



# Local and global factors affecting the coherent motion of gratings presented in multiple apertures

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## Abstract

Using stimuli composed of two independent gratings viewed through multiple apertures, we investigate a number of parameters affecting the integration of locally ambiguous motions into globally coherent motion. In four experiments, we varied local factors (grating spatial frequency, speed, contrast, duty cycle, orientation) and global factors (degree of similarity and common fate between the gratings, and symmetry in the configuration of the grating pattern) and examined their effects on global motion coherence. Our results, confirming accounts offered by previous investigators, indicate that local competition between motion signals generated by contours (ambiguous) and their line terminations (unambiguous) is important in determining global motion coherence in multiple-aperture stimuli. Our results also indicate that global factors can affect perceived coherence independently of local motion signals, suggesting the involvement of higher-level motion areas and a role for non-motion processes such as those involved in pattern and form perception. Comparing motion coherence with other two-dimensional (2-D) stimuli (plaids) shows that 2-D multiple-aperture stimuli are not analogous and that coherence models derived from plaid stimuli do not account for the data. © 1998 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Two-dimensional (2-D) motion perception has been a major area of research in the last decade or so, and several different paradigms have been developed as tools for examining the central questions this area poses. One question concerns how motion which is coherent at a global level can be derived from a variety of independent local motion signals. This has usually been investigated using either plaid stimuli [1], which require the visual system to find the unique motion which can accommodate the independent motion of the plaid's component gratings, or random dot stimuli, which require the visual system to average local motions into a globally coherent motion [55,56]. While these stimuli are presented within single apertures in almost all cases, there is an increasing interest in 2-D

motion stimuli presented within multiple apertures. Typically, these stimuli comprise single lines drifting within an array of spatially separated apertures [27,34,46]. Despite the fragmented nature of these stimuli, the visual system can nonetheless resolve coherent global motion. This suggests that local motion signals can be integrated across separate retinal locations, as well as within the same retinal location.

Like plaids, then, the presentation of oriented stimuli within multiple apertures provides another tool for examining 2-D motion perception, and it is one which allows important questions to be addressed in a different manner. For example, superimposed gratings in a single aperture (i.e. a plaid) can be used to study motion integration, but since the grating contours move through each other in the same depth plane it is not a stimulus which corresponds with the contours of real objects. To resolve this, plaid components are not always seen as moving coherently; sometimes they are perceived as ordered in depth. Plaid stimuli are ideally

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suiting to studying the resulting phenomenon of motion transparency and perceived occlusion [48,49,51,52]. A disadvantage, however, is that the superimposition of plaid components results in so-called ‘blobs’ [1] due to the summation of luminances at the grating intersections, and there is now a good deal of evidence suggesting that mechanisms responsive to these and other pattern features [6,52], rather than the component gratings, largely determine perceived plaid coherence [2,5,7,49].

Multiple-aperture displays (Fig. 1), then, allow component-based models of 2-D motion integration to be examined using spatially distributed contours. An important consequence of this is that the discrete moving contours must be integrated across space. This is a long-range motion integration process, as opposed to the short-range integration underlying plaid perception, and essentially mimics the situation commonly confronting the visual system when occlusion renders the contours of moving objects incomplete. Moreover, the implied occlusion allows the role of line terminators [47] in motion integration to be examined. Extrinsic line terminators arise whenever the contours of an object are terminated by an occluding object. When the occluded object is moving, the motion of these contour terminations do not reliably indicate the object’s motion and must be discounted. Alternatively, terminated contours belonging to the object itself are known as

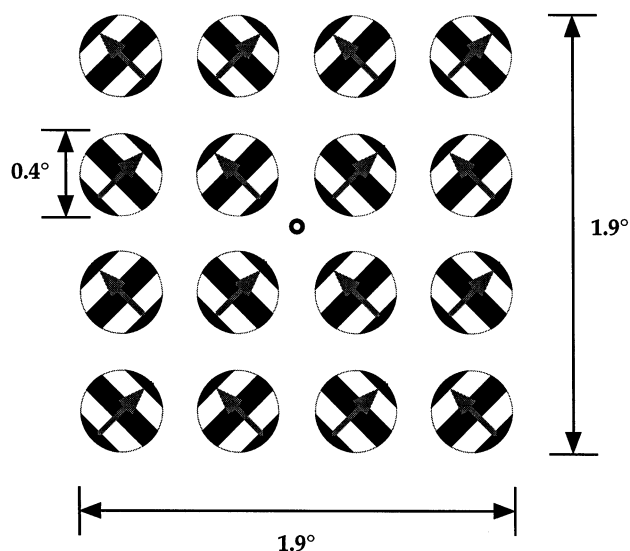


Fig. 1. A representation of the stimuli used in these experiments. The gratings were separated vertically and horizontally by  $0.1^\circ$  and the luminance of the area surrounding the apertures always had the same luminance as the high luminance regions of the gratings. Note that the gray circles around the apertures are only shown to clarify the figure and were not present in the experiments, and that the gratings generally had far lower contrasts than is shown. When subjects perceived the stimulus as moving coherently, it became perceptually organized into a global form which was phenomenally continuous behind the occluder.

intrinsic and their motions always correspond with the object’s motion.

The nature of contour terminations in multiple-aperture displays can be easily changed. Highlighting the perimeter of the apertures with a different color or luminance from the occluder [23,27], or covering the occluding surface with texture [47] makes the presence of an occluder clearly evident. This increases the likelihood that the terminations of the moving contours would be classed as extrinsic (resulting from occlusion), and thus their motions would be discounted. Consequently, the true motions of the contours behind the occluder are ambiguous and global motion coherence should be more likely because a single coherent object is not explicitly excluded by the presence of disambiguating, intrinsic contour terminations [27]. With plaid stimuli, by contrast, the presence of blob features generally provides an unambiguous motion signal in the pattern direction, irrespective of whether an occluder is explicitly present or not. There are, however, exceptional conditions under which the blobs are not represented as pattern features, most notably when the luminance of the grating intersections is manipulated to imply the occlusion of one grating by the other [49,51].

Of the studies which have used multiple-aperture motion displays to examine the integration of component motions into coherent 2-D motions, most have presented single, thin lines within each aperture of the array [4,23,26,27,34,46]. In the present study, we preferred to present moving gratings within our apertures to more readily study the effects of such factors as spatial frequency, contrast, velocity, etc., which are known to affect global coherence within single aperture stimuli (i.e. plaids). Our primary aim is to examine how these various local parameters affect the integration of grating motions into coherent global motion. However, our observation that amodal form completion always accompanied the perception of coherent motion implied the involvement of global form processes. Thus a secondary aim is to discuss how these processes might also have a role in global motion coherence.

## 2. General methods

### 2.1. Subjects

Two of the authors and two naive subjects served as subjects for these experiments. All were emmetropic or had suitably corrected vision.

### 2.2. Stimuli

The display consisted of square-wave gratings seen through 16 small apertures arranged in a  $4 \times 4$  array and were generated on an Amiga 2000 computer. The

apertures were circular with a diameter of  $0.4^\circ$  va and were arranged so that each aperture was equally spaced from its vertical and horizontal neighbour by  $0.1^\circ$  va at the viewing distance of 280 cm. The aperture array was presented on a Barco 6161 monitor with a resolution of  $640 \times 480$  pixels and subtended a square region with sides of  $1.9^\circ$  va. The luminance of the monitor beyond the apertures was always the same as the high luminance regions of the gratings, irrespective of grating contrast<sup>1</sup>. Two independently moving gratings could be seen through the apertures, with each grating occupying alternate diagonals of the array, like the black and white squares of a checker board (Fig. 1). The gratings were luminance-defined square waves which could be manipulated independently in terms of a range of variables, including: spatial frequency, contrast, orientation/direction, speed and duty cycle. With the exception of experiment 3, the gratings were always matched and differed only in their orientation/direction, and grating motions were always upward and symmetrical about vertical (that is, analogous to type I plaids). The phase of the gratings in each of the apertures of common orientation was identical. In the center of the display was a small, annular fixation point with an outer diameter of  $0.1^\circ$  va which served to reduce excessive eye movements [36]. When the gratings in the 16 apertures were seen to move coherently, they seemed to undergo a grouping process like ‘amodal completion’ [17], whereby they were perceived as four sets of complete (but partially occluded), concentric diamonds moving as if on a single surface behind the apertures. When incoherent motion was seen, the gratings appeared to move separately in orthogonal diagonal streams. In this case, amodal form completion was never seen, but 1-D amodal completion did occur across contours with the same orientation. 1-D amodal completion of contours across multiple apertures has been reported before by Shimojo et al. [47].

### 2.3. Procedure

All experiments were factorial designs except for experiment 4, which was a single-factor experiment. Subjects were given 10 brief presentations (except in experiment 4, where 40 were used) of each of the

<sup>1</sup> By using grating stimuli, the continual appearance of new contours with their terminations moving around the aperture perimeter implies an occluding surface with circular apertures, which would thus render the contour terminators extrinsic. This was almost always the case with the 1-s trials we used in these experiments and so a textured occluder or visible apertures were not needed. However, inspecting the stimulus for extended periods produced an alternating percept in which the contours were sometimes seen as intrinsic to the contours. In this case, the terminations were perceived to belong to contours which varied in length over time against a plain white background.

stimuli in a random order, with a 2-s pause between trials, and a 1-min break after every tenth trial. Shutters mounted in front of the subjects’ eyes were used to limit the presentations to 1-s. Subjects were required to indicate whether the gratings in the apertures appeared to move in a single direction (coherent motion) or not (non-coherent motion). The percentage of ‘coherent’ responses for each condition was measured, and the pooled data were analysed using factorial analyses of variance (ANOVAs). Data are shown in graphs which plot separately the results for each subject, together with a plot of the pooled data. Unless important interactions were obtained, only significant main effects are plotted since these are based on many more trials than the individual conditions.

### 3. Experiment 1: effects of motion direction, fundamental spatial frequency and contrast

This experiment tests the ability of subjects to group the independent motions of two gratings seen through 16 spatially separated apertures into a single, coherent motion while the fundamental spatial frequency, contrast and motion direction of the square-wave gratings are varied. The use of single lines in most earlier studies prevented the ready manipulation of spatial frequency and contrast. Using gratings overcomes this and allows comparison with the spatial frequency and contrast effects known to occur with other 2-D grating stimuli, such as plaids.

#### 3.1. Methods

The experiment factorially varied fundamental spatial frequency (2.5, 5, and 10 cycles/degree; corresponding respectively to 1, 2, and 4 grating cycles of the square-wave gratings within each aperture), contrast (5, 10, 20, 40 and 80%) and grating direction ( $0$ ,  $\pm 23$ ,  $\pm 45$ ,  $\pm 68$  and  $\pm 90^\circ$ ). Grating speed was  $1.67^\circ/\text{s}$ .

#### 3.2. Results and discussion

Grating direction ( $F_{4,12} = 32.77$ ;  $P < 0.01$ ) was a significant main effect, with coherence reported more often when the angular separation of component directions was small (see Fig. 2a). This pattern of dependence of perceived coherence on component direction is similar to that experienced with plaid stimuli [57]. The main effect of grating contrast was also significant (Fig. 2b), with  $F_{4,12} = 4.0$  and  $P < 0.05$ . Surprisingly, varying the fundamental spatial frequency of the gratings did not produce a significant main effect ( $F_{2,6} = 3.26$ ;  $P > 0.05$ ). We consider this is most likely due to the collapsing across contrast and direction in order to compute the spatial frequency main effect, as this in-

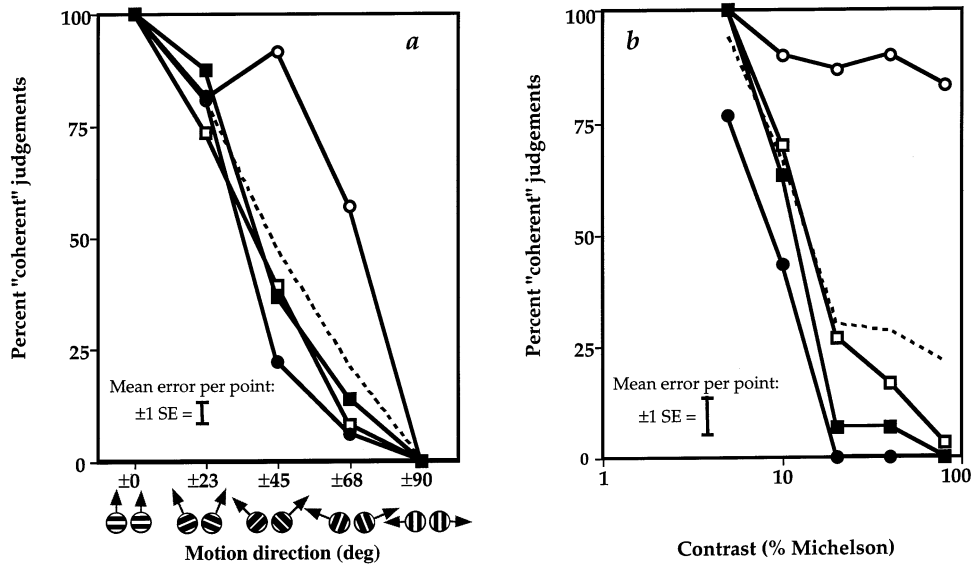


Fig. 2. Significant main effects from experiment 1; data points are based on 150 trials. (a) Judgments of global motion coherence as a function of local grating direction. The curves show four subjects separately, with the mean of the pooled data shown by the dashed line. A representative error bar is shown to avoid cluttering the graph. (b) Each curve represents global motion coherence as a function of grating contrast for four subjects. The conventions for representing the data in this and all the following graphs are as for (a).

cludes many conditions in which there was no coherent global motion (notably, those with large directional differences and high contrasts) thus compressing the range of the spatial frequency effect. Alternatively, it should be noted that while these gratings differed in their fundamental frequencies, they are spatially broadband stimuli with similar higher harmonics. Compounding this matter is the fact that contour terminations are inherently broadband features, and that 'hard' apertures add to the complexity of their spectra. In any event, further discussion of spatial frequency will be held over until it has been re-examined in the second experiment.

These results confirm that independent gratings presented in multiple-aperture arrays can result in coherent global percepts, just as has been reported with single line stimuli [27]. Our data show that motion coherence occurs particularly strongly when contrast is low and the directional difference between the gratings is small. At 10% contrast and  $\pm 23^\circ$  directional separation, the gratings are compellingly coherent, with 100% coherence observed at each of the three spatial frequencies. Under such conditions, subjects experienced an amodal completion of the stimulus such that the gratings were perceived to continue behind the occluding surface to create a single, global form. Typically, the gratings became globally organised into four sets of concentrically arranged diamonds, with the four apertures in each quarter of the stimulus array forming one such set. To the best of our knowledge, there are only two other reports of multiple-aperture global motion using grating stimuli. De Valois and De Valois [10] reported, in

an abstract, that sine-wave gratings presented in a  $2 \times 2$  array of Gaussian apertures produced coherent motion only in the periphery, and Ramachandran [41] briefly described observations of gratings seen through an array of circular apertures as not producing globally coherent motion unless in the extreme periphery. More detail than is present in those brief reports would be required to find the reasons for our differing results, although high grating contrast is the most likely reason.

Some investigations of multiple-aperture stimuli have used circular apertures [4,26,34], while others have used square ones [27,46]. The main difference is that circular apertures lead to changing line length as the contours pass through the apertures. This may vary the salience of the contour terminations since these have been shown to predominate more in short contours [8,20]. Also, the motion of the terminators provides the only unambiguous motion signals in the stimulus, and their vector sum specifies a motion direction orthogonal to the contour orientation (in rectangular apertures this can be varied by changing the orientation of the aperture) which may consequently prevent the assignment of another, global direction to the contours. However, this influence of changing contour lengths is likely to be secondary to the classification of the terminations as being intrinsic or extrinsic, since extrinsic contours are thought to be discounted by the visual system in any case. Moreover, recent work [3] indicates that changing line length is a critical condition for classification of contour terminations as extrinsic. Lorenceau and Shiffrar [27] used rapidly changing line lengths to create 'noisy' terminators and found that this increased coher-

ence, which is consistent with an attenuated influence from the contour terminators. In a similar vein, Scott-Brown and Heeley [44,45] randomly perturbed the positions of a set of lines and found that this reduced the influence of line terminators. Overall, presenting apertures in circular apertures was not an impediment to global motion when grating parameters were suitable and so should not prevent comparison with studies using other aperture shapes.

#### 4. Experiment 2: effects of fundamental spatial frequency and speed

With moving contour stimuli, both the contour itself and the contour's endpoints are cues which inform the visual system of the contour's motion. When moving (featureless) contours are viewed through apertures in an occluding surface, they become directionally ambiguous so that only motion perpendicular to the contour's orientation can be perceived. In this case, the motion of the contour terminations around the aperture perimeter provide the only unambiguous motion signal. Not surprisingly, then, the shape and configuration of the aperture(s) can influence perceived contour motion [20,21,27], revealing an important influence of contour terminations on motion perception. Illustrating this point, an obliquely moving grating viewed through a rectangular aperture is generally seen to move along the long axis. Thus, simply changing the orientation of a rectangular aperture can alter the perceived direction of an identical grating. This is the barber-pole illusion discussed by Wallach [54], who demonstrated related effects with a wide variety of other aperture configurations.

For multiple-aperture stimuli, Lorenceau and Shiffrar [27] proposed that the perception of local or global motion depends on a competition between the ambiguous motion signal from the contour segments and the unambiguous motion signal from contour terminations. They argued that global motion results from the integration of the ambiguous contour segments when they are predominant, whereas separate local motions are seen when the contour terminations predominate. Thus, for example, when Lorenceau and Shiffrar [27] presented drifting lines within multiple apertures defined by jagged, 'saw-toothed' boundaries (generating a noisy and unreliable motion signal from the terminators) performance on a global direction task increased. The increase is held to reflect an increased relative weight of the ambiguous contour segments resulting from the decreased salience of the terminator signal. This permits a global interpretation of the stimulus since it is no longer unambiguously specified as an array of local motions.

If competition between contour and terminator motions were to determine the nature of the motion percept, then any manipulation differentially activating the separate mechanisms signaling the motion of the contour segments and their terminations should cause changes in the level of global coherence. At low contrasts, for instance, global coherence predominates more than at high contrast. This is presumably due to the two cortical motion mechanisms having different modulation transfer functions; the end-stopped cells thought to signal the motion of contour terminations (see Hubel and Wiesel [16] and Orban et al. [39] for physiology; and Castet et al. [8] and Lorenceau et al. [28] for psychophysics) are not as effectively activated at low contrast as the simple cells signaling the motion of the contour segments [15]. With this 'competition' hypothesis in mind, experiment 2 introduces speed as a variable, and re-examines spatial frequency. Grating speed has not been examined in the studies published to date using multiple-aperture stimuli, and is a variable warranting examination since it is plausible that the contour and terminator motion mechanisms may also respond differentially as a function of speed. In addition, by varying speed and fundamental spatial frequency, we can determine whether global coherence varies as a function of the spatial or temporal frequency of the gratings. A lack of interaction between the two factors would suggest that temporal frequency is not a determinant of global coherence.

##### 4.1. Methods

The fundamental spatial frequency of the gratings (2.5, 5 and 10 cycles/degree) was varied across four levels of grating speed (0.83, 1.67, 3.33 and 6.67°/s). Grating contrast and orientation were, respectively: 10% and  $\pm 45^\circ$ . Subjects and procedure were as reported above.

##### 4.2. Results and discussion

Fundamental spatial frequency ( $F_{2,6} = 6.75$ ;  $P < 0.05$ ) and speed ( $F_{3,9} = 5.05$ ;  $P < 0.05$ ) were both significant main effects, with coherence being reported more often when spatial frequency was moderate and when the speed of the component gratings was low (see Fig. 3). There was no significant interaction between these factors ( $F_{6,18} = 0.60$ ;  $P > 0.7$ ).

Based on Lorenceau and Shiffrar's [27] 'competition' hypothesis, the effect of grating speed on global coherence suggests that the mechanisms responsive to contour terminations and contour segments are differentially sensitive to speed. More specifically, it suggests that the mechanism responsive to the contour terminations is less sensitive to low speed than the mechanism signaling the motion of the contour seg-

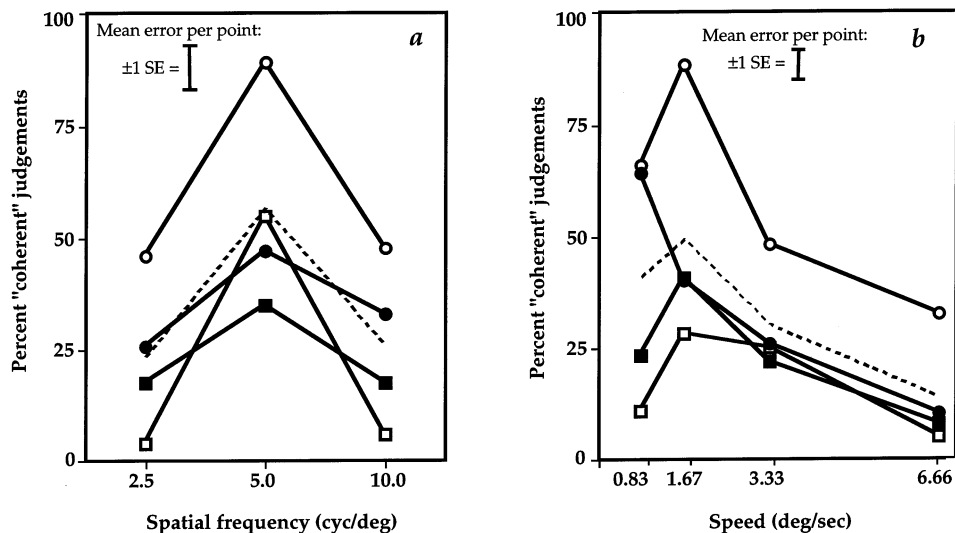


Fig. 3. Data from experiment 2. (a) The dependency of global motion coherence on grating spatial frequency shown separately for four subjects (40 trials per point), with the dashed line representing their mean. (b) The dependency of global motion coherence on grating speed for four subjects (30 trials per point).

ments. This is because low speed favoured global coherence, presumably reflecting the greater relative strength of ambiguous motion signals from contour segments at low speed. Increasing speed would render the disambiguating contour terminations relatively stronger, causing local motion to progressively dominate the percept. Thus, our data appear to be consistent with the competition hypothesis. However, it is possible that factors other than this competing dyad also influence perceived coherence. At higher speeds, for example, the process of amodal completion may become more difficult. Given that it is a form process, this is quite probable, and the absence of perceived global form would very likely reduce the incidence of globally coherent motion. Alternatively, grating speed may affect global coherence through the classification of contour terminations as either intrinsic or extrinsic, although empirical evidence addressing this question is lacking.

On the contrary, the interpretation of these data in terms of the 'competition' hypothesis is consistent with a report examining the perceived speed of single line segments [8]. Observers judged whether tilted, horizontally translating line segments moved faster or slower than the same segment oriented vertically. Tilted lines were perceived as translating more slowly than vertical lines and, importantly, the effect was more pronounced if speed was decreased. They argued that contributions from two mechanisms were involved. One mechanism, responsive to the line's endpoints, signals the *veridical* horizontal speed, and another signals the local speed *perpendicular* to the line segment. They reasoned that the greater speed misperception at the lower speed results from a stronger *perpendicular* signal at low speeds. Relating this to our stimuli, if the ambiguous

contour motion were to dominate at lower speeds, this would result in increased motion coherence.

Also relevant is a report by Nakayama and Silverman [37] examining the role of line terminators in the perceived rigidity of translating planar wave forms. They found that a translating line defining a cumulative Gaussian wave form was seen as highly non-rigid, whereas an identical wave form with two small gaps introduced (thereby introducing line terminators) was perceived as translating rigidly. They showed that the effect of line terminators on perceived rigidity was strongly dependent on speed, with non-rigidity seen at low speeds. They proposed that low speeds increase the dominance of the ambiguous, orthogonal motion, leading to perceived non-rigidity. This is another line of evidence suggesting that contour terminations lack salience at low speeds compared with motion perpendicular to contours.

As was expected in experiment 1, we clearly see an effect of fundamental spatial frequency, with perceived coherence greatest at 5 cycles/degree (Fig. 3a). Spatial frequency and speed did not interact: global coherence always peaked at a speed of 1.67°/s, regardless of spatial frequency, implying that temporal frequency of the local motions does not determine global coherence. This suggests that the critical neural locus for global coherence is not a low-level site such as area V1, where direction-selective cells are selective for temporal frequency [12]. Rather, global motion coherence is probably determined later in the motion processing stream, such as in area MT, where cells exhibit speed selectivity [31,33,42]. This implicates a different mechanism from that mediating the coherence of plaid stimuli, which is largely determined by a low-level, monocular mechanism [2,7].

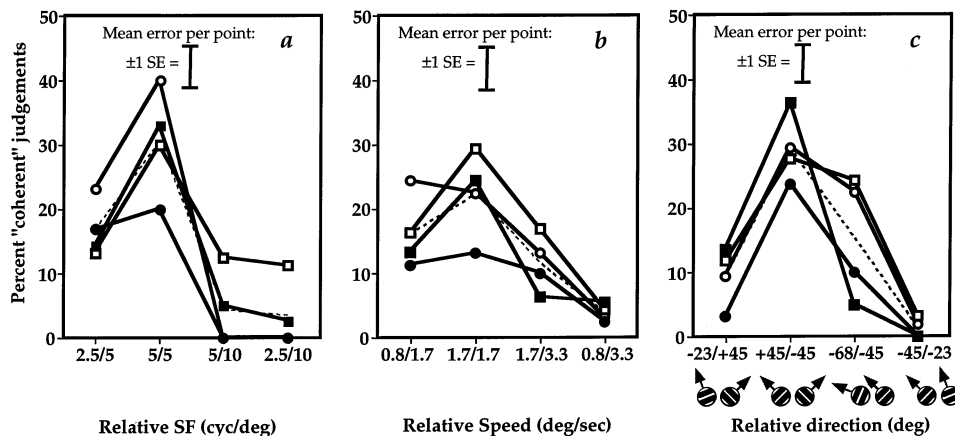


Fig. 4. Data from experiment 3 showing the effects of differences between component gratings on global motion coherence. Shown in (a) to (c), respectively, are the significant main effects of relative spatial frequency, speed and direction for four subjects. Note that all the local gratings with a common orientation (see Fig. 1) are assigned one value from the pairs of values shown on the abscissae, while the gratings with the other orientation have the other value. All data points are based on 160 trials.

### 5. Experiment 3: effects of relative differences in speed, direction and fundamental spatial frequency

The Gestaltists described several principles influential in determining global percepts, among them: similarity, proximity, common fate and continuity [19]. The similarity of the form and motion within each aperture is one factor likely to promote globally coherent motion. For example, the gratings in the preceding experiments are all identical in spatial frequency and phase and have no identifying texture or features, they are all rotationally symmetrical, have the same temporal frequency and are seen through identical apertures in a symmetrical  $4 \times 4$  array. The similarity (indeed, identity) between these factors no doubt favours a global interpretation, despite the motion of contour terminations providing disambiguating local motion cues. The close proximity of the local motions (their separation is only  $0.1^\circ$  va) adds further support to a global interpretation, as does the fact that common fate is upheld, since the ambiguous local motion of the contour segments ensures that each aperture contains a common motion vector. The extent to which global coherence depends upon these similarities is addressed in this experiment by introducing relative differences in terms of speed, spatial frequency and direction between the two gratings seen in the aperture array. Such manipulations have not been carried out previously with multiple-aperture stimuli, although Shimojo et al. [47] mentioned in a footnote (no data were presented) that global coherence would be likely to correlate with similarity among the local motions in terms of spatial structure and velocity.

#### 5.1. Methods

Subjects and procedure were as described above. All gratings were 10% contrast, but each of the pair of gratings in a given stimulus could be varied independently in terms of three variables. The following four pairs of fundamental spatial frequencies were used for the two gratings: 2.5 and 5, 5 and 5, 5 and 10 and 2.5 and 10 cycles/degree. The following four pairs of grating speeds were used: 0.83 and 1.67, 1.67 and 1.67, 1.67 and 3.33 and 0.83 and 3.33/s. These pairings of spatial frequency and speed are combinations of the values used in the first two experiments. Four pairs of grating direction were also used:  $-23$  and  $+45$ ,  $-45$  and  $+45$ ,  $-68$  and  $-45$  and  $-45$  and  $-23^\circ$  (where negative values refer to motions to the left of vertical; all gratings moved upwards). The three factors were combined factorially.

#### 5.2. Results and discussion

Relative speed, fundamental spatial frequency and direction were all significant main effects, respectively:  $F_{3,9} = 15.90$  ( $P < 0.005$ );  $F_{3,9} = 18.34$  ( $P < 0.005$ ); and  $F_{3,9} = 14.99$  ( $P < 0.005$ ). Fig. 4 plots these effects and shows clearly that globally coherent motion was drastically reduced by differences between the component gratings. Overall, manipulating these component differences has produced lower levels of coherence than in the preceding experiments, suggesting that coherence in multiple-aperture stimuli depends on agreement among a variety of component parameters, with any differences strongly detracting from perceived coherence. For fundamental spatial frequency (Fig. 4a) and relative

speed (Fig. 4b), a one-octave difference is sufficient to reduce global coherence by a factor of about 2, and a two-octave difference almost entirely eliminates it. Note that the graphs in Fig. 4 are not symmetrical: for spatial frequency (Fig. 4a), a one-octave difference in the fundamental frequency preserves coherence more for the lower spatial frequency pair than for the higher pair. Speed differences show a similar pattern (Fig. 4b). Interestingly, coherence is not a simple function of the directional difference between the gratings, as their separations (left to right in Fig. 4c) are 68, 90, 23 and 22°, since global coherence is strongest for the largest angular separation, and is weakest for the 22° separation.

These data are interesting in light of data from plaid stimuli. In a study by Kim and Wilson [18], gratings of different spatial frequencies were combined to form plaids, and grating direction was then varied to examine its effects on plaid coherence. They found that coherence under these conditions (similar to many of the conditions in the present experiment) is a function of directional separation: plaids were always coherent when separation was 53.2° or less. This is very different from the results in Fig. 4c, where a directional separation of just 22° was sufficient to prevent globally coherent motion for all spatial frequency combinations. These data suggest important differences between 2-D motion integration in single apertures and in multiple apertures, and caution against the use of coherence models derived from plaid data to explain coherence in multiple-apertures stimuli.

The competition hypothesis, however, also seems to have its limitations. On the assumption that terminator and contour motion mechanisms exhibit some form of tuning to fundamental spatial frequency or speed, it could be argued that stimuli composed of different gratings would inevitably create an asymmetry in which one grating would have more salient terminators than the other. Conceivably, with its direction specified by the salient terminators, that grating might thus be prevented from combining with the other grating to move globally in a different direction. Apart from its assumptions, this view ignores important dimensions of global organisation such as symmetry and *prägnanz* (figural goodness and closure [19]). With a symmetric configuration of grating direction/orientation, the grating contours project to form a symmetrical array of virtual corners arranged like four diamond figures. This represents good *prägnanz* since it neatly and symmetrically resolves the ambiguity of the stimulus by interpreting the contours as being part of a complete but occluded form. Closure has been shown to facilitate object detection [22] and may similarly facilitate the integration of related local velocities. On the contrary, when orientation is asymmetric, the contour projections are not symmetrically related to the aperture array and defy global organisation. This could reduce global coherence by inhibiting the cooperative processing which has been observed to occur

between corners and collinear segments [14,40], thereby preventing amodal form completion.

Overall, it is apparent that a number of factors determine global coherence in multiple apertures. Low-level signals from terminator and contour motions may be important, but these also appear to interact with factors concerning the global organisation. Global coherence will be maximal when there is total agreement among all the cues in the stimulus, and will weaken as conflict between one or more cues is introduced. Ultimately, the global percept in these stimuli is interpretative, and the bistability experienced with prolonged viewing may result from the concentric diamonds seen during coherence being ‘impossible’ figures, since no corners are seen during translation. Yet, as the visual system implements natural constraints by assuming properties such as object rigidity, a strong tendency to cohere can result if all available cues to the form and motion of the global object are in good agreement.

## 6. Experiment 4: effects of duty cycle

Shiffrar and Lorenceau [46] presented single red lines against a dark green background (there was also an equiluminant condition), and found that increasing line width from thin to thick progressively degraded global coherence. This was interpreted in terms of their competition hypothesis to mean that the perceptual salience of contour terminations increases with contour width to increasingly disambiguate the local contour motions and thus degrade global coherence. Experiment 4 tests their proposal using achromatic, square-wave gratings. We varied line thickness by manipulating duty cycle (defined here as the percentage of the grating’s wavelength represented by the light region of the wave) and tested a range of duty cycles symmetrically around the point of 50% duty cycle. Consistent with earlier observations concerning figure/ground segmentation [19,54], the thin bars in gratings which were not equally black and white were generally seen as the foreground and the thick bars as the background. Thus, gratings with high duty cycles (i.e. large light regions), were perceived as a series of thin dark lines on a light background. Conversely, low duty cycle gratings were seen as thin light lines on a dark background.

Shiffrar and Lorenceau’s reasoning predicts, for duty cycles above 50%, that global motion coherence should be an increasing function of duty cycle. For duty cycles below 50%, despite the thin light lines again being perceived as figure, a different pattern of results is expected. This is because thin light lines would not contrast with the equally light occluding surface, and thus strongly discount the interpretation of the line as being occluded. For this reason, coherence would be expected to continue to decrease below 50% duty cycle.



### 6.1. Methods

Subjects completed 40 trials with each stimulus rather than 10, and only three of the four subjects participated. One fundamental spatial frequency (5 cycles/degree), one speed (1.67°/s), and the following five levels of duty cycle were used: 17, 33, 50, 67, and 83%, which correspond, respectively, to (dark) line thicknesses of: 10, 8, 6, 4, and 2 arcmin. The data were entered into a single-factor ANOVA.

### 6.2. Results and discussion

The dependence of globally coherent motion on duty cycle was significant ( $F_{4,8} = 10.47$ ;  $P < 0.01$ ) and is plotted in Fig. 5. The increase in global motion coherence as duty cycle increases from 50% supports Shiffrar and Lorenceau's [46] proposal that thin lines are more readily integrated into global motion. Their data were obtained using line thicknesses of 6.4, 3.2 and 1.6 arcmin, which are similar to the line thicknesses used in this experiment for 50, 67 and 83%. However, as expected, increasingly thin light lines (below 50% duty cycle) did not yield increasing levels of global coherence as they do not contrast with the occluding surface and so they are not interpreted as being occluded. This bears out the importance of more global processes such as the assignment of figure and ground in visual images, and the interpretation of occlusion conditions. More generally, it indicates again that global coherence is

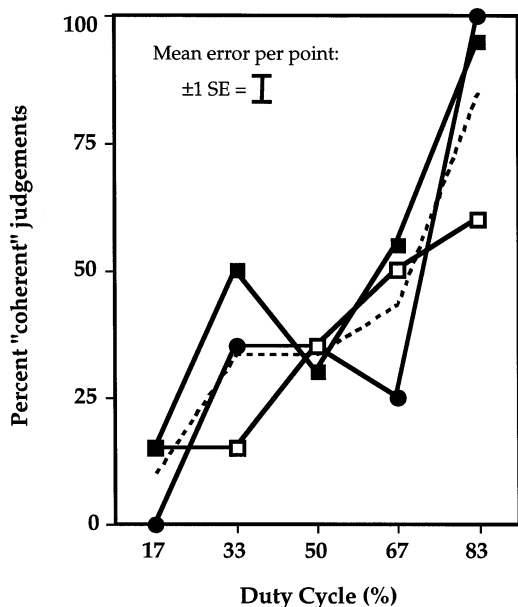


Fig. 5. Data from experiment 4 showing global motion coherence as a function of grating duty cycle (40 trials per point) for three subjects. Small values of duty cycle correspond to rectangular waves which are predominantly dark, while large values correspond to predominantly light rectangular waves.

determined by a broad range of factors, and that they must all provide converging evidence supporting global coherence if it is to occur.

Planned contrasts testing for first-, second- and third-order trend resulted in a significant linear trend ( $F_{1,4} = 35.51$ ;  $P < 0.001$ ), while cubic trend approached significance ( $P = 0.075$ ). The near-significant cubic trend reflects the acceleration of the curve above 50% duty cycle, which is probably inflated due to lower perceived contrast. Contrast is an important variable in determining coherent motion in multiple-aperture stimuli (see Fig. 2), particularly at low contrasts. Thus, for the low contrast used in this experiment (10%), any factor affecting perceived contrast would substantially affect global coherence. Where thin dark lines are located between broad light regions (high duty cycles), perceived contrast is reduced due to image blurring arising from its passage through the eye's optics. That is, blurring would cause light to spread from the broad white regions over the thin dark regions (only 4 and 2 arcmin wide), reducing perceived grating contrast and increasing global coherence. With predominantly dark gratings, blurring from the thin white lines would not extend far enough into the dark region to cause changes in perceived contrast. Thus, optical blurring can account for the observed asymmetry in the duty cycle function.

## 7. General discussion

Most literature concerning multiple-aperture stimuli focuses on competing motion signals from contour terminations and contour segments. Focusing on the local motion elements can account for many reported effects, but it constitutes only a partial explanation as it does not address the higher-level processes which underlie the subjective completion into a global form and those which pool local motions into a global one. Non-motion input from the form/color pathway, or parvocellular pathway [24,25], is likely to influence global motion coherence in multiple-aperture stimuli, despite findings showing that the absence of luminance contrast greatly impairs motion perception. The importance of parvocellular mechanisms is shown by Shiffrar and Lorenceau's [46] finding that global motion coherence for chromatic stimuli is enhanced at equiluminance. The epiphenomenon of amodal completion also suggests form processes. The 'perceptual interpolation' [17] of contours held to underlie this process promotes the perception of complete but partially occluded forms (diamond shapes, typically) moving globally behind the occluder. Shimojo et al. [47] also noted amodal completion of a moving grating presented behind three rectangular apertures into a phenomenally unified grating. The coincidence of amodal completion with global

motion, and its absence during local motion, suggests motion and form processes are tightly bound together for oriented stimuli within multiple-apertures.

In addition to psychophysical evidence, recent physiological work makes it increasingly clear that the form and motion pathways do interact considerably. Cells in the superficial layers of area V1 receive input jointly from magno and parvo cells [29,38,53] and, as early as layer 4B of V1, a substantial interaction between parvo and magno input has recently been demonstrated [43]. Thus, both parvo and magno streams would be expected to influence activity in the higher-level motion areas which receive strong input from layer 4B, such as areas V2 and MT. Further evidence suggests that the magno/parvo interaction increases in areas beyond V1 [13,50], and several of these subsequent stages important to form processing, such as V2 and V4 [32], project to MT [11,30] where their output might exert an influence on the computation of global motion.

The extent of motion and form interactions should not surprise since we need to recognise and identify moving *objects*, rather than motion per se. With multiple-aperture stimuli, identifying an object is difficult because the occluder renders the exact configuration of the gratings unknown. The globally organised percept, then, is an interpretation of *probable* form. Subjects occasionally reported seeing an array of crosses rather than diamonds (see Fig. 1), and this bistability<sup>2</sup> reflects two probable but mutually exclusive interpretations. The predominance of the phenomenal diamonds over the crosses may stem from their better closure and figural goodness (the Gestalt notion of *prägnanz* [19]). Kovacs and Julesz [22] examined the role of *prägnanz* in global structure. Against background noise, they presented long strings of elements forming either closed or open loops. Detection of closed loops tolerated greater element-separation than open loops by a factor of 2, suggesting a greater perceptual salience for figurally complete forms. Cognitive factors, too, may influence the bistability of the subjective form. Observations by the authors confirmed that cognitive strategies could be used to reverse the interpretation from phenomenal diamonds to crosses, or vice versa. Consistent with this, visual cortical areas crucial to form perception, such as V4 [32], are closely related to attentional processes [9,35] and thus might be selectively influenced by cognitive strategies.

Overall, this paper has attempted to clarify that a confluence of factors determines global coherence with multiple-aperture stimuli, with no single factor being the sole determinant. Global coherence is most likely to

occur when there is agreement between all or most of these factors, and is rendered less likely to the extent that their mutual agreement is violated. Useful accounts can be generated from local factors such as the relative contributions of contour and terminator motions but these are limited in that associated global phenomena of amodal completion and subjective form are not addressed. These phenomena demand an explanation in terms of mechanisms found in the parvo stream and a subsequent combination with the global motion processes from the magno stream.

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## References

- [1] Adelson EH, Movshon JA. Phenomenal coherence of moving visual patterns. *Nature* 1982;300:523–5.
- [2] Alais D, van der Smagt MJ, Verstraten FAJ, van de Grind WA. Monocular mechanisms determine plaid motion coherence. *Visual Neurosci* 1996;13:615–26.
- [3] Anderson BL, Sinha P. Reciprocal interactions between occlusion and motion computations. *Proc Natl Acad Sci USA* 1997;94:3477–80.
- [4] Ben-Av MB, Shiffrar M. Disambiguating velocity estimates across image space. *Vis Res* 1995;35:2889–95.
- [5] van den Berg AV, Noest AJ. Motion transparency and coherence in plaids: the role of end-stopped cells. *Exp Brain Res* 1993;96:519–33.
- [6] Bowns L. Evidence for a feature tracking explanation of why Type II plaids move in the vector sum direction at short durations. *Vis Res* 1996;36:3685–94.
- [7] Burke D, Alais D, Wenderoth P. A role for a low-level mechanism in determining plaid coherence. *Vis Res* 1994;34:3189–96.
- [8] Castet E, Lorenceau J, Shiffrar M, Bonnet C. Perceived speed of moving lines depends on orientation, length, speed, and luminance. *Vis Res* 1993;33:1921–36.
- [9] Connor CE, Gallant JL, Preddie DC, Van Essen DC. Responses in area V4 depend on the spatial relationship between stimulus and attention. *J Neurophysiol* 1996;75:1306–8.
- [10] De Valois RL, De Valois KK. Stationary moving Gabor plaids. *Invest Ophthalmol Visual Sci (Suppl)* 1990;31:171.
- [11] Felleman DJ, Van Essen DC. Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex* 1991;1:1–47.
- [12] Foster KH, Gaska JP, Nagler M, Pollen DA. Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *J Physiol* 1985;365:331–63.
- [13] Gegenfurtner KR, Kiper DC, Fenstemaker SB. Processing of color, form, and motion in macaque area V2. *Visual Neurosci* 1996;13:161–72.
- [14] Grossberg S, Mingolla E. Neural dynamics of motion perception: Direction fields, apertures and resonant groupings. *Percept Psychophys* 1993;53:243–78.

<sup>2</sup> The global percept was always stable within a single trial for the brief exposure time used in this experiment (1 s). However, during prolonged inspections, say 20 s, subjects reported that the global percept would occasionally alternate between crosses and diamonds.

- [15] Hubel DH, Wiesel TN. Binocular interaction in striate cortex of kittens reared with artificial squint. *J Neurophysiol* 1965;28:1029–40.
- [16] Hubel DH, Wiesel TN. Receptive fields and functional architecture of monkey striate cortex. *J Physiol* 1968;195:215–43.
- [17] Kanizsa G. Organization in vision: Essays on Gestalt perception. New York: Praeger, 1979.
- [18] Kim J, Wilson HR. Dependence of plaid motion coherence on component grating directions. *Vis Res* 1993;33:2479–89.
- [19] Koffka K. Principles of Gestalt psychology. New York: Harcourt, Brace and Company, 1935.
- [20] Kooi FL. Local direction of edge motion causes and abolishes the Barberpole illusion. *Vis Res* 1993;33:2347–51.
- [21] Kooi FL, De Valois KK, Switkes E. Higher order factors influencing the perception of sliding and coherence of plaids. *Perception* 1992;21:583–98.
- [22] Kovacs I, Julesz B. A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation. *Proc Natl Acad Sci USA* 1993;90:7495–7.
- [23] Lappin JS, Norman JF, Loken KB, Fukuda H. The visibility globally coherent motion behind multiple apertures. *Invest Ophthalmol Visual Sci (Suppl)* 1990;31:240.
- [24] Livingstone MS, Hubel DH. Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *J Neurosci* 1987;7:3416–78.
- [25] Livingstone MS, Hubel DH. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* 1988;240:740–9.
- [26] Lorenceau J, Boucart M. Effects of a static textured background on motion integration. *Vis Res* 1995;35:2303–14.
- [27] Lorenceau J, Shiffrar M. The influence of terminators on motion integration across space. *Vis Res* 1992;32:263–73.
- [28] Lorenceau J, Shiffrar M, Wells N, Castet E. Different motion sensitive units are involved in recovering the direction of moving lines. *Vis Res* 1993;33:1207–17.
- [29] Malpeli JG, Schiller PH, Colby CL. Response properties of single cells in monkey striate cortex during reversible inactivation of individual lateral geniculate laminae. *J Neurophysiol* 1981;46:1102–19.
- [30] Maunsell JHR, Van Essen DC. The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *J Neurosci* 1983;3:2563–86.
- [31] Maunsell JHR, Van Essen DC. Functional properties of neurons in middle temporal area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *J Neurosci* 1983;3:2563–86.
- [32] Merigan WH. Basic visual capacities and shape discrimination after lesions of extrastriate area V4 in macaques. *Visual Neurosci* 1996;13:51–60.
- [33] Mikami A, Newsome WT, Wurtz RH. Motion selectivity in macaque visual cortex, I: mechanisms of direction and speed selectivity in extrastriate area MT. *J Neurophysiol* 1986;55:1308–27.
- [34] Mingolla E, Todd JT, Norman JF. The perception of globally coherent motion. *Vis Res* 1992;32:1015–31.
- [35] Motter BC. Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J Neurophysiol* 1993;70:1–11.
- [36] Murphy BJ, Kowler E, Steinman RM. Slow oculomotor control in the presence of moving backgrounds. *Vis Res* 1975;15:1263–8.
- [37] Nakayama K, Silverman GH. The aperture problem II: Spatial integration of velocity information along contours. *Vis Res* 1988;28:747–53.
- [38] Nealy TA, Maunsell JHR. Magnocellular and parvocellular contributions to the responses of neurons in macaque striate cortex. *J Neurosci* 1994;14:2069–79.
- [39] Orban GA, Kato H, Bishop PO. End-zone region in receptive fields of hypercomplex and other striate neurons in the cat. *J Physiol* 1979;42:818–32.
- [40] Peterhans E, von der Heydt R. Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *J Neurosci* 1989;9:1749–63.
- [41] Ramachandran VS. Visual perception in people and machines. In: Blake A, Trascianko T, editors. *AI and the Eye*. New York: Wiley, 1990:21–77.
- [42] Rodman HR, Albright TD. Coding of visual stimulus velocity in area MT of the macaque. *Vis Res* 1987;27:2035–2048.
- [43] Sawatari A, Callaway EM. Convergence of magno- and parvocellular pathways in layer 4B of macaque primary visual cortex. *Nature* 1996;380:442–6.
- [44] Scott-Brown K, Heeley DW. Topological arrangement affects the perceived speed of tilted lines in horizontal translation. *Invest Ophthalmol Visual Sci (Suppl)* 1995;36:261.
- [45] Scott-Brown K, Heeley DW. Random perturbation of the length or the position of horizontally drifting tilted lines affects their perceived speed. *Invest Ophthalmol Visual Sci (Suppl)* 1996;37:3406.
- [46] Shiffrar M, Lorenceau J. Increased motion linking across edges with decreased luminance contrast, edge width and duration. *Vis Res* 1996;36:2061–7.
- [47] Shimojo S, Silverman GH, Nakayama K. Occlusion and the solution to the aperture problem for motion. *Vis Res* 1989;29:619–26.
- [48] Stoner GR, Albright TD. The interpretation of visual motion: evidence for surface segmentation mechanisms. *Vis Res* 1996;36:1291–310.
- [49] Stoner GR, Albright TD, Ramachandran VS. Transparency and coherence in human motion perception. *Nature* 1990;344:153–5.
- [50] Tamura H, Sato H, Katsuyama N, Hata Y, Tsumoto T. Less segregated processing of visual information in V2 than in V1 of monkey visual cortex. *Eur J Neurosci* 1996;8:300–9.
- [51] Trueswell JC, Hayhoe MM. Surface segmentation mechanisms and motion perception. *Vis Res* 1993;33:313–28.
- [52] Vallortigara G, Bressan P. Occlusion and the perception of coherent motion. *Vis Res* 1991;31:1967–78.
- [53] Van Essen DC, DeYoe EA. Concurrent processing in the primate visual cortex. In: Gazzaniga MS, editor. *The Cognitive Neurosciences*. Cambridge, MA: MIT Press, 1994.
- [54] Wallach H. Über visuell wahrgeommene bewegungsrichtung. *Psychol Forschung* 1935;20:325–80.
- [55] Watamaniuk SNJ, Sekuler R, Williams DW. Direction perception in complex dynamic displays: the integration of direction information. *Vis Res* 1989;29:47–59.
- [56] Williams DW, Sekuler R. Coherent global motion percepts from stochastic local motions. *Vis Res* 1984;24:55–62.
- [57] Wilson HR, Kim J. A model for motion coherence and transparency. *Visual Neurosci* 1994;11:1205–20.