PERGAMON

Vision Research 42 (2002) 991–1003

Vision Research

www.elsevier.com/locate/visres

Self-organized pattern formation: experimental dissection of motion detection and motion integration by variation of attentional spread

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Received 19 June 2001; received in revised form 8 October 2001

Abstract

The formation of global motion patterns depends on the stimulus activation of local motion detectors as well as integrative excitatory and/or inhibitory interactions among the activated detectors. The counterphase row-of-elements [Vis. Res. 34 (1994) 1843] is an ideal stimulus for examining the relationship between the activational/energizing effect of the stimulus and interaction among the activated detectors. This is because the formation of the alternative unidirectional and oscillatory motion patterns for this stimulus requires the stimulation of local motion detectors, but there is no information in the stimulus that specifies either of the patterns. Their formation depends instead on the relative contributions of excitatory and inhibitory interactions to detector activation; the temporal patterns are self-organized. Broadly spread attention affects motion integration by changing the balance of excitatory versus inhibitory interactions, increasing the perception of unidirectional compared with oscillatory motion. (It likewise increases the perception of group compared with element motion for the Ternus stimulus.) There is, however, little if any effect of attentional spread on the luminance contrast required for the perception of single-element motion. The results indicate that the balance of integrative excitatory and/or inhibitory detector interactions can be modified by the perceiver's spread of attention, and further, that such changes need not be mediated by changes in the local, stimulus activation of the detectors.

Keywords: Attention; Motion; Global; Local; Interaction; Integration

A pattern is said to be self-organized when there is no agent, and thus, no list of to-be-followed rules that governs its creation. Self-organization requires the continual supply of energy to a system through the stimulation of its constituent elements (systems capable of self-organization are dissipative), but there is no information in the energy that specifies the to-be-formed pattern. Self-organized patterns are therefore emergent; they are defined by and receive their "shape" from interactions among the locally energized constituents of the system. Because the stimulus does not specify the pattern, stimuli for which patterns are self-organized provide an ideal experimental framework for examining the relationship between the energizing or activational effects of the stimulus and the integrative, excitatory and inhibitory interactions among the activated elements that are responsible for the formation of coherent patterns. Within such a framework, the objective of the research reported in this article is to determine whether the relative contributions of excitatory and inhibitory interactions to the formation of global motion patterns can be modified (in the current study, through variation in the perceiver's attentional spread), without such modifications being mediated by changes in the activation level of the patterns' constituent elements.

The formation of coherent global motion patterns depends on properties of the activating stimulus combined with excitatory and/or inhibitory interactions among stimulus-activated motion detectors. Psychophysical and modeling studies indicate that such detector interactions can enhance weakly specified motion directions, integrate similar stimulus-specified directions to create an averaged motion direction, and select which among many possible motion directions will be realized

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0042-6989/02/$ - see front matter
PII: S0042-6989(02)00026-3

in experience (i.e., provide solutions to the motion correspondence problem). In experiments concerned with global pattern formation for random cinematograms, weak stimulus specification is introduced by biasing the motion direction for a relatively small percentage of the elements composing the random cinematogram or restricting the range of their possible motion directions. Excitatory and inhibitory interactions among detectors with different directional selectivities increase the activation of the weakly specified direction relative to other, randomly occurring motion directions, resulting in its dominance of the global motion pattern (Chang & Julesz, 1984; Van Doorn & Koenderink, 1983; Williams & Sekuler, 1984; Williams, Phillips, & Sekuler, 1986). Interaction also has been implicated in the formation of moving plaid patterns from the stimulus-specified motion of overlapping, drifting gratings. Excitatory and inhibitory interactions increase the relative activation of detectors selective to intermediate motion directions that are partially activated by both of the drifting gratings, resulting in more activation for an intermediate, average direction than for the directions specified by the drifting gratings (Adelson & Movshon, 1982; Wilson & Kim, 1994). For motion quartets with stimulus-specified horizontal and vertical motion directions, inhibitory detector interactions are the basis for solutions to the motion correspondence problem. They determine whether horizontal or vertical motion patterns are formed (Bartsch & van Hemmen, 1997; Hock, Schöner, & Giese, submitted for publication; Hock, Schöner, & Hochstein, 1996).

In the above examples, the structures of the global motion patterns are directly specified by information in the stimulus. The global motion perceived for a random cinematogram is in the direction specified by the biased local motion directions, the perceived-motion direction of the plaid is intermediate to the similar motion directions specified by its constituent gratings, and the alternative horizontal and vertical motion patterns perceived for the bistable motion quartet correspond alternatively to the horizontal and vertical motion directions specified by local element motions. To our knowledge, there is only one reported example of a bistable stimulus for which there is no stimulus specification of the global structure for the perceived patterns.

This example is the counterphase row-of-elements, a bistable, directionally ambiguous apparent motion stimulus composed of a long row of small, evenly spaced squares (Hock & Balz, 1994; Hock, Balz, & Eastman, 1996). Over a succession of frames, the same row of squares is shifted 180° such that the squares fall in the exact midpoints of the squares presented during the preceding frame. (The row extends far enough into the retinal periphery for motion at its ends to be undetectable.) Because of the midpoint placements during successive frames, leftward and rightward motion are equally likely; both are equally specified by the stimulus during every frame. Nonetheless, leftward and rightward motion are never perceived simultaneously, and there are never random frame-to-frame changes between the two directions. Instead, spatially and temporally coherent unidirectional and oscillatory motion patterns are formed. For the unidirectional motion pattern, which predominates for relatively small inter-element distances, all the squares are perceived moving in the same direction over a succession of frames. For the oscillatory motion pattern, which predominates for relatively large inter-element distances, all the squares are perceived moving in the same direction during one frame, then all are perceived moving in the opposite direction during the next frame, and so on over a succession of frames. However, there is no information in the counterphase stimulus that specifies how the perceived-motion direction will evolve over time. (Inter-element distance predicts which pattern is most likely to be perceived, but detecting inter-element distance is not the same as detecting information specifying the temporal repetition—or alternation—of motion direction.) It can be concluded, therefore, that the temporally coherent unidirectional and oscillatory motion patterns that are formed for the counterphase stimulus are self-organized.

Because stimulus specification for the counterphase row-of-elements is always equal for leftward and rightward motion, the symmetry in activation for detectors that respond selectively to these motion directions must be broken by random fluctuations in detector activation. Activation-increasing excitatory interactions among detectors selective to the same motion direction must predominate with the onset of each frame for both the unidirectional and oscillatory patterns; otherwise, all the elements would not be perceived moving in the same direction (excitatory interactions presumably increase activation for both leftward and rightward motion, the alternatives being resolved by random fluctuations in activation and inhibitory competition between the opposing directions). Moreover, the formation of the unidirectional pattern indicates that the contributions of excitatory interaction to the activation of detectors selective to the just-perceived-motion must be relatively strong; otherwise, the same perceived-motion direction would not persist from one frame to the next. Finally, the formation of the oscillatory motion pattern indicates that there must be a contribution from activation-decreasing inhibitory interactions among detectors selective to the just-perceived-motion direction; otherwise, the perceived-motion direction would not systematically reverse during successive frames. The oscillatory motion pattern requires that the excitatory contribution to detector activation be sufficient for all the elements to move in the same direction with the onset of each frame. However, by the end of the frame, and thus the beginning of the frame that follows, the contribution of excitation to detector activation must become relatively weak compared with the contribution of inhibiting interactions in order for the perceived-motion direction to reverse. [1] Whether the unidirectional or oscillatory pattern is formed therefore depends on the relative contributions of excitatory versus inhibitory interactions to the activation of directionally selective motion detectors. It cannot be based on the detection of pattern-specifying stimulus attributes because there are no such attributes to detect.

Although there is no information in the counterphase stimulus specifying the temporal structures of the perceived unidirectional and oscillatory motion patterns, their formation would not be possible if the stimulus did not activate local motion detectors. Moreover, it is fundamental to the relationship between local detector activation and interaction that the interactive influence of a detector on the activation of other detectors depends on the extent to which it is itself activated; weakly activated detectors would not be expected to have as much of an interactive influence on the activation of other detectors as strongly activated detectors (Giese, 1999; Grossberg, 1973; Hock et al., submitted for publication). If it is also the case that excitatory contributions of a detector to the activation of other detectors vary more with the detector's level of activation than inhibitory contributions (i.e., if the gain is greater for excitatory than inhibitory interactions), the level of stimulus activation of local motion detectors could affect global pattern formation by affecting the relative contributions of excitatory and inhibitory interaction to the activation of other detectors. On this basis, the unidirectional motion pattern formed for the counterphase row-of-elements would predominate for small inter-element distances if: (1) there is more feed-forward detector activation for individual element motions over shorter motion paths, and (2) increased detector activation enhances the influence of excitatory relative to inhibitory detector interactions. Experimental evidence for the first premise has recently been provided by Gilroy, Hock, and Ploeger (2001), who have shown that more time-varying luminance contrast is required for single-element motion to be perceived as frequently for long motion paths as it is for short motion paths. In addition, modeling studies have demonstrated the plausibility of such differences in the stimulus activation of local motion detectors affecting the relative contribution of excitatory and inhibitory detector interactions to detector activation, and thereby, the relative frequency with which unidirectional and oscillatory motion patterns are formed for the counterphase row-of-elements (Park et al., 2001).

The question addressed in this article is whether changes in the excitatory/inhibitory balance (as measured by the relative frequency of perceiving the unidirectional versus the oscillatory motion pattern) can occur only through changes in local motion detector activation (the latter resulting from either changes in the motion stimulus, or changes in the sensitivity of the detectors responding to the motion stimulus). More specifically, we investigated whether top-down effects of attention can directly influence the relative contribution of excitatory and inhibitory interactions to global pattern formation, independent of any modulating influence of attention on the sensitivity (responsiveness) of local detectors to the motion stimulus. (If there is pattern-specifying information in the counterphase stimulus—there is not—we would not be able to determine whether attention was influencing the detection of this information or the balance of excitatory/inhibitory detector interactions.)

Hock, Balz, and Smollon (1998) have shown that when the perceiver's attention is broadly spread over a relatively large region of space compared with when it is narrowly focused at a particular location along the counterphase stimulus, the range of inter-element distances over which unidirectional motion is perceived increases (and oscillatory motion commensurately decreases). The perceiver's attentional state when presented with the counterphase stimulus was manipulated in two ways: (1) with a secondary task involving the detection of luminance increments (this included a procedure for confirming that there was indeed a difference in attention between the Broad and Narrow Attention conditions), and (2) by instruction. With both methods, more broadly spread attention enhanced the formation of the unidirectional pattern. Experiment 1 of the current study replicates these results with a similar instruction-based manipulation of attentional spread, and Experiment 2 extends the manipulation of attentional spread to the Ternus stimulus, another bistable motion stimulus for which pattern formation depends on inter-element distance (Pantle & Petersik, 1980). The effect of attentional spread on the detection of individual motions is then investigated in Experiment 3. Using the same instructional manipulation as in Experiments 1 and 2 (and the same subjects), we assess the effect of attention on the detection of single-element apparent motion over distances corresponding to displacements

[1] A non-linear dynamical model has been developed that accounts for the formation of unidirectional and oscillatory motion patterns for the counterphase row-of-elements (Hock, Park, & Schöner, 2001; Park, Hock, & Schöner, 2001). The model incorporates: (1) feed-forward contributions of the stimulus to the activation of motion detectors selective to leftward or rightward motion, (2) local stability (leftward and rightward motion detectors have stable, fixed-point activation values), (3) contributions of each detector to the activation of other detectors with similar directional selectivity through excitatory and inhibitory interactions that depend non-linearly on the detector's activation level, and (4) inhibitory competition among leftward and rightward detectors that results in one or the other being activated, not both at the same time.

of individual elements for the counterphase and Ternus stimuli in Experiments 1 and 2. The key to the three experiments is to obtain evidence for different effects of attentional spread on global pattern formation compared with the perception of individual element motions. The results are remarkably convergent with recent neurophysiological evidence for attentionally modulated context effects (Ito & Gilbert, 1999).

1. Experiment 1

Since our over-all objective is to compare global and local effects of attentional spread with a common attentional task and common subjects, we began by replicating Hock et al.'s (1998) results with a similar instructional manipulation of attentional spread. Subjects were instructed to simultaneously attend to four small green dots presented in the corners of an imaginary square prior to and during the presentation of the counterphase row-of-elements. The area enclosed by the four "attention" dots was approximately seven times larger in the Broad than the Narrow Attention condition. When presented, the counterphase stimulus passed through the center of the square defined by the four attention dots (Fig. 1a).

1.1. Method

1.1.1. Subjects

Three subjects, students at Florida Atlantic University with normal or corrected-to-normal vision, participated in this and the following two experiments (the experiments were conducted in the order in which they are reported). Only CP, an author, was aware of their purpose.

1.1.2. Stimuli

Stimulus presentation and the recording of responses were controlled by a Power Macintosh 7300/180. Viewing distance was maintained at 86 cm with a head restraint. Each trial began with the presentation of four small green dots (size $= 2.5 \times 2.5$ min; luminance $= 11.8$ cd/m^2) arranged in a square and centered in the screen

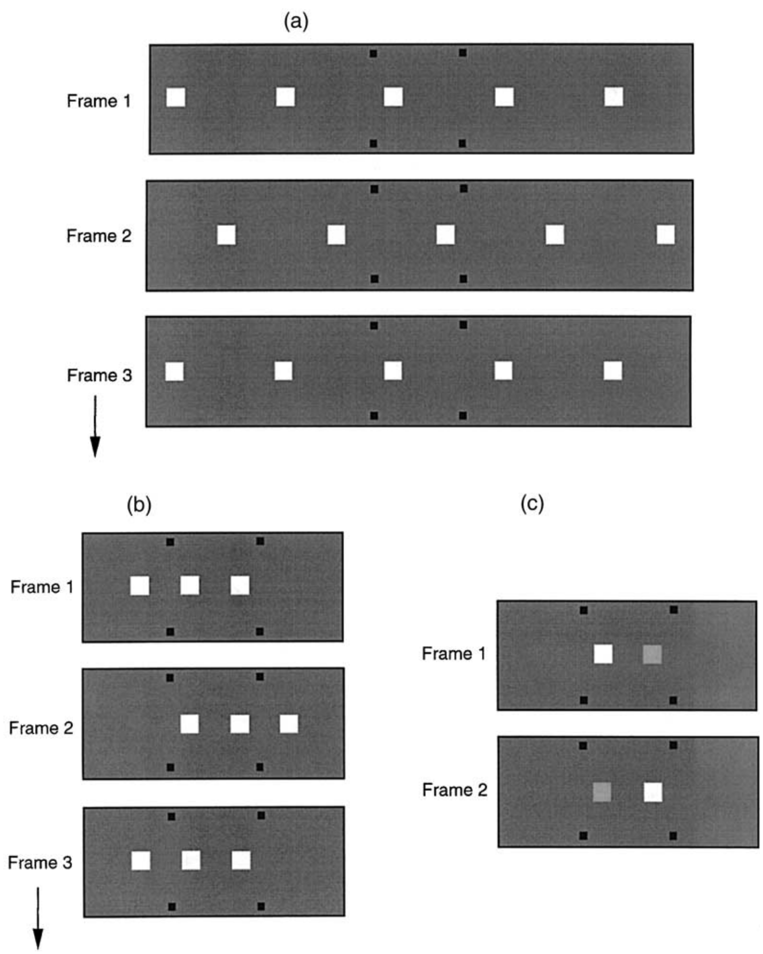

Fig. 1. (a) Illustrations of the counterphase row-of-elements stimuli studied in Experiment 1, (b) the Ternus stimuli studied in Experiment 2 and (c) the generalized single-element apparent motion stimuli studied in Experiment 3. Element sizes and distances are not to scale.

(luminance = 3.6 cd/m^2) of a ViewSonic 15GA monitor. The horizontal and vertical distances between these green attention dots were 188 min in the Broad Attention condition, and 70 min in the Narrow Attention condition. They remained on the screen for the entire trial. At the start of each trial, the subject pressed the spacebar of the computer keyboard to indicate that he or she was attending to the green dots, as instructed, and was thus prepared for the presentation of the test stimulus. Thereupon, a long (9.8°) horizontal row of evenly spaced white squares (size = 10.0 × 10.0 min; luminance = 17.1 cd/m^2) was presented midway between the top and bottom attention dots. The inter-element distance for the counterphase stimulus varied randomly from one trial to the next. It was either 30, 40, 50, 60, 70, 90, 100, or 120 min (center-to-center). The initially presented row was horizontally displaced by one-quarter of the inter-element distance (90°) with respect to the center of the four attention dots. Over a succession of eight 267 ms frames (the inter-frame interval was 0 ms), the row of squares was shifted by half the inter-element distance (180°), so each square was located at the midpoint between the squares presented during the preceding frame. Local element motions therefore occurred over distances ranging from 15 to 60 min (half the inter-element distance).

1.1.3. Design

Subjects were tested in blocks of 64 trials (8 inter-element distances, each presented 8 times). Order was randomized within sub-blocks of 8 trials. There were four blocks of trials during each testing session (alternating between the Broad and Narrow Attention conditions), and four testing sessions per subject.

1.1.4. Procedure

Subjects were instructed to simultaneously attend to all four attention dots prior to the presentation of the test stimulus, to press the space bar when they were meeting the attentional requirement—this resulted in the immediate presentation of the counterphase row-of-elements—and to maintain the required attentional spread for the remainder of the trial. At the end of each trial they indicated, by pressing designated keys on the computer keyboard, whether the first motion pattern they perceived was unidirectional or oscillatory. This judgment was based on subjects' experience with biased versions of the counterphase row-of-elements presented during practice. (A more precise criterion, for example, "unidirectional motion if the perceived motion is in the same direction for *N* consecutive frames," was not practical; frame durations were too brief for the number of frames to be discerned while unidirectional motion was being perceived.) Subjects were instructed to ignore switches to the alternative pattern, and to press the spacebar if they were unsure of their response. Trials with "unsure" responses were not replaced.

1.1.5. Practice

Prior to formal testing, the two naive subjects (DN and RK) began a series of practice sessions. To be sure that they understood the difference between the unidirectional and oscillatory patterns, each practice session began by showing them biased versions of the counterphase row-of-elements that always resulted in the perception of unidirectional motion or always resulted in the perception of oscillatory motion. The rest of each session entailed practice establishing the required attentional spread prior to the presentation of the to-be-tested counterphase stimuli and maintaining it for the entire trial. DN and RK were never told that unidirectional motion was expected to be perceived less often (and oscillatory motion more often) for increased inter-element distance, or that attentional spread was expected to affect the relative frequency with which unidirectional and oscillatory motion patterns would be perceived.

Fluctuating attention during the practice sessions was inferred from instability in subjects' reports of unidirectional versus oscillatory motion as a function of inter-element distance (e.g., oscillatory motion might be perceived most frequently for intermediate inter-element distances during some blocks of trials, and for large inter-element distances during other blocks of trials). Feedback entailed telling subjects that they were not maintaining attention in the instructed manner, and reinforcing those instructions. DN's data were stable from the start of practice, so formal testing for him began after just a few practice sessions. RK required more extended practice until her data were sufficiently stable to begin formal testing. Whether the perception of unidirectional motion decreased with increased inter-element distance, and whether attentional spread affected the relative perception of unidirectional versus oscillatory motion, were not considerations in determining when practice was terminated. [2]

1.1.6. Results

The results, which are presented in Fig. 2, are based on trials for which subjects indicated whether they perceived unidirectional or oscillatory motion (subjects pressed the spacebar on an average of 1.6% of the trials to indicate that they were unsure of their response).

[2] We were unaware of any implicit demand for subjects to report more unidirectional motion in the Broad Attention condition. Even if there were such a demand, there was no basis for it transferring to Experiment 2, which involved completely different patterns and was initiated after a brief practice session familiarizing subjects with the response alternatives (as was also the case for Experiment 3). There was no way for subjects to have learned that broadly spread attention was expected to increase the perception of group motion for the Ternus stimulus in Experiment 2.

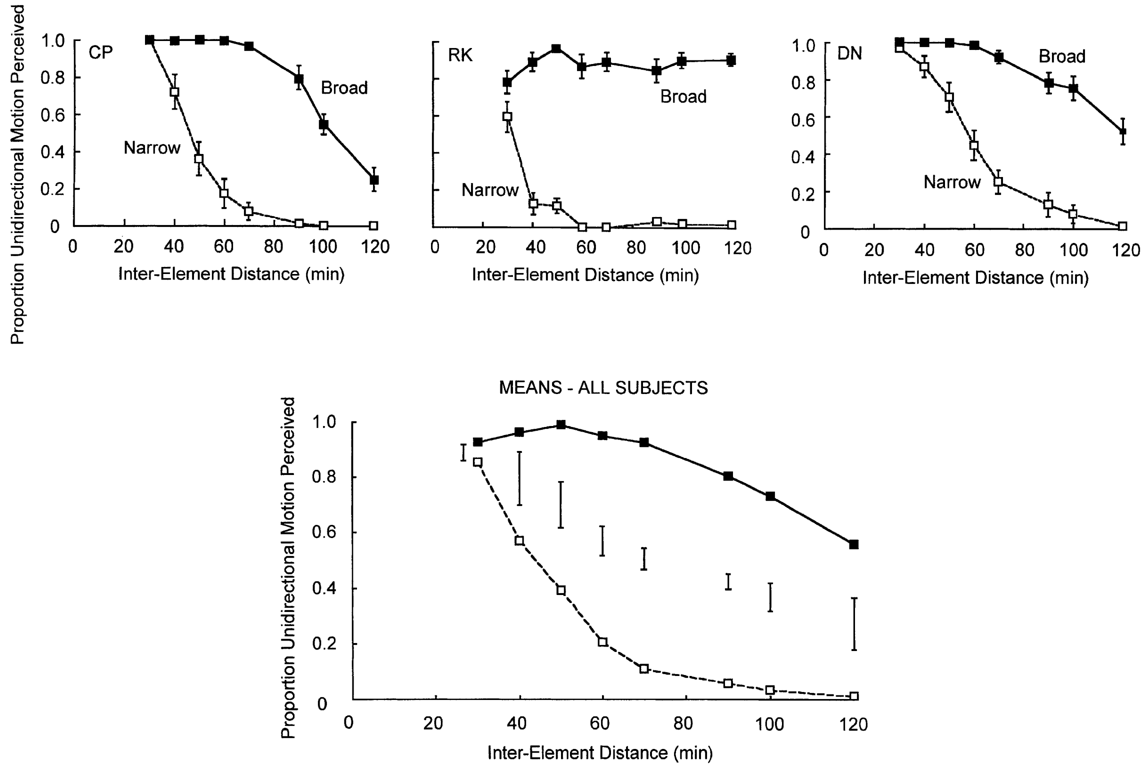

Fig. 2. Experiment 1: effect of attentional spread (Broad versus Narrow) and inter-element distance on the perception of the unidirectional motion pattern for the counterphase row-of-elements. (The proportions for the perception of the oscillatory motion pattern are the complement of the proportions for unidirectional motion.) For each subject, the standard error bars are based on the means for each of 8 blocks of Broad Attention and 8 blocks of Narrow Attention trials. The standard error bars in the bottom graph are based on the mean Broad/Narrow difference in the perception of unidirectional motion for each subject. The path length of individual motion components was one-half the inter-element distance.

Graphed in the figure are the proportions of trials for which unidirectional motion was the first pattern perceived; the proportions for the oscillatory motion pattern are the complement of those for unidirectional motion. As in previous studies (Hock & Balz, 1994; Hock et al., 1996, 1998), the perception of the unidirectional motion pattern decreased as the inter-element distance of the counterphase stimulus was increased, the exception being that the frequency of perceiving unidirectional motion was near ceiling for RK's Broad Attention condition. For all three subjects, the perception of the unidirectional pattern extended into much larger inter-element distances in the Broad compared with the Narrow Attention condition. The effect of attentional spread was consistent for each subject, and was also consistent across subjects. This replicated results obtained by Hock et al. (1998) with a similar instructional manipulation of attention, and with an attentional manipulation involving the detection of luminance increments.

1.1.7. Experiment 2

The purpose of this experiment was to show that the effect of attentional spread on global motion pattern formation is not limited to the counterphase row-of-elements. The methodology of Experiment 1 was therefore extended to the Ternus stimulus (Ternus, 1926). For the particular version we studied (Fig. 1b), two square elements were presented in the same location during every frame, and a third square was presented to the left or right of the two static squares during alternating frames (distances between the three squares were equal during every frame). Either an "element motion" or "group motion" pattern is formed for this stimulus, even in the absence of a blank interframe interval (Kramer & Rudd, 1999; Pantle & Petersik, 1980), which was at one time thought necessary for the formation of the group motion pattern (Pantle & Picciano, 1976). For small inter-element distances, all three squares are perceived moving as a unit, including the static "inner" squares (i.e., group motion). For larger inter-element distances, the inner static squares are perceived as stationary, and only the "outer" square is perceived in motion (i.e., element motion). Based on previous results for the counterphase row-of-elements, it was anticipated that the range of inter-element distances over which group motion is perceived would increase in the Broad compared with the Narrow Attention condition.

1.1.8. Method

Although the stimuli and to-be-reported patterns were different, this experiment was methodologically the same as Experiment 1 with respect to subjects, design, and procedure. Once again, the green attention dots remained on the screen until the subject pressed the spacebar of the computer keyboard to indicate that he or she was attending to them, as instructed. Thereupon, three equally spaced white squares were presented (same size and luminance as in Experiment 1). The two inner squares, which remained in the same location during every frame of a trial, were equidistant left and right from the center of the four attention dots. The third square was presented to the left of the two inner static squares during odd-numbered frames, and to their right during even-numbered frames. There were eight 267 ms frames per trial (the inter-frame interval was 0 ms). The distances between the three squares were equal during the entire trial, and varied randomly from one trial to the next. The inter-element distance was either 12.5, 15.0, 17.5, 20.0, 25.0, 30.0, 45.0 or 60.0 min (center-to-center), so local element motions occurred over distances ranging from 12.5 to 60.0 min when the group motion pattern was formed, and from 37.5 to 180.0 min when the element motion pattern was formed. After each trial, subjects indicated whether they first perceived the group motion pattern (defined by all the elements moving) or the element motion pattern (defined by only the outer element moving). They pressed the spacebar when unsure of their response.

1.1.9. Results

The results presented in Fig. 3 are based on trials for which subjects indicated whether they perceived the group or element motion pattern (subjects pressed the spacebar to indicate they were unsure of their response on an average of 1.1% of the trials). Graphed in the figure are the proportions of trials for which group motion was the first pattern perceived; the proportions for the element motion pattern are the complement of those for group motion. The results are consistent with Pantle and Petersik's (1980) in indicating that the perception of group motion decreases as the inter-element distance of the Ternus stimulus is increased (the perception of element motion commensurately increases). For all three subjects, the perception of group motion for the Ternus stimulus extended into larger inter-element distances for the Broad compared with the Narrow Attention condition. However, the enhancement of group motion by Broad Attention occurred at different inter-element distances for each subject, so standard errors based on each subject's Broad/Narrow difference in the perception of

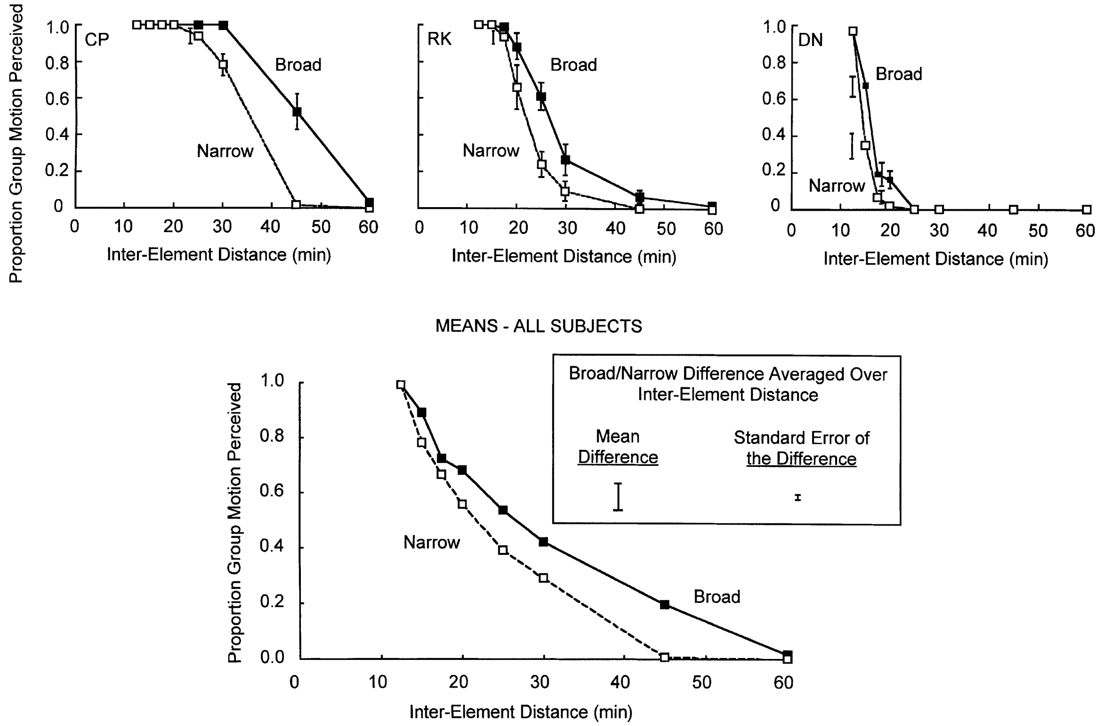

Fig. 3. Experiment 2: effect of attentional spread (Broad versus Narrow) and inter-element distance on the perception of the group motion pattern for the three-element version of the Ternus stimulus. (The proportions for the perception of the element motion pattern are the complement of the proportions for group motion.) For each subject, the standard error bars are based on the means for each of 8 blocks of Broad Attention and 8 blocks of Narrow Attention trials. Included in the bottom graph is the difference between the Broad and Narrow conditions averaged over all 8 inter-element distances, as well as the standard error of this difference (based on the mean Broad/Narrow difference in the perception of group motion for each subject). The path length of individual motion components corresponded to the inter-element distance when group motion was perceived.

group motion were determined only after averaging the results over all eight inter-element distances. As indicated at the bottom of Fig. 3, the overall effect of attention on group motion was much greater than the standard error of the Broad/Narrow difference.

2. Experiment 3

The results for the first two experiments join those of Hock et al. (1998) in providing evidence that the perceiver's attentional spread affects global pattern formation (although the size of the attention effect was smaller in Experiment 2 than Experiment 1). The critical question in this experiment is whether or not attentional spread, manipulated as in the first two experiments, also affects local motion perception. Subjects were instructed to simultaneously attend to all four small green dots presented in the corners of an imaginary square. Now, however, a pair of squares with different luminance values was simultaneously presented with the four attention dots (in the center of the attention area). Subjects were required to indicate whether they perceived motion between the two squares following a single, 267 ms exchange of their luminance values (Fig. 1c). Each trial in this experiment was kept brief in order to give the greatest opportunity for an effect of attention to be observed; fluctuations in attentional spread over the course of a multi-frame trial would tend to dilute differences between the Broad and Narrow Attention conditions. [3]

The test stimulus for this experiment is based on a generalized version of single-element apparent motion first described by Johansson (1950) and studied systematically by Hock et al. (1997). Pairs of elements (small squares) of different luminance are simultaneously visible, and the two luminance values are exchanged during one or more successive frames. Whether or not motion is perceived depends on the background-relative luminance contrast (BRLC), for each element (i.e., the frame-to-frame change in luminance divided by the difference between the average luminance and the luminance of the background; Hock et al., 1997). The greater the BRLC, the more likely it is that motion will be perceived. (For standard apparent motion—when only one element is visible at a time—the BRLC is 2.0 regardless of the particular luminance values.)

The rationale for the experiment is based on Albrecht and Geisler's (1991) evidence that the activation of motion-sensitive cortical neurons increases with increased luminance contrast. It can be inferred from these neurophysiological results that if detector activation is relatively weak for one of the attentional conditions, more time-varying luminance contrast (higher BRLC values) would be required in order to increase activation to the level required for motion to be perceived as frequently as it is perceived in the other attentional condition.

[3] Brief trials were not an option for the counterphase row-of-elements studied in Experiment 1 because multiple frames were required in order for the unidirectional and oscillatory motion patterns to emerge. Experiment 2, whose purpose was to demonstrate that the effect of attentional spread on pattern formation generalized to stimuli other than the counterphase row-of-elements, maintained the design of Experiment 1.

2.1. Method

Each trial again began with the presentation of the four green attention dots. In this experiment, however, the attention dots were accompanied from the start of the trial by two small squares (size $= 10.0 \times 10.0$ min, as in the preceding experiments) presented equidistant left and right from the center of the attention dots. Their luminance values were always different, either 65.4/71.6, 59.3/77.7, 53.1/83.9, 46.9/90.1, 40.8/96.2, 34.6/102.0, 28.4/108.6, 22.3/114.7, or 16.1/120.9 for the left and right squares, respectively. As in the preceding experiments, subjects pressed the spacebar when they were meeting the attentional requirement of simultaneously attending to all four green attention dots. Thereupon, the luminance values of the two elements were exchanged. The BRLC values resulting from the luminance exchange were 0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, 1.5, or 1.7; background luminance $= 6.9$ cd/m^2. BRLC values varied randomly from trial to trial, as did the distance between the squares (either 15, 30, or 45 min, center-to-center). The latter, which established the length of the motion path, corresponded to the inter-element distances of 30, 60 and 90 min for the counterphase stimuli of Experiment 1 (motion paths were half the inter-element distance), and to the inter-element distances (and motion paths) of 15, 30, and 45 min when group motion was perceived for the Ternus stimuli of Experiment 2.

There were 6 testing sessions, with 2 blocks of 270 trials per session (one block in the Broad and one in the Narrow Attention condition; their order alternated during successive sessions). The blocks of 270 trials were formed from the orthogonal combination of 3 inter-element distances, 9 BRLC values, and 10 repetitions (order was randomized within sub-blocks of 27 trials). Subjects were instructed to simultaneously attend to the four attention dots, to press the space bar when they were meeting the attentional requirement, and to maintain the required attentional spread for the remainder of the trial. When the space bar was pressed, the luminance values of the two elements were exchanged for a duration of 267 ms. At the end of each trial subjects pressed designated keys on the computer keyboard to indicate whether or not they perceived-motion between the two element locations. They were instructed to press the space bar if they were unsure of their response.

2.2. Results

As in Hock et al. (1997) and Gilroy et al. (2001), the proportion of trials for which motion was perceived increased with the BRLC. It can be seen for the averaged results presented in Fig. 4 that attentional spread had little effect on the BRLC values required for motion to be perceived.

In order to quantitatively assess the results, the BRLC values required for motion to be perceived for half the trials (the 50%-threshold) was determined by probit analysis for each subject in each of the six conditions (three inter-element distances × Broad/Narrow Attention). As indicated in Fig. 5, the 50%-threshold increased with increases in inter-element distance (motion path length), replicating Gilroy et al.'s (2001) results. However, the effects of attentional spread were small and inconsistent. Subjects CP and RK perceived single-element motion for smaller BRLC values in the Narrow compared with the Broad Attention condition for the smallest inter-element distance, but DN required larger BRLC values in the Narrow than the Broad Attention condition to perceive motion, and then only for the larger inter-element distances.

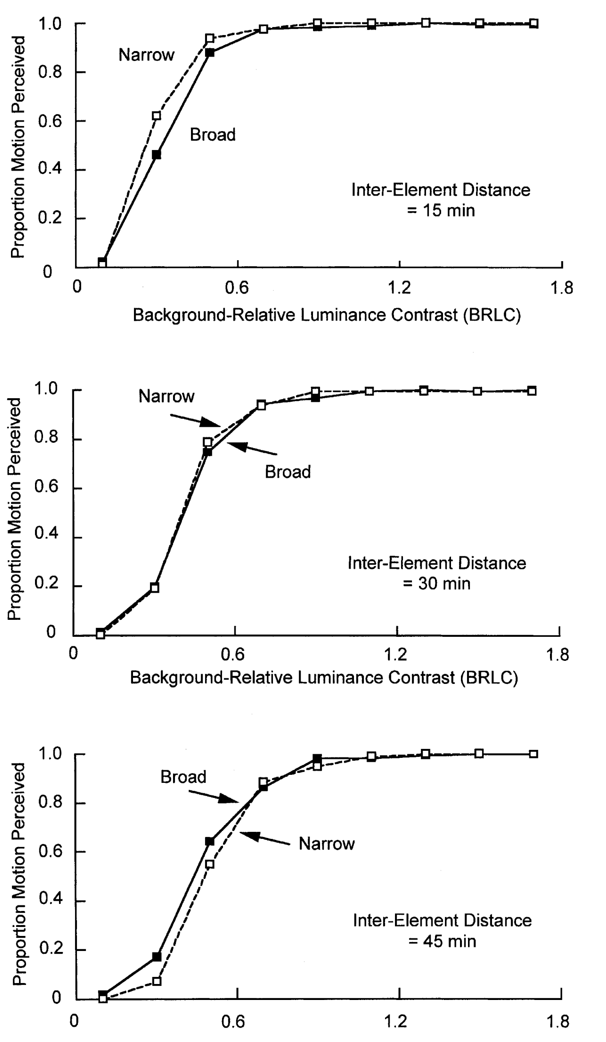

Fig. 4. Experiment 3: effect of attentional spread (Broad versus Narrow), inter-element distance, and BRLC on the perception of motion for the generalized single-element apparent motion stimulus (averaged over the three participating subjects).

The consistency over subjects in the effect of inter-element distance is indicated by standard errors based on each subject's difference between the 15 and 30 min inter-element distances, and between the 30 and 45 min inter-element distances (the left side of the bottom graph in Fig. 5). Standard errors of these differences were substantially smaller than the differences in BRLC value required for 50% motion perception. In contrast, standard errors based on each subject's difference between the Broad and Narrow Attention conditions (for each inter-element distance; bottom graph, Fig. 5) were much larger than the Broad/Narrow differences in the BRLC value required for 50% motion perception; i.e., the effect of attentional spread was small and unreliable.

2.2.1. Additional results

Although attentional spread affected pattern formation for the counterphase row-of-elements and the Ternus stimulus (Experiments 1 and 2), it had little, if any effect on the activation of local motion detectors in this experiment. However, single-element motion in this experiment was tested with BRLC values less than 2.0 (generalized apparent motion), whereas motion for the counterphase and Ternus stimuli in experiments 1 and 2 was based on a BRLC value of 2.0 (standard apparent motion). In order to determine whether this difference might have been a factor in attentional spread affecting pattern formation, but not the perception of single-element motion, we created a version of the counterphase row-of-elements for which the BRLC value was 0.9 (luminance values for this BRLC value alternated between 40.8 and 96.2 cd/m^2, and the background luminance was 6.9 cd/m^2). All element locations are simultaneously visible for this stimulus (illustrated at the top of Fig. 6), high luminance elements spatially alternating with low luminance elements. Motion is perceived when the luminance values are exchanged during successive frames, local motions beginning at locations where luminance decreases toward the luminance value of the background, and ending at locations where luminance increases away from the background luminance (Hock et al., in press). Inter-element distances were 50% smaller for this version of the counterphase stimulus compared with Experiment 1 because all element locations are simultaneously visible (individual motion components nonetheless had the same path length as in Experiment 1). The manipulation of attentional spread as well as other aspects of the experiment was identical to Experiment 1. The subject, DN, participated in two

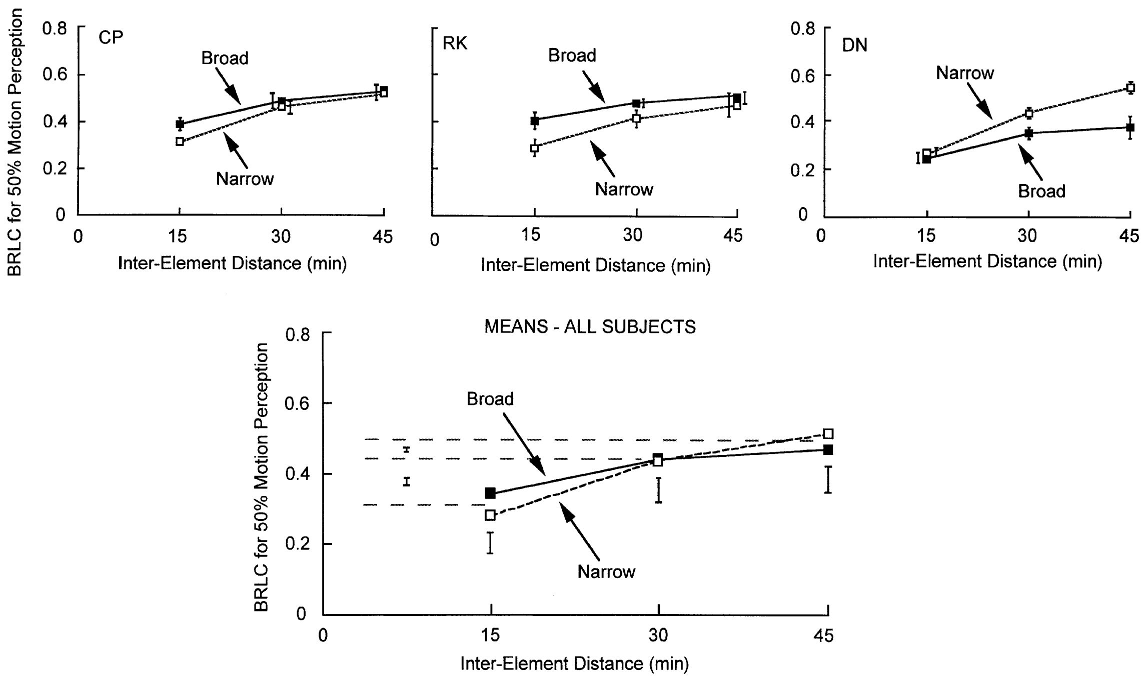

Fig. 5. Experiment 3: effect of attentional spread (Broad versus Narrow) and inter-element distance on the perception of motion for the generalized single-element apparent motion stimulus. The dependent measure is the probit-determined value of BRLC that results in the perception of motion on 50% of the trials. For each subject, the standard error bars are based on the means for each of 6 blocks of Broad Attention and 6 blocks of Narrow Attention trials. Error bars on the left side of the bottom graph indicate the standard error of the difference in motion perception between the 15 and 30 min inter-element distance, and between the 30 and 45 min inter-element distance (based on the mean difference for each subject). Standard errors based on each subject's mean Broad/Narrow difference are presented in the bottom graph for each inter-element distance.

testing sessions, with four blocks trials per session (alternating between the Broad and Narrow Attention conditions).

The results were very similar to DN's Experiment 1 results in indicating that broadly spread attention increases the frequency with which the unidirectional motion pattern is perceived for the counterphase row-of-elements (Fig. 6). Now, however, local motions were based on a BRLC value of 0.9 rather than 2.0. This indicated that the differential effect of attentional spread on pattern formation versus single-element motion was unlikely to have been the result of differences in BRLC among the experiments.

3. Discussion

The results for Experiment 3 are consistent with Gilroy et al. (2001) in indicating that single-element motion produces more activation of local motion detectors when inter-element distances are relatively small. That is, more luminance contrast (higher BRLC values) is required to increase the activation of motion detectors (Albrecht & Geisler, 1991) to the level required for motion to be perceived as frequently for large inter-element distances as it was perceived for small inter-element distances. Based on the assumption that the contributions of excitatory interaction to detector activation are more dependent on the level of local detector activation than the contributions of inhibitory interaction, the greater local activation for smaller inter-element distances could have enhanced the perception of unidirectional motion by increasing the relative contribution of excitatory interactions to the activation of detectors with similar directional selectivity (Park et al., 2001).

A similar possibility is not indicated for the effects of attentional spread. The results of Experiment 1 replicated previous evidence (Hock et al., 1998) that broadly spread attention increases the relative contribution of excitatory versus inhibitory interactions to detector activation for the counterphase row-of-elements (thereby increasing the range of inter-element distances over which the unidirectional motion pattern is perceived). However, the results for Experiment 3 do not indicate that this is the result of broadly spread attention increasing the stimulus activation of local motion detectors (such an effect would have been attributable to attention modifying the sensitivity/responsiveness of local motion detectors). Effects of attention were small and inconsistent across subjects and inter-element distances, despite the fact that the manipulation of attentional spread and the subjects were the same as in the experiments showing reliable effect of attentional spread

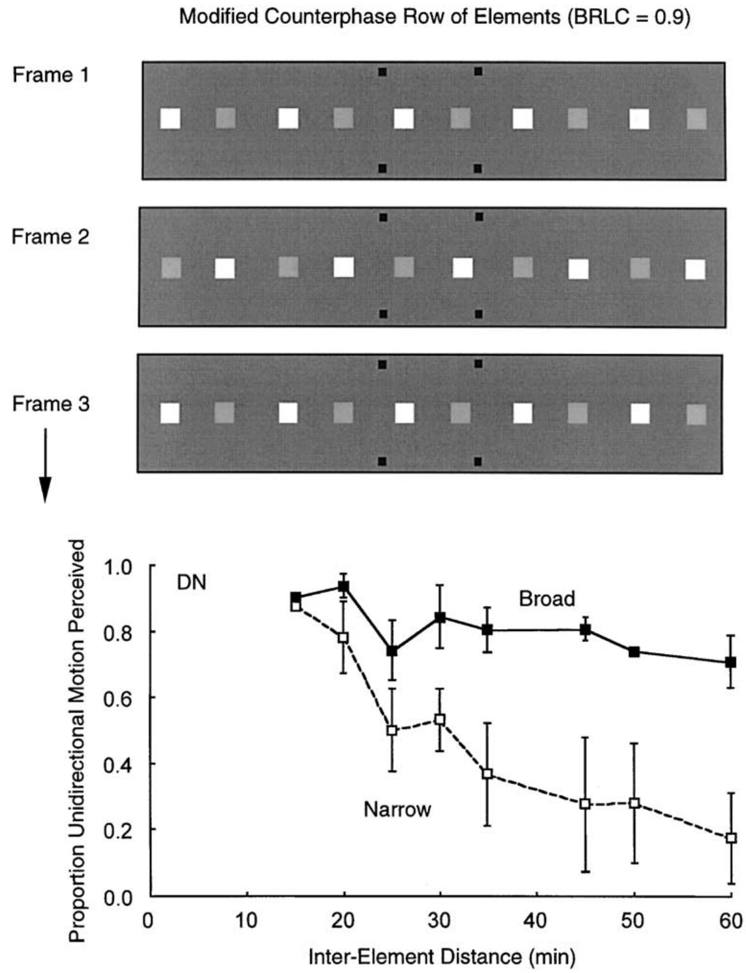

Fig. 6. Experiment 3: additional results. Top: Illustration of counterphase row-of-elements for which local motions are based on BRLC values of 0.9 rather than 2.0. Element sizes and distances are not to scale. Bottom: Effect of attentional spread (Broad versus Narrow) and inter-element distance on the perception of the unidirectional motion pattern for the counterphase row-of-elements with BRLC = 0.9. The standard error bars for each mean were based on 4 blocks of Broad Attention and 4 blocks of Narrow Attention trials. The path length of individual motion components corresponded to the inter-element distance (although the inter-element distances are smaller for this version of the counterphase stimulus compared with Experiment 1, individual motion components have the same path length as in Experiment 1).

on pattern formation. There was a small advantage of Broad Attention for the perception of single-element motion in Experiment 3 only for the inter-element distance of 45 min (unreliable because it was due entirely to the results for one subject, DN) that was consistent with the effect of broadly spread attention on pattern formation in Experiment 1 when the inter-element distance was 90 min (i.e., when the path length for individual motion components was 45 min). However, similarly strong effects of broadly spread attention on pattern formation also were observed in Experiment 1 for the 60 min inter-element distance (path length for individual motion components = 30 min), but in Experiment 3 there clearly was no influence of attentional spread on the perception of single-element motion for the corresponding motion path length. Moreover, even if the observed effect of attention on the perception of single-element motion was reliable (it was not), it was much smaller than the effect of inter-element distance. That is, averaging over the three subjects, differences among the three inter-element distances in Experiment 3 accounted for 77% of variance in reports of single-element motion, more than four times the variance accounted for by the effects of attention (18%). If attention effects on pattern formation for the counterphase row-of-elements occurred as a result of differences in local detector activation, differences in inter-element distance would likewise be expected to have a much larger effect on reports of unidirectional motion than differences in attentional spread. This was the opposite of what was observed in Experiment 1. That is, differences among the three inter-element distances in Experiment 1 with motion path lengths corresponding to those of Experiment 3 accounted for 30% of variance in reports of unidirectional motion, 0.6 of the variance accounted for by the effects of attention (51%).

It can be concluded, therefore, that broadly spread attention enhances the formation of the unidirectional motion pattern by changing the balance between the contributions of excitatory and inhibitory interactions to detector activation, and this occurs independently of any influence on the activation of local motion detectors (or the detection of higher-order stimulus properties specifying unidirectional or oscillatory motion—there were no such properties to detect). One possibility is that broadly spread attention increases the interactive influence of a detector on the activation of other detectors, and does so more for excitatory than inhibitory interactions (i.e., it increases the excitatory relative to the inhibitory gain). Another possibility is that broadly spread attention increases detector activation by expanding the range over which local motion detectors interact (as proposed by Hock et al., 1998). In either case, the same level of feed-forward detector activation would result in a larger contribution of excitatory than inhibitory interaction to the activation of detectors with similar selectivity in the Broad Attention condition, high activation levels constituting the basis for the formation of the unidirectional motion pattern.

The effects of attentional spread on pattern formation for the Ternus stimulus in Experiment 2 were parallel to (though smaller than) those obtained for the counterphase stimulus in Experiment 1. Broadly spread attention increased the range of inter-element distances over which unidirectional motion was perceived for the counterphase row-of-elements and group motion was perceived for the Ternus stimulus. The formation of the unidirectional pattern reflects the presence of relatively strong, activation-increasing excitatory interactions that are boosted by broadly spread attention (so the activation of motion detectors selective to the just-perceived-motion is sufficient for the same perceived-motion direction to persist from one frame to the next). The parallel results for the group motion pattern perceived for the Ternus stimulus suggests that its formation is likewise dependent on excitatory detector interactions.

Results convergent with those of the current article have been reported by Ito and Gilbert (1999), who studied the effect of distributed versus focussed attention on the context effects obtained in a brightness discrimination task. Two monkeys judged whether a reference line segment near the fixation point was brighter or dimmer than one of four peripherally presented line segments (a receptive field in V1 was identified for each of these potential target stimuli). On some trials the line segments were presented alone, on others they were accompanied by flanking, co-linear line segments (the contextual stimuli) that fell outside the receptive fields of the four potential target stimuli. Finally, attention was either focused by a pre-cue on the location of the target (the peripheral line segment that differed from the reference line), or it was distributed among all four peripheral line segments.

Ito and Gilbert found that there was little effect of distributed versus focussed attention on either brightness judgments or neural activation in the absence of interactive influences from flanking line segments (i.e., when there were no contextual stimuli). This was parallel to the results obtained in Experiment 3 of the current article, for which there was little, if any difference between the Broad (distributed) and Narrow (focussed) attention conditions with respect to the perception of single-element motion. In contrast with this "local" attention independence, Ito and Gilbert found that when the flanking context lines were present, their influence depended on whether attention was distributed or focussed. For the monkey who received the most training, distributed attention enhanced the facilitating effect of the context on both brightness judgments and neural activation. This was parallel to the results obtained in Experiments 1 and 2 of the current study, when each element motion was seen in the context of other, simultaneous element motions. It was found then that attention mattered; broadly spread (distributed) attention enhanced the formation of the unidirectional motion pattern for the counterphase stimulus and the group motion pattern for the Ternus stimulus. It should be noted, however, that Ito and Gilbert's results were very different for the monkey with less training. For that monkey, focussed rather than distributed attention enhanced the facilitating effect of the context on brightness discrimination and neural activation. This reversal suggests that perceptual learning might be similarly critical for how attentional spread affects motion pattern formation for the counterphase and Ternus stimuli investigated in the current study.

4. Conclusion

In conclusion, the results of the experiments reported in this article show that the integrative excitatory and inhibitory detector interactions responsible for the formation of global motion patterns can be modified (in the current case, by attentional spread), independent of any effect on local detector activation. This, however, does not rule out the possibility that differences in local detector activation could not also alter the excitatory/inhibitory balance. We've previously indicated that the distance over which local motions are perceived affects the activation of local motion detectors (Gilroy et al., 2001, and Experiment 3), and discussed how this might influence the balance of excitatory/inhibitory interactions in global pattern formation (leading to more perception of the unidirectional motion pattern for small inter-element distances). Other evidence along the same lines has been reported by Hock and Park (1999), who have shown that both local detector activation and global pattern formation for the counterphase row-of-elements are affected by disparities in the size and shape of the elements at the start and end of each motion path. Additional influences on global pattern formation could come from adaptation; Varela, Song, Turrigiano, and Nelson (1999) have shown that excitatory synapses are more depressed by repetitive activation than inhibitory synapses. As stated at the beginning of this article, stimuli for which pattern formation is self-organized (like the counterphase row-of-elements) provide an ideal psychophysical framework for the study of these potential contributions to the balance of excitatory and inhibitory interactions because in the absence of pattern-specifying stimulus information, the global structure of self-organized patterns can provide a direct indication of how the relative strength of these interactions determines the pattern that is formed.

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