

Monocular mechanisms determine plaid motion coherence

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Abstract

Although the neural location of the plaid motion coherence process is not precisely known, the middle temporal (MT) cortical area has been proposed as a likely candidate. This claim rests largely on the neurophysiological findings showing that in response to plaid stimuli, a subgroup of cells in area MT responds to the pattern direction, whereas cells in area V1 respond only to the directions of the component gratings. In Experiment 1, we report that the coherent motion of a plaid pattern can be completely abolished following adaptation to a grating which moves in the plaid direction and has the same spatial period as the plaid features (the so-called “blobs”). Interestingly, we find this phenomenon is monocular: monocular adaptation destroys plaid coherence in the exposed eye but leaves it unaffected in the other eye. Experiment 2 demonstrates that adaptation to a purely binocular (dichoptic) grating does not affect perceived plaid coherence. These data suggest several conclusions: (1) that the mechanism determining plaid coherence responds to the motion of plaid features, (2) that the coherence mechanism is monocular, and thus (3), that it is probably located at a relatively low level in the visual system and peripherally to the binocular mechanisms commonly presumed to underlie two-dimensional (2-D) motion perception. Experiment 3 examines the spatial tuning of the monocular coherence mechanism and our results suggest it is broadly tuned with a preference for lower spatial frequencies. In Experiment 4, we examine whether perceived plaid direction is determined by the motion of the grating components or the features. Our data strongly support a feature-based model.

Keywords: Motion perception, Motion coherence, Monocular, Aperture problem, Spatial tuning

Introduction

Much discussion in the two-dimensional (2-D) motion literature over the last decade or so has focused on how the visual system overcomes the “aperture problem” (Ullman, 1986) to signal the coherent motion of objects. The “problem” is that the edges of moving objects seen through small apertures (receptive fields, by analogy) are directionally ambiguous, since only their perpendicular motion is visible, and this could be due to any motion in the family of oblique motions which shares the same perpendicular component. Yet, in most circumstances, our perception of moving objects does not reflect the ambiguity which is held to occur in the front-end of the visual system and objects are seen to move coherently. One common method for examining motion coherence in the laboratory has been to use plaid stimuli (Adelson & Movshon, 1982). Plaids are compound stimuli constructed by superimposing two gratings (the components)

which move in different directions and have different orientations. When the component gratings are similar (in terms of contrast, spatial frequency, color, etc.), a moving plaid will result. That is, a coherently moving pattern with a single direction will be seen, rather than the independent motion of the components. If the component gratings differ markedly, then plaid coherence is not seen and the components are seen instead to slide transparently over each other.

Motion coherence is one of three motion-related questions which the human visual system must solve when it is confronted with moving images on the retina. In such circumstances, the visual system must decide which of the motions on the retina belong to single objects (motion *coherence*), and what are the *directions* and *velocities* of these objects. It can be argued that motion coherence is the most fundamental of these questions and that it must logically precede the others, since the visual system can only signal the direction and velocity of an object after first deciding which of the motion signals on the retina constitute a single object. Despite its primacy, motion coherence remains the least understood of the three general questions in motion perception. This can be partially related to the fact

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that we often know that a moving object we perceive is a physically rigid entity and should thus have a single direction of motion. Many researchers have traditionally assumed (tacitly, at least) that our perception of objects simply reflects our knowledge of them. However, researchers in the 1980s started to acknowledge that the detection of moving objects is not so straightforward, and that as a consequence of the visual system receiving its input through small circular receptive fields on the retina, the edges of moving objects are directionally ambiguous. The consequence of this has been to direct the attention of some vision researchers to consider how the visual system resolves this ambiguity to produce percepts of rigid, coherent motion.

Of the studies which have used plaid stimuli to examine motion coherence, most have invoked the Movshon et al. (1985) Intersection-of-Constraints (IOC) model as an explanatory account. The IOC model postulates a neural implementation of a simple geometric rule (Fennema & Thompson, 1979) which provides a mathematical solution to the directional ambiguities associated with viewing moving objects through small circular receptive fields. The IOC model is based upon neurophysiological findings (Movshon et al., 1985) which showed that, while visual area 1 (V1) of the cortex acts as a series of independent directional filters, interactions between signalled directions do occur in the middle temporal (MT) area, where, in response to a moving plaid, a minority of cells (25%) would respond to the direction of the coherent plaid (pattern-selective cells) and not to the component directions. The remainder of MT cells responded much like those in V1 (component-selective cells). Accordingly, the model states that two stages of processing are involved in 2-D motion processing. In the first stage, the plaid (or 2-D object) is effectively decomposed into its grating components (object edges or contours) by direction and orientation-selective cells found in area V1. These separate signals then feed forward to a second stage where the pattern-selective motion cells in area MT integrate the component signals according to an IOC-like algorithm to provide the plaid (object) direction.

As this brief summary indicates, the IOC model is primarily an explanation of perceived plaid direction. It provides a useful account of how two independently moving components can produce a pattern moving in a third direction, but says very little about how the resulting plaid appears to move coherently (or noncoherently), or about what mechanism might underlie coherence. The model presumes that coherence results from the activation of pattern-selective MT cells, which then inhibit the component-selective MT cells. Most studies which have examined motion coherence using plaid stimuli have manipulated the relative values of various component parameters, such as spatial frequency, contrast, velocity, direction, color, relative depth, and component direction, in order to identify the factors which prevent plaid coherence (Adelson & Movshon, 1982; Adelson, 1984; Movshon et al., 1985; Krauskopf & Farell, 1990; Kooi et al., 1992; Smith, 1992; Kim & Wilson, 1993). Essentially, these studies have found that plaid components must be the same or similar on most or all of these factors for coherence to occur. To explain these observations, it is generally concluded, in line with the IOC model, that stimulus differences between the plaid components prevent the activation of the pattern-selective MT cells, so that the component-selective MT cells dominate the percept. Conversely, noncoherent plaid motion is taken to reflect the opposite relationship. Thus, most studies using plaid stimuli have suggested area MT as the neural site of motion coherence

(although this suggestion has also been advanced by researchers using other stimuli, see Yang & Blake, 1994) and the inhibition of component-selective cells by pattern-selective cells as the essential mechanism.

In the present study, we use plaids composed of textured gratings (see Figs. 1a and 1b) to examine motion coherence. The textured gratings are square-wave luminance gratings with a fine, random dot array on the high luminance regions (Fig. 1a). Whereas drifting gratings would normally be directionally ambiguous and always appear to drift orthogonally to their orientation (the aperture problem), textured gratings provide the visual system with sufficient directional cues to disambiguate

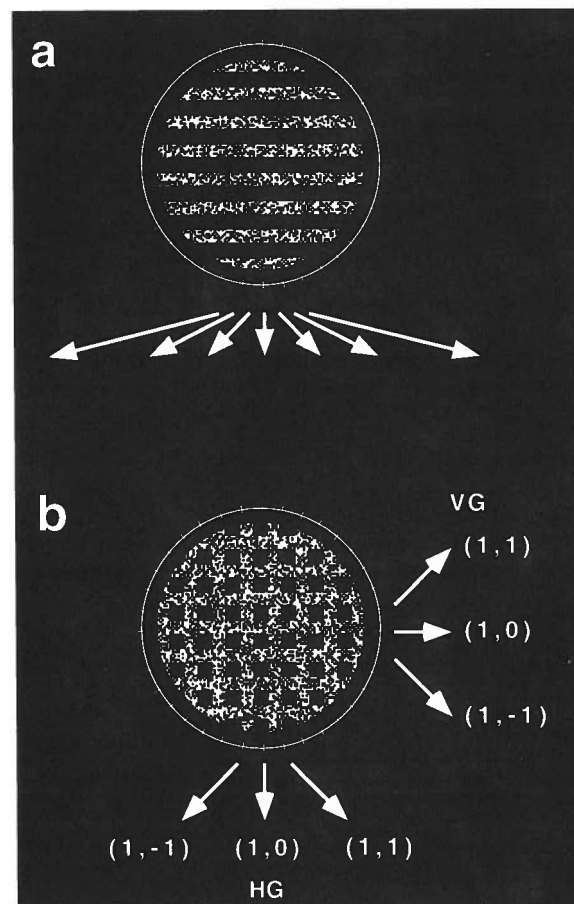


Fig. 1. An example of the stimuli used in this experiment. (a) High-luminance regions of square-wave gratings were covered with small (1 arc min^2) texture elements. The texture and the grating form a single stimulus and they do not move independently of each other, allowing the decoupling of orientation and direction. The component velocity ratios express the perpendicular and parallel displacement combinations used to produce the motion of each component, and the perpendicular value is given first. A positive value for parallel displacement indicates that the grating translated anticlockwise of perpendicular, irrespective of whether it was oriented vertically or horizontally. (b) Two textured gratings were superimposed to form textured plaids. The gratings were oriented vertically (VG) and horizontally (HG) and their motion directions are shown by the arrows. Their perpendicular movement component was always constant (0.83 deg s^{-1}), and their parallel movement component could be varied to alter their direction. Where the textured regions intersect, the texture elements were combined according to XOR logic (see Methods).

their motion direction. It has been shown elsewhere that the direction of these stimuli is accurately perceived irrespective of whether they drift orthogonally or in a range of directions oblique to their orientation (van den Berg & van de Grind, 1993; Alais et al., 1995). It has also been shown that, despite their unambiguous directions, plaids composed of obliquely moving textured gratings will combine to form coherently moving plaids, although the coherence is dependent upon such factors as component spatial frequency, the size of the texture elements, and inspection duration (van den Berg & van de Grind, 1993). The rationale for using textured plaids is to provide a test of component recombination models, such as the IOC model and others (Wilson et al., 1992; Wilson & Kim, 1994). Importantly, we find that the perceived direction of a coherently moving textured plaid does not depend on the disambiguated directions of its components. Rather, as our Experiment 4 shows, a mechanism responsive to the motion of the plaid's intersection features, the so-called "blobs" (Adelson & Movshon, 1982), seems to determine the direction of textured plaids, since their perceived direction is invariant as long as the direction of their blobs is invariant.

As well as suggesting that a feature-sensitive motion mechanism determines the perceived direction of textured plaids, this result suggests that the same mechanism must also be involved in determining their coherence. This is because there is a conflict of moving textures in textured plaids, as each grating component has a fine random texture whose motion direction conflicts with that of the other textured component. This is clearly evident when viewing textured plaids which are not perceived to move coherently, where the impression is one of strips of fine, random texture streaming in different directions and segregated in depth, and the blobs are not evident (essentially the same percept as occurs with conventional plaids). This typically occurs when the textured gratings are of lower spatial frequency or have large texture elements (van den Berg & van de Grind, 1993). In a coherently moving textured plaid, while both of these textures are still physically in conflict, they appear in the same depth plane and as background noise in a rigidly moving orthogonal form, the plaid, which has an unambiguous direction determined by the moving array of dark blobs visible in Fig. 1b. Thus, apart from defining the direction of the textured plaid, it seems that the presence of the drifting array of low spatial-frequency blob features also determines the coherence of the plaid, despite the conflicting motion of the high spatial-frequency random texture. In this respect, it is interesting to consider that the coherent motion of textured plaids may share a common mechanism with motion capture, since they have a similar phenomenology: motion capture occurs most effectively when the capturing stimuli (a drifting sine-wave grating, for example) is of low spatial frequency (Ramachandran & Inada, 1985), when it can even capture the motion of random dots drifting in an opposite direction (Ramachandran & Cavanagh, 1987).

Experiment 1

In the present study, we test the proposal that the perception of plaid coherence is determined by a mechanism responsive to the motion of the plaid's blob features. This will be done using an adaptation paradigm to manipulate the salience of the plaid blobs, a paradigm which has been used successfully in this capacity before (Burke et al., 1994). The method involves testing plaid

coherence before and after a period of adaptation to a moving grating, with subjects reporting whether the plaid appears to move coherently or noncoherently. The grating is oriented orthogonally to the motion direction of the plaid blobs, matches their spatial period, velocity and direction, and is thus designed to fatigue the mechanism responding to the motion of the blobs. If the feature-sensitive motion mechanism responding to the motion of the blobs were to determine plaid coherence, then postadaptation testing of coherence should produce less "coherent" judgements than preadaptation testing, reflecting the reduced output of the mechanism following adaptation. Similar adaptation procedures have been used elsewhere (Movshon et al., 1985; von Grünau & Dubé, 1993), although without the emphasis on the feature-sensitive motion mechanism. What distinguishes the present experiments from these earlier studies is that it evaluates recent research implicating a feature-sensitive motion mechanism in the perception of plaid direction and coherence which has suggested that the mechanism is monocular (Alais et al., 1994; Burke et al., 1994; Wenderoth et al., 1994; Alais et al., 1996b). We test this claim by presenting preadaptation and postadaptation test stimuli monocularly to the same eye, but comparing the effects of exposure to the adapting stimulus between the tested and untested eye. If the feature-sensitive motion mechanism were truly monocular, then any effects of monocular adaptation to the grating on coherence judgements will be confined to the exposed eye, such that there will be no effect when coherence judgements are tested interocularly. If this result is obtained, it will support the claimed monocularly of the mechanism and argue against claims that the site of plaid motion coherence is a higher level, binocular mechanism such as cortical area MT.

Methods

Observers

Three of the authors and two naïve observers served as the subjects in these experiments. All wore corrective lenses if they were normally required to do so.

Apparatus and stimuli

Three plaid stimuli were used in this experiment, all composed of square-wave, luminance-defined component gratings which were orthogonally oriented (vertical and horizontal) and had a spatial frequency of 5 cycles/deg. The component gratings had a texture of random dots "painted" on the regions of high luminance (Fig. 1), with each dot formed by a small square of 1×1 min of arc at the viewing distance of 2.8 m. The dots were assigned the same luminance as the dark and bright regions of the underlying square-wave and were black or white with equal probability. This effectively halved the space-averaged luminance of high-luminance regions. The luminance of a fully textured region was about 25 cd/m², and the Michelson contrast between the dark regions and the textured (bright) regions of the square-wave was more than 0.9. In the regions of the plaid where the textured stripes of each component grating overlap, XOR logical combination was used to ensure an equal percentage of dark and light texture in these and the nonoverlapping regions. This ensures that the intersection luminances are not compatible with physical transparency, as this encourages the perception of noncoherent motion (Stoner et al., 1990; Trueswell & Hayhoe, 1993; van den Berg & van de Grind, 1993). Since the texture on each grating was random, the texture array in

the overlapping regions varied each frame. When viewed from close range, these features appeared to “twinkle,” although this could hardly be seen at the viewing distance used for the experiments, from where only the dark blobs were perceived as clear, distinguishable features. Thus, unlike plaids composed of sine- or square-wave gratings, where the term “blobs” refers to the doubly dark and doubly light local regions formed by luminance summation at the grating intersections, the blobs in textured plaids are slightly different. While the dark blobs are formed in the same manner, the light blobs are in fact small regions of twinkling texture which are equal in luminance to the nonoverlapping regions of texture.

All gratings had a 50% duty cycle and were generated by an Amiga 2000 computer using a program described elsewhere in detail (van den Berg & van de Grind, 1993). A textureless, square-wave, luminance grating oriented at 45 deg and matched for the spatial period, velocity, and direction of the blobs was used as an adapting stimulus. The plaid components were set in motion by displacing the patterns of each frame. The frame rate was 50 Hz, and by varying the step-size of the displacement (in pixels), a range of velocities was available. By combining perpendicular and parallel displacement (relative to the orientation of each component grating) of each frame, it was possible to move the textured gratings obliquely relative to their orientation, so that their direction of motion could be manipulated independently of their orientation. Thus, while the three plaids were all composed of orthogonally oriented, textured grating components, the directions of the textured gratings were not constrained to be perpendicular to orientation. However, for all three plaids, the *perpendicular* displacements of each textured grating component were constant and equal, so that the plaid direction would always be downwards to the right at 45 deg (the direction of motion of the blobs). The directions of the grating components for the three plaids were symmetrical around the plaid (blob) direction and are shown by the arrows in the three panels of Fig. 2. The component velocity ratios shown for each component in Fig. 2 express the perpendicular value first, and a positive value of parallel displacement means that the displacement was anticlockwise of perpendicular. Note that the plaid represented in Fig. 2a corresponds to a conventional, textureless plaid insofar as the components each move perpendicularly to their orientation. The stimuli subtended a circular area of 1.5-deg diameter, in the center of which was a small computer-generated fixation point (an annulus of 20 arc-min diameter) to help prevent excessive eye movements. A circle with tickmarks surrounded the stimuli, as shown in Fig. 1, which aided direction judgements (see Experiment 4).

Procedure

Subjects sat in a darkened laboratory and their task was to judge whether the plaids they were presented with moved coherently or not. The procedure was a two-alternative forced-choice between coherent or noncoherent motion, and the percentage of “coherent” judgements was measured. Subjects completed 10 trials with each of the three plaid configurations, in both the Mon-Mon and IOT conditions. This required a 90-min session, with a break of 60 s between trials. The order of conditions was alternated between subjects. Subjects were instructed to fixate the central fixation spot throughout the experiments and to make their judgements as quickly as they could be accurately made. Head position was held steady by a chin and forehead

rest. Viewing was monocular in all conditions and plaids were presented for 3 s immediately prior to and immediately following a 30-s, monocular presentation of the adapting stimulus. The preadaptation and postadaptation plaid coherence tests were always made with the same eye; however, in separate conditions, the adapting stimulus was monocularly presented either to the tested eye (Mon-Mon condition) or to the untested eye. The latter condition tests for the interocular transfer of the effects of adaptation to the grating, and will be referred to as the IOT condition.

Results and discussion

The data are graphed in Fig. 2 and show that prior to adaptation, all plaids were judged to be “coherent” for 100% of the trials, in both the Mon-Mon and IOT conditions. However, the level of postadaptation coherence depends on whether or not the adapting grating was presented to the eye from which the coherence judgements were obtained. The Mon-Mon data (dark columns) show the coherence judgements made by the same eye that was adapted. In panels (a) and (b), the postadaptation Mon-Mon coherence judgements have been reduced from 100% prior to adaptation to 14% and 2.5%, respectively, and neither of these values is significantly different from zero ($t_4 = 2.24$ and $t_4 = 1.0$; $P > 0.05$ in both cases). The IOT data (grey columns) show the coherence judgements for the conditions where adaptation and testing are of different eyes, and it is clear from panels (a) and (b) that this left coherence judgements almost entirely unaffected, with postadaptation coherence judgements remaining at near-100% level and subjects reporting compellingly coherent plaids. This indicates that, unlike in the Mon-Mon condition, the coherence mechanism was not adapted in the IOT condition. The remarkably low level of interocular transfer of adaptation effects suggests very strongly that the mechanism mediating the coherence judgments in our stimuli is monocular. Thus, while cells in area MT would undoubtedly be adapted by exposure to our adapting stimuli, adaptation at this level could not explain our data, since MT is a highly binocular area (Felleman & Kaas, 1984; DeYoe & Van Essen, 1988) and therefore its adaptation would be evident by a decrease in coherence judgements no matter which eye was tested. Rather, the fact that these adaptation effects on coherence are confined to the adapted eye suggests that plaid coherence is mediated by a monocular mechanism.

The data shown in panel (c) are invariant. For both the Mon-Mon and IOT conditions, plaids were judged to be coherent 100% of the time in both the preadaptation and postadaptation conditions. The reason for this is that there is no conflict of motion signals in this stimulus at all, since the direction and velocity of the blobs and of both textured components is identical. Thus, the likely effect of an adapting stimulus also moving in that same direction at the same velocity would be to adapt the component and the blob mechanisms similarly. Of course, even if this were not the case and the component and blob mechanisms are not similarly adapted (since the adapting stimulus was not designed to match the texture on the component gratings), there would still be no conflict of motion signals in the stimulus. Thus, no change at all is expected from preadaptation to postadaptation coherence judgements for this plaid configuration and the invariant data in panel (c) are as expected.

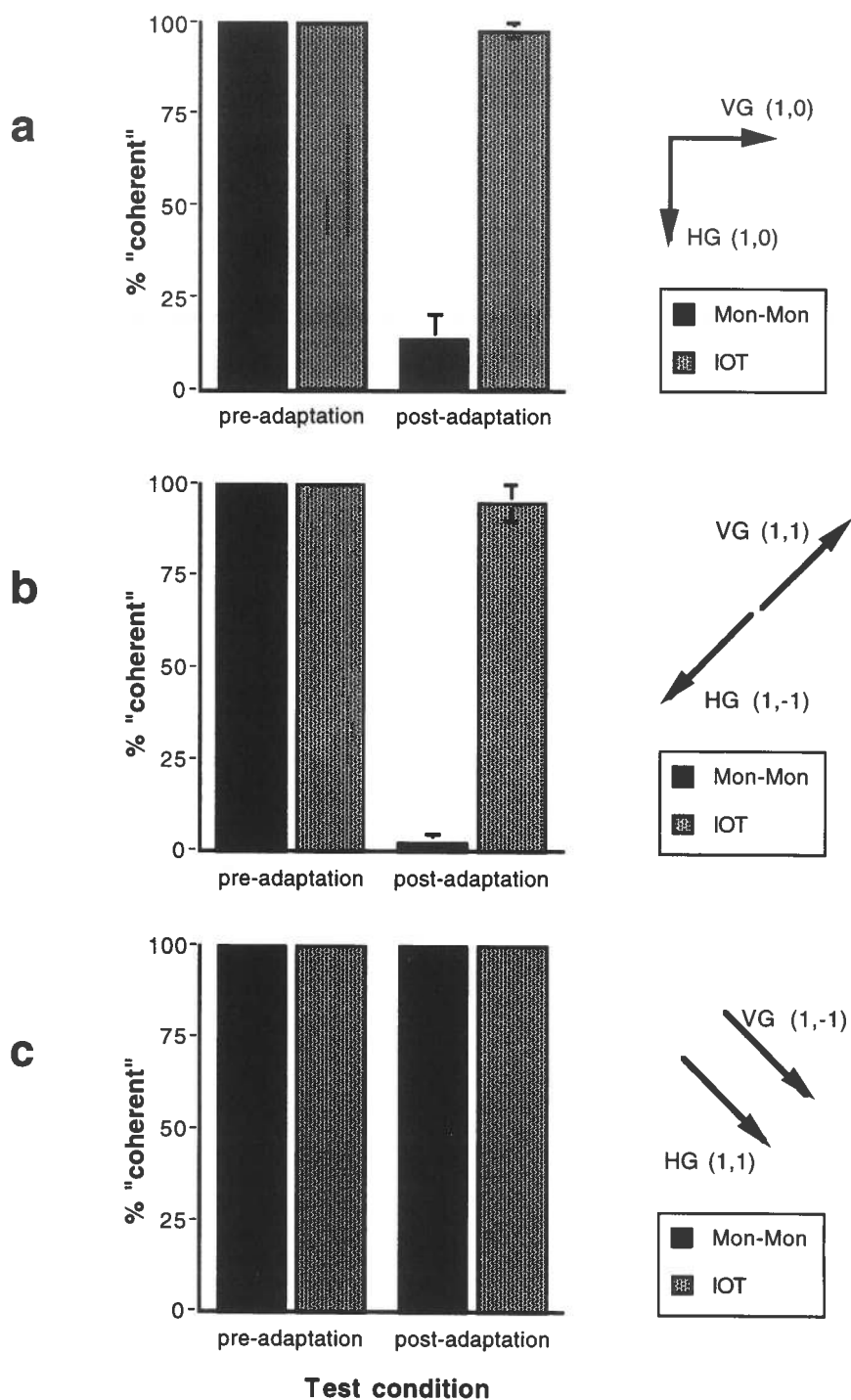


Fig. 2. The frequency of “coherent” judgements before and after adaptation to a square-wave grating designed to match the array of plaid blobs. While the direction and velocity of the coarse texture (“blobs”) is constant in all three graphs, the directions of the textured plaid’s component gratings vary, as indicated by the arrows. The plaid represented in (a) corresponds to a conventional, textureless plaid insofar as each component moves perpendicularly to its orientation. In (a) and (b), the fine texture conflicts, and in (c) it coincides. The data in (a) and (b) indicate that the response from the feature-sensitive mechanism mediating coherence is reduced following exposure to the adapting grating, such that the conflicting motion of fine texture is visible, producing a clear percept of incoherence. In (c), there is no conflicting fine texture, and coherence is unaffected following adaptation. These data suggest a spatially tuned coherence mechanism with a greater sensitivity to the coarse array of blobs than to the fine random texture.

Experiment 2

This experiment is designed to test further the conclusion that the perception of plaid coherence is determined by a monocular motion mechanism. Whereas a monocular coherence mechanism was implied in Experiment 1 by the lack of IOT of adaptation effects, this experiment will use adaptation to purely binocular motion to test this conclusion. The method will be similar to that used in Experiment 1, in that adaptation to a square-wave grating will be used to bring about changes in per-

ceived plaid coherence. The main difference is that two gratings will be presented dichoptically and fused using a stereoscope (at zero disparity). In the experimental condition (dichoptic motion), the stimuli were arranged in such a way that each of the monocular views was of a directionally ambiguous grating (alternating between 0 deg and 180 deg in one eye and 90 deg and 270 deg in the other), but the cyclopean view was of a coherently drifting grating moving in steps of 90 deg of phase. In the control condition (dichoptic flicker), the stimuli were arranged so that the ambiguous motion presented to each eye did not com-

bine into coherent motion. Thus, if plaid coherence is determined by a monocular mechanism, there should be no difference between the dichoptic motion and dichoptic flicker conditions because the coherent drift in the dichoptic motion condition is a purely binocular percept and adaptation to its motion would not affect the level of activity in a monocular mechanism. Experiment 2 tests this prediction.


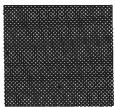

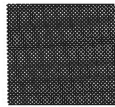
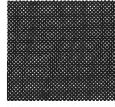

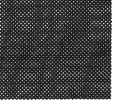





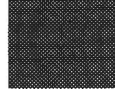



Methods

The subjects and apparatus were essentially the same as described in the methods of Experiment 1 except that only two of the authors and two naïve subjects served as subjects, another monitor, a Barco 6161, was used instead of the Amiga monitor, and all stimuli were viewed either binocularly (in preadaptation and postadaptation testing) or dichoptically (during adaptation). The stimuli, however, differed in a number of ways. Two windows of 1.5-deg diameter were drawn on the display monitor, each containing a textureless, square-wave, 5 cycles/deg grating oriented at 45 deg which were displaced each frame in steps of 90 deg of phase. Animation of the stimuli was created by cycling through a sequence of four frames, and by presenting the stimulus alternately to the left and right eyes, interposed with a blank field, the two dichoptic conditions summarized in Table 1 were created. In the dichoptic motion condition, each

monocular view is of a directionally ambiguous, counterphase grating, but the two views are 90 deg out of phase so that the cyclopean percept is of unambiguous motion. In the dichoptic flicker condition, the monocular views are again of a counterphase grating, and so is the cyclopean percept. Thus, the dichoptic flicker condition controls for adaptation to monocular flicker in each eye, which might affect the monocular coherence mechanism, since adaptation to flicker is known to affect velocity coding and sensitivity to moving gratings (Green, 1981; Smith, 1985). It also ensures that any differences between the two conditions are due to the additional presence of binocularly coherent motion in the experimental condition. The preadaptation and postadaptation stimulus was the same as one of the textured plaids used in Experiment 1 (see Fig. 2a) and the adaptation stimuli again matched the velocity and direction of the plaid's array of blob features.

For this experiment, a different dependent variable was used to quantify the effects of adaptation on perceived plaid coherence. Instead of the percentage of "coherent" judgements, we measured the total duration of perceived plaid transparency in a 15-s period immediately following adaptation, which gave us a continuous and more sensitive measure of the adaptation effects. Subjects were required to judge whether they perceived the plaid to be transparent or coherent when it first appeared, and then to monitor each change in the plaid percept over the

Table 1. A summary of the two dichoptic adaptation conditions used in Experiment 2^a

Frame	Dichoptic motion		Dichoptic flicker	
	Left eye	Right eye	Left eye	Right eye
1	 0°		 0°	
2		 90°		 0°
3	 180°		 180°	
4		 270°		 180°

^aBoth dichoptic conditions are similar in two significant ways. First, the grating alternates each frame between the left and right eyes, interposed with a blank field, and second, the monocular view in each eye is of a counterphasing and therefore directionally ambiguous grating. The important difference between the conditions is that when the monocular views are combined stereoscopically, the gratings in the dichoptic motion condition are arranged in a quadrature phase relation and form a vivid percept of a coherently drifting grating, whereas the gratings in the dichoptic flicker condition remain directionally ambiguous.

15-s period. Thus, the experimenter could measure the cumulative duration of the “transparency” percept using a stopwatch. Subjects were tested in this manner five times in each adaptation condition, with the adaptation duration being 30 s and a pause of 1 min between the trials. The data for each condition were averaged into a single estimate, and since the pattern of results was very similar for each subject, the four subjects’ data were pooled and are presented in Fig. 3. Also, since plaids which normally appear to move coherently may often switch between transparent and coherent during prolonged viewing, we also measured (binocularly) the total duration of perceived plaid transparency in a 15-s period without any prior exposure to an adapting stimulus. This established a transparency baseline for the plaid and is shown in Fig. 3 by the dashed line.

Results and discussion

Two conclusions can be drawn from the data in Fig. 3. The first, since there is clearly no difference between the dichoptic motion and dichoptic flicker conditions, is that plaid coherence is not determined by a binocular mechanism. The second is that adaptation to flicker alone is sufficient to adapt the coherence mechanism. The first conclusion is consistent with the prediction outlined in the introduction to this experiment, which followed from the findings of Experiment 1. Together, the results of the two experiments constitute strong evidence that the mechanism

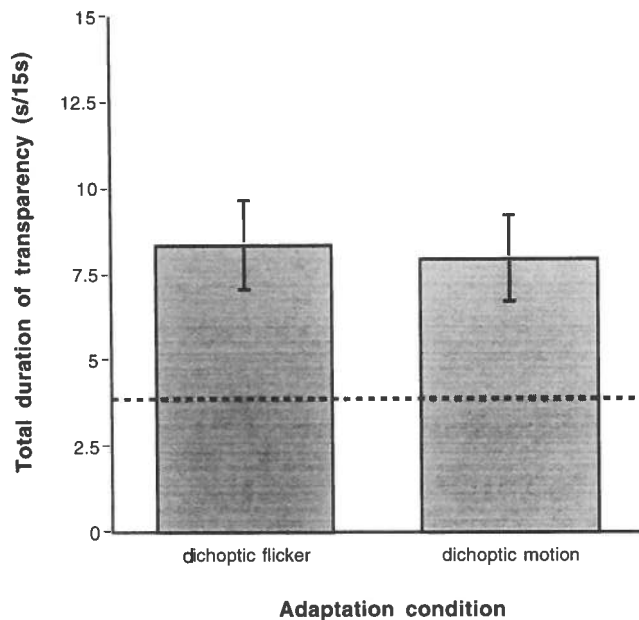


Fig. 3. The total duration of transparency in the 15-s period immediately following adaptation to dichoptic flicker and dichoptic motion. The dashed line represents the binocular baseline level of transparency for the same period without adaptation. The elevation in transparency above baseline is due to the effects of adaptation to the counterphase, flickering gratings presented to each eye during the dichoptic conditions. In the dichoptic motion condition, where the monocular flicker in each eye is interleaved to produce cyclopean motion, there is no elevation above the dichoptic flicker condition, in which the cyclopean percept is directionally ambiguous (see Table 1). This suggests that the plaid motion coherence mechanism is monocular, since it is not adapted by purely binocular motion.

determining plaid coherence is monocular, or at least very largely so. Indeed, the data of this experiment would suggest that there is no role at all for a purely binocular mechanism, although the small amount of IOT of adaptation effects found in Experiment 1, and the similarly small effects reported by Burke et al. (1994) using a similar paradigm, suggest that there is a small role for a binocular mechanism. Irrespective of whether the plaid coherence mechanism is largely monocular or entirely monocular, it is clear that such a mechanism would be peripheral to area MT, which has been proposed as a likely coherence mechanism (Movshon et al., 1985; Newsome & Paré, 1988; Rodman & Albright, 1989).

Turning to our second conclusion, the key point is that in both the dichoptic flicker and dichoptic motion conditions, each of the eyes was presented with counterphase, flickering gratings. The difference between the conditions is only whether the presentations to the left and right eyes were in phase (dichoptic flicker) or 90 deg out of phase (dichoptic motion). Thus, the significant elevation in perceived transparency above the level of the no-adaptation baseline in both conditions ($t_6 = 3.77$ and $t_6 = 3.48$ for the flicker and motion conditions respectively; $P < 0.05$ for both conditions) can only be attributable to flicker adaptation. A likely explanation stems from the fact that the flickering, counterphase grating seen by each eye is directionally ambiguous and its displacement could be equally due to motion in either of the directions orthogonal to its orientation. Thus, in terms of motion detectors, it would be expected that detectors responsive to motion in each direction would be activated in roughly equal numbers, with the result that there would be no net motion (Levinson & Sekuler, 1975; Watson et al., 1980). This is sensible, too, from a mathematical point of view, since a counterphase grating can be decomposed into two, equivalent, half-amplitude gratings moving in opposite directions.* Thus, we can assume that there is monocular motion adaptation in both of the dichoptic conditions, except that it is occurring equally for two opposing directions. Usually, the opposing motions would not be evident as they would cancel each other, but by presenting a moving plaid in our test condition, we isolate the effect of adaptation on only one of the directions, the direction of plaid drift. The result of this, as in Experiment 1, is to cause the plaid to be perceived as less coherent, but, importantly, there is no additional effect in the dichoptic motion condition due to binocular motion adaptation.

Using essentially the same method to produce dichoptic motion as we have used, Carney and Shadlen (1993) reported that adaptation to dichoptic motion produced robust motion aftereffects (MAEs), although they were somewhat lesser in magnitude than binocularly adapted MAEs. In piloting this experiment, we found that dichoptic motion did result in MAEs, but they were very weak, and certainly much weaker than those reported by Carney and Shadlen. This is likely to be accounted for by the fact that they adapted for 5 min to dichoptic motion, whereas we did so for only 30 s. Of course, the fact that they used such an extraordinarily long adaptation period was undoubtedly due to the weaker MAEs which resulted from more conventional periods of adaptation to this type of stimulus, but

*The type of counterphase grating used in this experiment is more strictly known as an ON-OFF grating, as Sekuler et al. (1978) have pointed out, and it contains a static component which is not present in other counterphase gratings which are made by combining two half-amplitude gratings moving in opposite directions.

the occurrence of these MAEs does show that this method is capable of causing adaptation of binocular motion detectors, and so should also adapt the coherence mechanism mediating plaid coherence if it had any binocular component. That this does not occur indicates that the plaid coherence mechanism is not binocular. Possibly, prolonged adaptation (say, 5 min) to our dichoptic motion stimulus would have reduced plaid coherence, but the key point is that whereas 30 s of monocular adaptation almost completely destroyed coherence in Experiment 1, the same period of dichoptic motion adaptation has no effect. This suggests that the plaid coherence mechanism is at least largely monocular.

Experiment 3

One possible interpretation of the results obtained in Experiment 1 is that the mechanism underlying motion coherence is tuned to lower spatial frequencies. This stems from the fact that, in textured plaid stimuli, there are two sets of high spatial-frequency texture elements which move in conflicting directions, and a low spatial-frequency array of blobs moving in a third direction. Since these three conflicting motions are simultaneously present in the same region of the visual field, the two likely perceptual outcomes are either: two, rigid but transparent objects moving over each other, or, a single, but not entirely rigid object, moving in a third direction (the direction of the blobs). In the latter case, a single, coherently moving object is seen despite some high spatial-frequency “noise” in the object (the conflicting fine texture), which is not unlike the motion of many real and naturally occurring objects which may move across the visual field but not be fully rigid. The twitching markings on a running animal, for example, may move locally in many directions, yet, at a coarser spatial scale, the animal’s form moves consistently in a single direction. Thus, from an ecological point of view, a coherence mechanism would need to give greater weight to lower spatial frequencies in order to function

in a robust and consistent manner. The aim Experiment 2 is to sketch the spatial tuning of the coherence mechanism by using the same adaptation paradigm as in Experiment 1 in conjunction with the textured plaid represented in Fig. 2a. Specifically, in this experiment, we will examine how perceived coherence is affected by adaptation to a range of gratings of various spatial frequencies.

Methods

The methods are essentially the same as for Experiment 1, with the same apparatus being used and two of the authors and two naïve observers serving as subjects. The preadaptation and postadaptation stimulus was again an orthogonally oriented, 5 cycles/deg textured plaid, and the gratings’ directions of motion were orthogonal to their orientations (as represented in Fig. 2a). The adaptation stimuli were again monocularly viewed square-wave gratings designed to match the velocity and direction of the plaid’s array of blob features, but unlike the first experiment, the spatial frequency of the adapting grating was varied. On a given trial, the adapting grating could have a spatial frequency of either 0.625, 1.25, 2.5, 5.0, 10.0, or 20.0 cycles/deg. In another adaptation condition, a field of random dot texture, with texture elements matching those on the plaid’s textured gratings, was used as an adapting stimulus, making a total of seven adaptation conditions. As in Experiment 2, we measured the total duration of perceived transparency in the 15 s immediately following adaptation as our dependent variable. Subjects were tested five times in each adaptation condition, with the adaptation duration being 30 s and a pause of 1 min between trials. The data for each condition were averaged into a single estimate, and since the pattern of results was very similar for each subject, the four subjects’ data were pooled and are presented in Fig. 4. We also measured monocularly the duration of perceived transparency without adaptation to establish a transparency baseline for the plaid (the dashed line in Fig. 4).

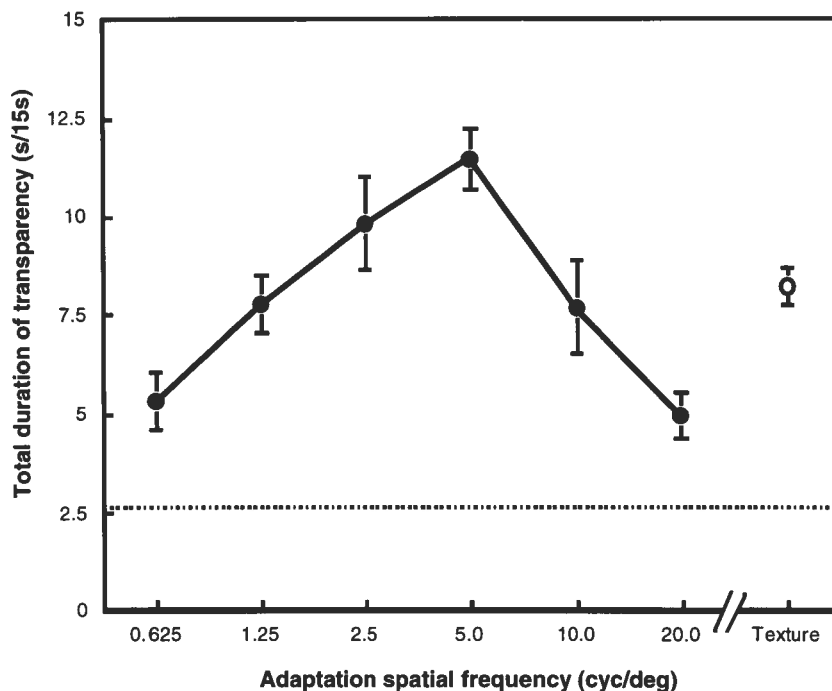


Fig. 4. The total duration of transparency in the 15-s period immediately following monocular adaptation to square-wave gratings of various spatial frequencies. The dashed line represents the monocular baseline level of transparency for the same period without adaptation. All spatial frequencies elevated the level of transparency, as did random texture, although lower spatial frequencies were more effective.

Results and discussion

The data are graphed in Fig. 4 and show that following adaptation to all stimuli, the duration of plaid transparency is greater than the no-adaptation baseline level (dashed line). The smallest effects, which occurred following adaptation to gratings of 0.625 cycles/deg and 20.0 cycles/deg, both differ significantly from the baseline ($t_6 = 3.25$ and $t_6 = 3.26$, respectively; $P < 0.05$ in both cases). However, there is a clear effect of the spatial frequency of the adapting stimulus, with the 5 cycles/deg adapting grating being maximally effective in causing transparency (i.e. the duration of plaid coherence is least in this condition). On either side of this point, the effectiveness of the adapting stimuli for causing postadaptation transparency decreases. Note that for 10 cycles/deg, one octave above the maximum, the elevation in duration of transparency above baseline is reduced by approximately one half, but that below the maximum, a decrease of two octaves is required to reduce the duration of transparency by a similar amount. Thus, the roll-off is greater for spatial frequencies above the 5 cycles/deg point than for those below it. This suggests a bias towards lower frequencies in the spatial tuning of the coherence mechanism. In the texture condition, the duration of transparency following adaptation is 8.18 s and the average duration of transparency in the six grating conditions is 7.78 s. This difference is not significant ($t_{21} = 1.24$; $P > 0.05$), which is consistent with the fact that, on average, a field of random dots contains all spatial frequencies in equal proportion.

Experiment 4

The preceding experiments provide strong evidence that a monocular mechanism sensitive to the motion of the plaid's blob features determines perceived plaid coherence. Other evidence suggests that a monocular feature-sensitive motion mechanism is also involved in determining perceived plaid direction (Alais et al., 1994; Wenderoth et al., 1994; Alais et al., 1996a), although it is often difficult to evaluate feature-based and component-based models of plaid direction perception because they often make identical predictions. Adelson and Movshon (1982), in their original plaid paper, considered both kinds of model but dismissed a feature-based model in favor of the component-based IOC model on the grounds of masking experiments which showed orientation tuning and therefore supported a model based on oriented components. However, the problem remains that both models predict the same direction. By using textured plaid stimuli, the importance of plaid blobs in determining perceived plaid direction can be examined under conditions where component-based models and feature-based models make distinct predictions. This arises from the fact that the perceived direction of the textured gratings which make up the textured plaid is not constrained to be orthogonal to its orientation (the aperture problem). Rather, the texture disambiguates the motion direction of the grating so that its orientation is decoupled from its motion direction.

In previous experiments, it has been shown that the direction of textured gratings can be accurately perceived when moving in a wide range of directions which are oblique with respect to orientation (van den Berg & van de Grind, 1993; Alais et al., 1995). Using textured gratings, a plaid can be composed of grating components which are, say, orthogonal in orientation, but whose direction may still be independently manipulated. This

differs from conventional sine-wave or square-wave plaids where specifying the orientation of the components necessarily specifies their direction too, since the direction and orientation of the gratings are yoked and inextricably confounded. Thus, textured plaids permit a test which discriminates between feature-based and component-based models. The test capitalizes on our earlier finding that textured gratings which move obliquely (i.e. a combination of perpendicular and parallel movement) are accurately perceived, and on the fact that the motion of a plaid's blobs is determined only by the perpendicular movement of its grating components. We construct plaids out of textured gratings which have a constant perpendicular movement (thus holding blob direction constant) while varying the parallel movement component of the gratings (to alter their perceived direction). Since component-based models of plaid perception calculate plaid direction by first extracting the directions of the grating components, before recombining them according to either the IOC rule (Movshon et al., 1985) or a vector sum of the Fourier and non-Fourier components (Wilson et al., 1992; Wilson & Kim, 1994), they must predict changes in plaid direction due to (nonsymmetrical) changes in component direction. On the contrary, by keeping the perpendicular movement of the gratings constant, the blobs will be constant in velocity and feature-based models would predict no change in perceived plaid direction. In Experiment 4, we evaluate these predictions.

Methods

The plaids used in this experiment were all composed of orthogonally oriented textured grating components (vertical and horizontal) with a spatial frequency of 5 cycles/deg and were viewed binocularly. Each grating component of the textured plaids could have any one of three directions, as shown in Fig. 5, but their perpendicular movement was held constant and only their parallel movement was varied. The three directions for each component were combined factorially to make a total of nine plaid combinations, and the stimuli were presented in random order for 5 s each and subjects were required to judge plaid direction. They did so by placing a mouse-operated pointer on a graduated circle drawn just beyond the stimulus perimeter and clicking the mouse button. The computer recorded the directions. Five replicated measures of each plaid direction were taken and averaged for each subject.

Results and discussion

The important result of this experiment (see Fig. 5) is that the perceived direction of the textured plaids is nearly invariant over the nine combinations of component direction. These data provide a strong challenge to component-based models in that the various combinations of component directions have apparently not been recombined to yield the expected variety of plaid directions such models would predict. The IOC model, for example, predicts a range of plaid directions greater than 180 deg for these nine combinations of component directions. This result replicates and extends a similar finding reported by van den Berg and van de Grind (1993). Moreover, these data specifically support a feature-based model in that the direction in which all nine plaids were seen to move corresponds to the direction of the blob features, which is determined by the sum of the perpendicular movement only of the grating components. Since the perpendicular movement of the grating components were or-

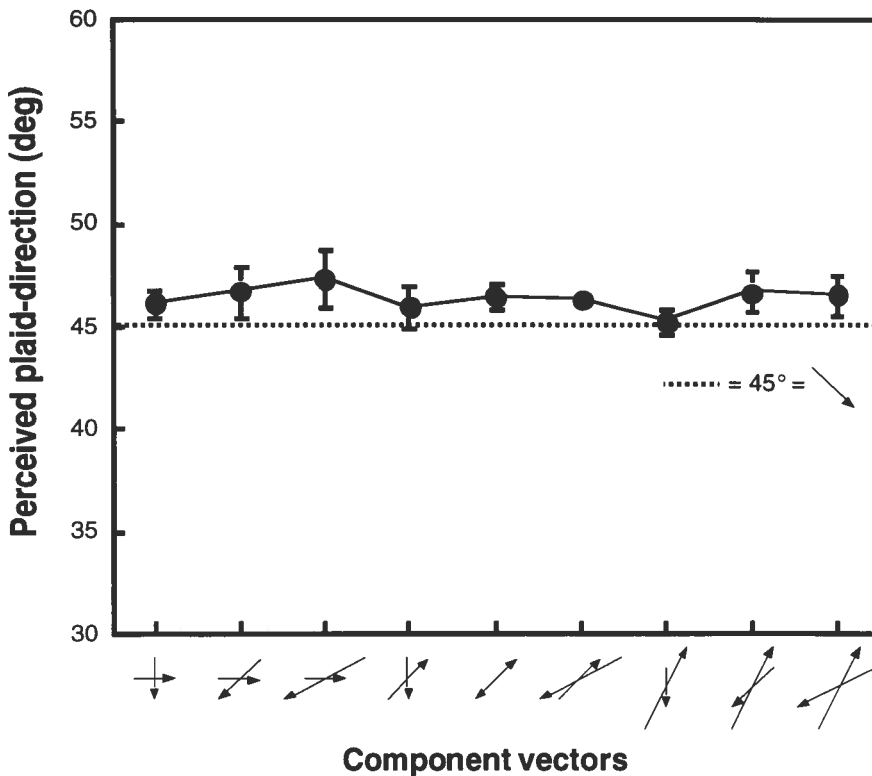


Fig. 5. Perceived directions of nine textured plaids whose component directions and speeds are manipulated as shown by the vectors on the abscissa. In all nine plaids, the component gratings moved with a constant perpendicular movement component, while the parallel movement component was varied. This has the effect of varying the direction of the plaid's component gratings, while the direction of the blobs, which is determined only by the perpendicular movement of the gratings, is kept constant (represented by the dashed line). This should result in a range of perceived plaid directions of over 180 deg according to component-based theories of plaid direction perception, such as the IOC model. Our data strongly suggest the motion of the blobs determines perceived plaid direction, and thus favors a feature-based model.

thogonal and equal in magnitude, they sum to a direction of 45 deg (downward and to the right). It is also noteworthy that the IOC model cannot provide a solution for the fifth plaid (5th combination on the abscissa of Fig. 5), since the constraint lines never intersect, and that the IOC-predicted direction for the ninth plaid is directly opposite the direction indicated by our subjects.

General discussion

From the results reported in these four experiments, we draw a number of conclusions: (1) that the mechanism determining the coherence of textured plaids responds to the motion of plaid's blob features; (2) that a similar feature-sensitive mechanism also determines the direction of textured plaids; (3) that this coherence mechanism is monocular, and thus (4) that it is located at a low level in the visual system and peripherally to the binocular mechanisms commonly held to underlie 2-D motion perception; and (5) that the coherence mechanism is spatially tuned to coarse texture or features rather than fine texture.

Our first conclusion adds to a growing body of evidence suggesting that motion coherence is determined by the local motion signals associated with the motion of object texture and features (Derrington & Badcock, 1992; Burke et al., 1994; Yang & Blake, 1994). More specifically, the data from Experiment 3 suggest that the spatial tuning of the coherence mechanism is such that it prefers the coarse texture of the blob array to the fine texture of the component gratings. The results of Experiment 1 make this point clearly, since in two of the plaids [panels (a) and (b) in Fig. 2], the fine random texture on each component moved in conflicting directions, yet a rigid plaid was still seen to move coherently in the direction of the low spatial-frequency array of blobs. It was only after adapting the mech-

anism responding to the motion of the blobs that the conflicting fine texture was visible and incoherent motion reported. Our third and fourth conclusions shed light on an unanswered question: where does plaid coherence occur in the motion pathway? A coherence mechanism which is very largely monocular, as these data and those of Burke et al. (1994) suggest, is most likely to have a relatively low-level neural site where eye of origin information is still available. In terms of a probable neural site for this mechanism, a cortical location is most likely limited to the middle layers of V1, primarily layers 4Ca and 4Cb, where the input from the two eyes remains largely separated and there are many monocular simple cells. Most cells in other layers of V1 are substantially or fully binocular, and higher level cortical sites in the motion pathway, such as V2 and MT, are highly binocular. At a lower level, another possibility would be a subcortical structure like the lateral geniculate nucleus, where the alternately layered inputs from the left eye and right eye are essentially independent (Rodiek, 1971). Another midbrain structure, the superior colliculus (SC), sends strong projections to MT (Maunsell & Van Essen, 1983; Ungerleider et al., 1984) and might therefore be involved in motion processing and coherence; however, the data from Experiments 1 and 2 render this possibility unlikely as most SC cells can be driven by input to either eye (Gordon & Presson, 1977; Marrocco & Li, 1977).

Regardless of its particular neural site, a monocular motion coherence mechanism would certainly be peripheral to area MT, a highly binocular area which is often labelled a specialist motion mechanism and is frequently presumed to underlie two-dimensional motion perception. If the coherence mechanism were low level and monocular, it would make good sense in ecological terms since it would provide a robust means of signalling motion coherence with a single eye, whereas a binocular mechanism would likely require activation from two eyes to be optimally

activated, due to binocular synergism (Hubel & Wiesel, 1977). Also, the immediate challenge facing the visual system when it receives visual input is image segregation, to establish figures from their backgrounds, depth relations, to group contours and textures into objects, etc. When the visual input contains moving objects, image segregation and the grouping of contours and textures into objects (motion coherence) has a particular computational importance in that it must precede the calculation of the direction and velocity of the moving objects. It is sensible, then, that a mechanism signalling object coherence be located early in the visual system and prior to higher level, specialized motion mechanisms concerned with object direction and velocity, such as area MT (Albright, 1984; Rodman & Albright, 1987). Moreover, our perception of moving objects is likely to be even more robust if the coarse texture or features of an object are given greater weight than the fine features, since many moving objects are not physically rigid, in which case conflicting local motion signals are more likely on a fine spatial scale than on a coarser spatial scale. The oscillating leaves on a swaying tree, for example, may move in many local directions, but the trunk and branches are a good cue to the swaying movement of the tree. Thus, the bias of the coherence mechanism towards lower spatial frequencies reported in Experiment 3 is consistent with this rationale.

A motion coherence mechanism responsive to moving texture or features is sensible because regions of similar texture in a retinal image are reliable cues for delineating the spatial extent of objects, and this is very useful in aiding the initial task of image segregation (together with other cues, such as motion parallax, color, etc.). Moreover, for several reasons, a coherence mechanism of this kind would be more reliable for defining an object's direction, velocity, and spatial extent than one based on an object's edges. Not only are edges subject to the aperture problem, but recent studies using multiple apertures to view rigid, moving shapes defined by lines which are not spatially coextensive (a diamond, for example, but not a plaid) have shown that the lines are not grouped into a coherent object, except at low contrast levels (Lorenceanu & Shiffrar, 1992). Thus, models of 2-D motion perception which are based on the extraction of velocities from edges, such as the IOC model, would not be likely to provide a robust foundation for a coherence mechanism unless information from other features, such as corners or surface texture and features, were also included. Considering plaid stimuli in this light suggests that the important element determining perceived coherence does not stem from the components *per se*, but from the components being spatially coextensive, which thereby creates an array of blob features and makes the plaid more like a textured surface than a pattern composed of two, independent gratings. Experiment 4 showed the importance of the blobs in determining perceived plaid direction when the component gratings are manipulated independently and supports the contention that the motion signal generated in response to the moving array of blobs is crucial in our perception of moving plaids.

It was mentioned in the Introduction that the array of dark blobs dominate the textured plaid percept, and that the twinkling, textured blobs at the grating intersections do not seem nearly so salient. We examined the role of the dark blobs in a pilot experiment by changing the textured plaid so that rather than being composed of textured bars moving over a dark background, the textured bars instead moved over a textured background. The difference between the two stimuli is that the former

creates an array of dark blobs which appear to be shunted along by the moving bars, whereas in the latter, the static, textured background is clearly visible and dynamic occlusion cues indicate the textured bars sweeping over it. Thus, in the latter case, there are no dark blobs, only the twinkling, textured blobs at the grating intersections, and the effect of this is dramatic: textured plaids of this kind (otherwise identical to the one shown in Fig. 2a) were perceived to move completely incoherently, with no hint of coherence. This demonstrates that the twinkling, textured blobs alone are insufficient to cause the textured plaid to be perceived coherently, and therefore indicates that the dark blobs are the critical features determining the perceived coherence of the textured plaids.

Of course, whether it is the dark blobs or the light, textured blobs which are most important for the perceived coherence of our stimuli, the results in these four experiments are consistent with other studies which have shown that perceived plaid coherence is directly affected by manipulations of blob luminance (Stoner et al., 1990; von Grünau & Dubé, 1993; Trueswell & Hayhoe, 1993), or by obscuring them (Vallortigara & Bressan, 1991). On the contrary, the studies of plaid coherence mentioned in the Introduction which showed that large relative differences in component spatial frequency, color, velocity, direction, contrast, etc. destroys plaid coherence may actually show more about image segregation cues used by the visual system than about object coherence. That is, these component differences might have led to the components being signalled as separate objects because they differed sufficiently in terms of variables which are normally robust segregation or depth cues to produce a percept of separate, independently moving gratings. Presumably, under these circumstances, the cues indicating that the component gratings are separate objects become perceptually dominant in spite of the consistent motion of the plaid's array of blobs to suggest a single object.

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