is entirely conceivable that, in this circumstance, there would be an independent binocular interaction for form and motion.

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