Integration and segregation of local motion signals: the role of contrast polarity

Maarten J. van der Smagt *, Wim A. van de Grind

Department of Comparative Physiology and Helmholtz Instituut, Universiteit Utrecht, Padualaan 8, NL-3584 CH Utrecht, The Netherlands

Abstract

In the initial stages of visual processing in primates, more or less separated ON and OFF pathways have been shown to exist. There is ample evidence, that this separation includes the initial stages of motion processing. In the present study, experiments were conducted to investigate whether this ON versus OFF distinction persists into the integration stage of local motion information. We constructed stimuli that consisted of clusters of checks with equal contrast polarity, which could be varied in size, and compared them to stimuli with a random polarity distribution. We found that the ON versus OFF distinction remains partly intact, while interactions between the two systems are also apparent. These interactions prove to be highly correlated with the spatial structure of the stimulus. We propose a mechanism of contrast-sign specific integration of local motion signals, after which these separate ON and OFF pools engage in mutually inhibitory interactions. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

For organisms (like humans) that rely heavily on vision to perceive the spatial structure of their environment, it is essential that their visual system is able to determine which parts of the retinal image belong to any given object. The relative motions of these parts of the image can serve as an important clue for object segregation (Braddick, 1993). However, the visual system may have to integrate many distinct local motion signals to establish an object to be separate from its surroundings. For instance, the moving object might be partially occluded and thus give rise to non-connected object components (Lorenceau & Shiffrar, 1992; Mingolla, Todd & Norman, 1992). Furthermore, natural scenes tend to contain an excess of spurious motion signals, for example waving cornfields or rustling leaves, which might mask the object's motion (Williams, Phillips & Sekuler, 1986; Braddick, 1995; Watamaniuk, McKee & Grzywacz, 1995; Croner & Albright, 1997). The visual system is faced with the difficult task to determine which motion signals should

be integrated and which should be segregated to detect a moving object.

There are a number of cues, that might indicate which local motion signals are most likely to originate from the same object. Obvious and well-explored are common speed and direction, generally referred to as the Gestalt law of common fate (Koffka, 1935). Small distances between the motion signals in space-time also increase the likelihood that they stem from one object (Snowden & Braddick, 1990; Fredericksen, Verstraten & van de Grind, 1994; Ben-Av & Shiffrar, 1995; Shiffrar & Lorenceau, 1996), as does a spatial arrangement of the signals that resembles a form or an edge (Koffka, 1935; Lorenceau, 1996; Shiffrar & Lorenceau, 1996). Also, similar colour or contrast polarity (Stoner & Albright, 1993; Croner & Albright, 1997) might bind the local motion signals. In this paper, we will focus on the latter: The role of contrast polarity in merging and/or separating object components in motion vision.

In the retina, ON-centre and OFF-centre ganglion cells respond to the onset of a bright and dark visual stimulus, respectively (Wiesel & Hubel, 1966; Famiglietti Jr. & Kolb, 1976; Schiller, 1992). The ON and OFF systems remain independent through LGN and possibly even parts of the primary visual cortex (Hubel &

Wiesel, 1968; Horton & Sherk, 1984; Schiller, 1984; Schiller, Sandell & Maunsell, 1986; Hubel & Livingstone, 1990). Evidence suggesting that motion stimuli of opposite contrast polarities are processed separately in the front-end visual system, was found in electrophysiological studies of the monkey primary visual cortex (Schiller, 1982; Schiller, Sandell & Maunsell, 1986; Sherk & Horton, 1984), as well as in psychophysical work (Shechter & Hochstein, 1990; Mather, Moulden & O' Halloran, 1991; Wehrhahn & Rapf, 1992; Edwards & Badcock, 1994).

It seems reasonable to assume that this separate processing persists up to a level at which local motion signals are integrated. Only then can contrast polarity be a cue about two or more local motion signals arising from one moving object. On the other hand, the visual system must compare these signals to other motion signals that do not originate from the same object (and which would have the opposite polarity). Consequently, if contrast polarity is to provide (one of) the object clues, interactions between the ON and OFF system are expected as well.

Two psychophysical studies, Edwards & Badcock (1994) and Croner & Albright (1997), have addressed the question on how ON and OFF systems interact when global motion is extracted. However, even though they used a similar experimental paradigm (a variant of the one used by Newsome & Paré (1988)), these studies produced contradicting results. In their Experiment 1, Edwards & Badcock (1994) used a stimulus consisting of a grey background on which the global motion signal was carried by bright dots only. The noise either consisted of bright dots only, or contained dots of both polarities. They found that direction discrimination thresholds were similar for both conditions. From these results, they concluded that the global-motion system does not process ON and OFF signals independently. In contrast, using a similar stimulus, Croner & Albright (1997) found that direction discrimination improved when the contrast-sign distribution of the signal dots differed from that of the noise dots.

We think, as discussed above, that both separate integration of ON and OFF signals, as reported by Croner & Albright (1997), and interaction between the ON and OFF systems, as reported by Edwards & Badcock (1994), represent essential components of a visual motion mechanism that uses contrast polarity as an object segregation cue. In this paper we will thus re-examine the controversy between those studies by trying to answer two related questions: (1) Does the separate processing of motion signals of opposite contrast polarity persist into the stage where local motion information is combined to reveal the object's motion (i.e. are Croner & Albright (1997) right)? (2) Do the ON and OFF systems interact at this stage (i.e. are Edwards & Badcock (1994) right) to enhance object segregation, and if so how?

In an experiment to answer these questions, the dots that define the object's motion cannot be distributed randomly within the stimulus window. Therefore, we use a different stimulus paradigm. Our coherently moving stimuli consist of 'checks' of both contrast polarities (dark or bright). The mean luminance of our moving stimuli is identical to that of the static background, which also consists of dark and bright checks. Thus, the checks carrying the coherent motion signal can only be identified as such when they move. The moving checks, however, are distributed in the stimulus window in such a way, that together they resemble a moving edge or line.

We manipulate the contrast polarity of individual checks. By creating clusters of checks with the same polarity, local regions arise where checks of equal polarity carry the coherent motion signal. Changing the size of this region, results in a change of the area within which the motion signals of equal contrast polarity can be integrated. For example, a performance increase with increasing equal-polarity cluster-size, would suggest that integration of equal polarity checks is a stronger object segregation cue than integration across opposite contrast polarities. This would imply that the separation of ON and OFF systems would remain at least partly intact in the motion integration stage.

2. General methods

2.1. Stimulus generation

The motion stimuli were generated on custom image generation hardware, controlled by a Macintosh IIfx computer and presented on a CRT display (Electro-Home EVM-1200, P4 phosphor, base display rate 90 Hz). The display screen was 14 cm and 256 pixels square, each pixel subtending 0.55 mm. At a viewing distance of 2 m, this resulted in a display area of 4° arc and a pixel size of 0.94 min arc.

The stationary background consisted of a 256×256 random-pixel-array (RPA). The stimuli moved coherently (velocity $= 1.41°$ s^{-1}) either to the left or to the right, starting at the centre of the screen. They moved 'in front' of the background, thus sequentially occluding pixels of the background pattern.

All moving stimuli consisted of 1 pixel wide columns of 64 'checks', which were 1×1 pixel in size[1]. The checks were thus always aligned vertically. Within one column the individual checks could be vertically adja-

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[1] The 'checks were identical in shape and luminance to the dark or bright background pixels. However we will use the term 'checks' instead of pixels to distinguish them from the stationary background pixels, as well as the multi-pixel round dots used by Edwards & Badcock (1994) and Croner & Albright (1997).

cent to the next check (a sequence of vertically contiguous checks defines a 'segment'), or vertically separated by a certain number of pixels from the next check. The mean luminance of all stimuli was equal to that of the background[2]). The contrast-polarity (dark or bright) was distributed over the moving checks either randomly or in clusters of equal contrast polarity. Figs. 1, 4 and 6 show examples of the stimuli used in the experiments.

An uncorrelated dynamic 'noise' RPA was superimposed on both the background and the moving stimuli. The mean luminance (L) of the signal-plus-noise pattern was set to 50 cd m^{-2}, its average contrast (C) to 70%. Both L and C were held constant while the 'luminance signal-to-noise ratio' (LSNR) could be increased or decreased, depending on the observer's response.
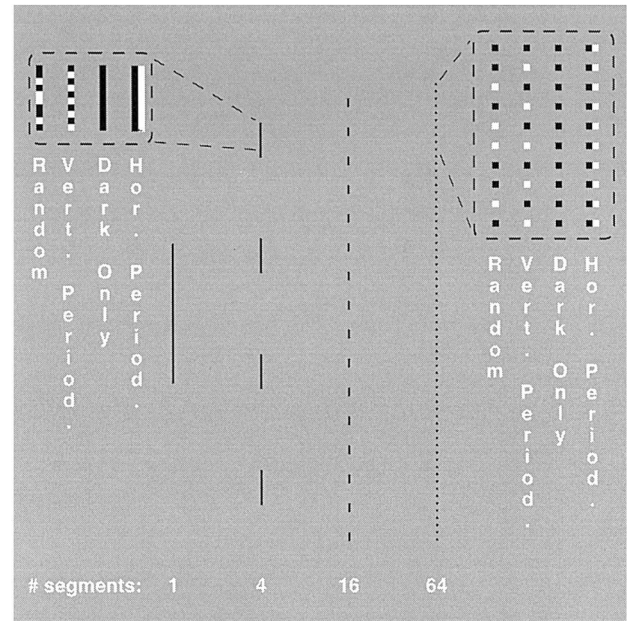
2.2. LSNR method

On every frame, every bright ($L + \Delta L$) and dark ($L - \Delta L$) pixel of stimulus and background is randomly increased or decreased in luminance by a noise value ΔN. Mean square contrast of the 'signal' part is $r_s^2 = (\Delta L/L)^2$ and mean square contrast of the 'noise' part is $r_n^2 = (\Delta N/L)^2$. By definition, $\underline{\text{LSNR} = r_s^2/r_n^2}$ and the total rms contrast equals $C = \sqrt{(r_s^2 + r_n^2)}$. From C, L and the chosen LSNR-value, the computer determines ΔL and ΔN (van de Grind, Koenderink & van Doorn, 1997). Fig. 2 illustrates the implementation of the LSNR method in the form of space-time diagrams of a single row of moving checks.
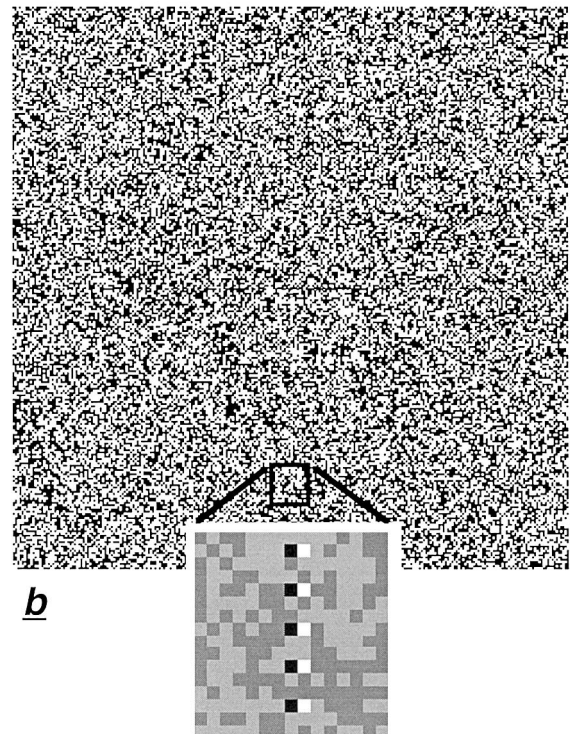
2.3. Procedure

Motion direction thresholds were measured in a two-alternative forced-choice (2AFC) horizontal (left-right) direction discrimination task. The LSNR-thresholds were determined using a staircase procedure that pursued the 79% correct level; three consecutive correct direction discriminations resulted in a lowering of the LSNR value, while any incorrect direction discrimination raised the LSNR value by the same amount. In all staircase sequences there were ten reversals, the thresholds were calculated as the average of the final six. Staircases where convergence was absent were regarded as incomplete and discarded before analysis. As an objective measure for convergence of the staircase, the 95% confidence interval of the calculated average had to be within ± 5% of this value. Although this measure is rather strict, only a minor fraction of the staircases needed to be discarded. In order to decrease

the duration of the experiment, the observers were asked to change the LSNR manually prior to the staircase, until it was just above subjective threshold. For each data point three staircases were completed and the three threshold-values averaged.

a

b

Fig. 1. (*Continued*)

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[2] All stimuli had the same mean luminance as the background, except for the 'dark only' condition in Fig. 1. This condition is used in both Experiments 1 and 2a. A double-column dark only condition is used as a control in Experiment 2b.

The experiments were performed in a darkened room, where the only light came from the monitor. Observers used a head rest and viewed the stimuli binocularly. Observers were instructed to fixate on a black dot (diameter 3.76 min arc) in the centre of the screen and to maintain fixation while the stimulus was shown. The presentation time for each stimulus was 1 s, after which the stimulus was replaced by a uniform grey screen (50 cd m^{-2}) until the observer indicated the perceived motion direction by pressing the arrow-keys on the computer keyboard. The first author and two experienced observers, who were unaware of the aim of this study, served as observers in these experiments. All had normal or corrected to normal vision.

3. Experiment 1

This experiment served as an initial comparison between four different contrast polarity distributions: random distribution of contrast polarity across the checks, two regular distributions of contrast polarity and a condition where all the moving checks had one contrast polarity (dark). The two regular distributions were obtained by introducing a vertical periodicity in one column or a horizontal periodicity when two adjacent columns were used. Fig. 1a illustrates the stimulus conditions used in this experiment (except the two-column random condition). We divided the moving check-columns in 1, 4, 16 and 64 segments. As a result, the moving columns resembled partially occluded moving edges or borders, thus containing non-connected object components. This set-up is analogous to the occluded lines used in some studies involving multiple apertures (Ben-Av & Shiffrar, 1995). The size of the components and the (vertical) distance between them could be varied, to mimic occluding surfaces of different size and density. The idea behind this stimulus design is that the quantification of the threshold as a
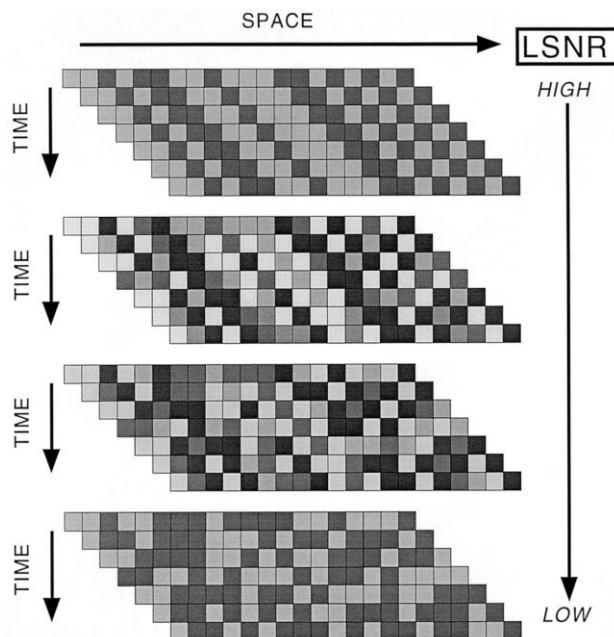

Fig. 2. LSNR method example. Shown are four space-time diagrams of a moving row of pixels at different luminance signal-to-noise ratios. The top diagram shows the moving pixels without noise, i.e. with an infinite LSNR. The individual pixels have a luminance of $L - \Delta L$ (dark) or $L + \Delta L$ (bright). Note that the top-left to bottom-right orientation, which depicts the directional motion energy in the stimulus, is clearly visible. The bottom diagram shows the noise pattern, i.e. the LSNR value approaches zero. The individual pixels have a luminance of $L - \Delta N$ (dark) or $L + \Delta N$ (bright). No specific orientation can be observed here. The two middle diagrams are combinations of the signal and noise pattern. They are combined in such a way, that the mean luminance and contrast remain equal. In the second diagram (from the top) the strength of the signal in the combined pattern is still sufficient to reveal the top-left to bottom-right orientation (adapted from van Wezel, 1996).

Fig. 1. (a) Example of the stimuli used in Experiment 1. The vertical columns above the number of segments (1–64) depict the form of the moving stimulus. The insets show the appearance of the different stimulus conditions, for a subset of the stimulus checks, in the four segments and 64 segments condition. The two column, random condition (not shown) consisted of two (uncorrelated) single random columns. vert. period. means vertical periodicity; hor. period. horizontal periodicity. The grey background in this figure symbolises a random-pixel-array (see b), which would make it virtually impossible to see the difference between (most of) these stimuli in a static representation. (b) One frame of an actual stimulus situation. The background consists of a 256 × 256 array of pixels, which have a 50% chance of being dark or bright. In the centre of the random-pixel-array a '64 segment, horizontal periodicity' stimulus occludes the background pixels. No noise is added to stimulus or background. The inset shows a magnification of the bottom five segments of the stimulus. The background pixels in the inset are drawn in grey to facilitate identification of the stimulus segments.

function of such a segmentation will allow us to deduce the properties of the contrast-sign specific (or non specific) spatial summation. The values four and sixteen are relatively arbitrary. However the one and 64 segments conditions are two extremes: one segment where all checks were contiguous (one large aperture), 64 segments where no check was vertically adjacent to the next (64 narrow apertures).

As mentioned before, a segment is defined by a group of vertically contiguous checks. Between two segments there is an interval, containing stationary background pixels. In this experiment, one segment means 64 vertically contiguous checks. Four segments means sixteen vertically contiguous checks and a 32 pixels (vertical) interval between neighbouring segments. Sixteen segments means four vertically contiguous checks and an interval of eight pixels and 64 segments means each check was vertically separated by two pixels from its nearest neighbour. The interval between the segments is thus twice the segment size. Pilot experiments with equal segment size and interval size resulted in lower
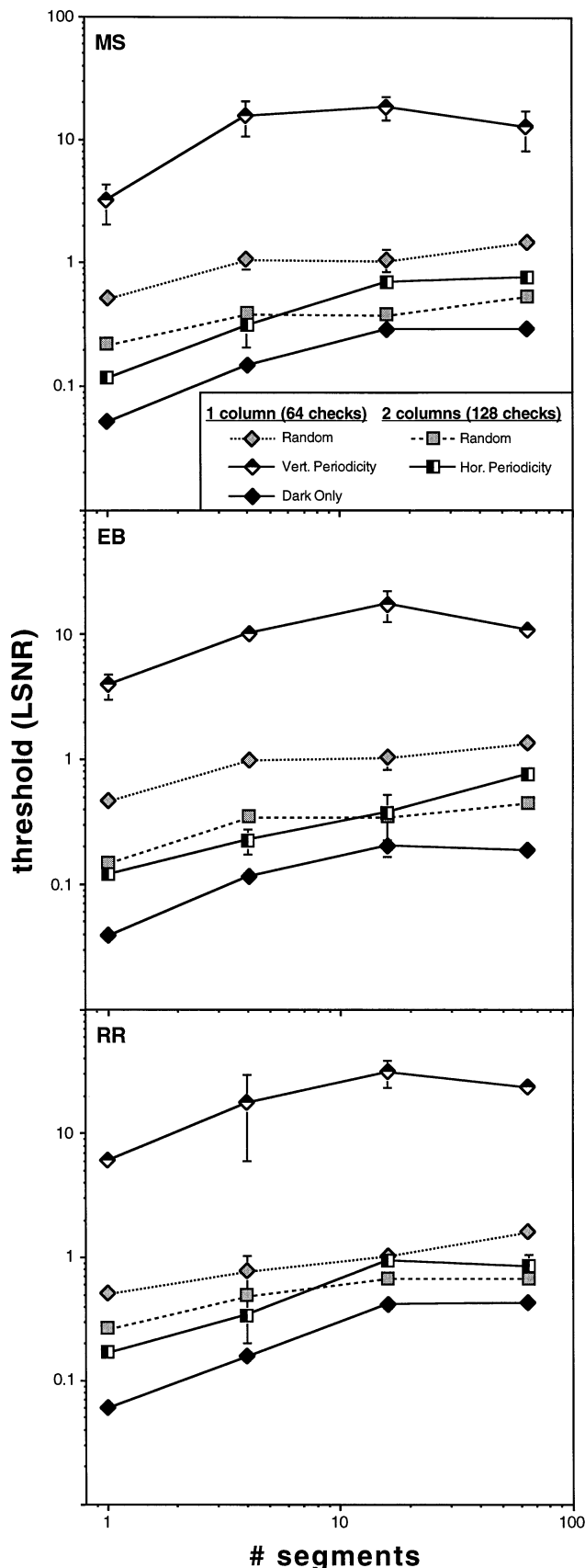
Fig. 3.

thresholds. However, the overall results were similar. We used either one or two adjacent columns. When two columns were used, they had an equal number of segments, which were aligned.

A single column with a random distribution of contrast polarity (as in the background pattern) was compared to a vertical periodicity condition and a dark only condition (see insets in Fig. 1a). The vertical periodicity condition consisted of 64 clusters of one check. That is, the bright and dark checks were alternated. Consequently, contrast polarity was evenly distributed across all moving checks. In the dark only condition the moving stimulus contained only dark checks, thus resulting in a mean luminance which differed from that of the background pattern. One would expect a contrast-sign specific integration mechanism to favour the dark only over the random condition, and favour the random over the vertical periodicity condition, since the latter never contains two neighbouring equal polarity checks.

When the stimulus contained two adjacent columns (i.e. 128 checks) a random polarity distribution was compared to a horizontal periodicity condition (see Fig. 1b and insets in Fig. 1a; random condition not shown). The horizontal periodicity consisted of one column of dark checks, always followed by one column of bright checks (thus containing two clusters of 64 identical checks). Thus the mean luminance of the stimulus was equal to that of the background, although the luminance of both columns differed substantially. Pilot experiments revealed that there was no difference in sensitivity to horizontal periodicity with reversed contrast sequence (i.e. a bright column followed by a dark column), or random contrast sequence (i.e. within a staircase, the leading column had a 50% chance of being dark or bright while the following column had the opposite contrast polarity). Here, one would expect a contrast-sign specific integration mechanism to favour the horizontal periodicity condition, since it contains a 'dark only' column and a 'bright only' column.

3.1. Results

Fig. 3 shows, that an increase in the segmentation of the columns results in a slight increase of direction detection thresholds. The thresholds for the 128 check stimuli with a random contrast polarity distribution (grey squares) are clearly lower than those for the

Fig. 3. The results of Experiment 1 for three subjects. The direction discrimination thresholds (LSNR) as a function of the number of segments. Error bars show the SEM. Diamonds represent the data for the three stimulus conditions with one column (grey = random, black and white = vertical periodicity, black = dark only), whereas squares represent the two-column conditions (grey = random, black and white = horizontal periodicity).

random stimuli containing 64 checks (grey diamonds). This is intuitively reasonable, since the 128 check stimuli contain twice as many possible correlations. However, instead of a decrease by a factor of $\sqrt{2}$, which would be expected from a simple spatial summation (Lappin & Bell, 1976; van Doorn & Koenderink, 1982, 1984), this factor is roughly between two and three. This difference might be accounted for by a temporal integration mechanism like that proposed by Fredericksen, Verstraten & van de Grind (1994).

There are two results from this experiment, that are of particular interest to this study. If one compares the curves that represent the one column (64 checks) stimuli (diamonds) there is a huge difference in thresholds for the three conditions: vertical periodicity or contrast polarity alternation, random contrast distribution and dark only (black and white, grey, and black diamonds, respectively). For the dark only condition the average luminance of the stimulus differs from that of the background, and this might account for the decrease in thresholds, compared to the random condition. However, we do not expect this to be the case (at least it cannot be the complete story), since the vertical periodicity condition has the same mean luminance as the background and as the random condition. Yet, the threshold increase for the vertical periodicity, compared to the random condition, is even larger than the decrease for the dark only condition. It seems that local imbalances in polarity distribution are important factors that determine direction discrimination performance. In Experiment 2a we will elaborate on this topic.

The other interesting result concerns the two column (128 checks) stimuli. As mentioned above, one column of only dark checks, results in much lower direction detection thresholds, than a column containing checks with a random possibility of being dark or bright. Van der Smagt & van de Grind (1996) showed that thresholds for columns containing only bright checks are similar to those for dark columns. One would thus expect the threshold for the horizontal periodicity condition (black and white squares in Fig. 3), which consist of one bright column adjacent to a dark column, to be much lower than two adjacent columns with random distribution of contrast polarity (grey squares in Fig. 3). It is clear from Fig. 3 that this is not the case! A *t*-test revealed that only the one-segment condition for subject MS is significantly different ($P < 0.05$). The other differences between the two column random and horizontal periodicity conditions and all differences between these conditions for the other subjects were not significant. The interaction between the bright and dark columns, which results in this threshold elevation is studied further in Experiment 2b.
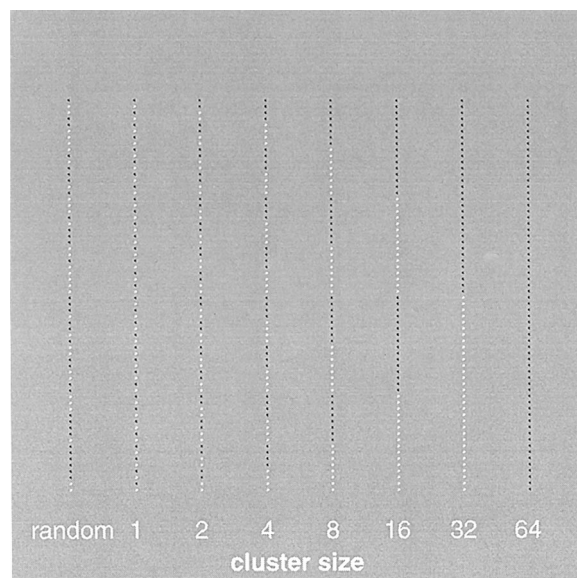

Fig. 4. Experiment 2a (vertical periodicity). Only the 64 segment condition is shown. Note that the random condition depicted is only one of 2^{64} possible contrast polarity distributions. A new random distribution was shown every trial. The background is depicted grey, but during the experiments it consisted of a 256×256 random-pixel-array.

4. Experiment 2

In Experiment 1 we found that within a single column, a local clustering of equal polarity checks improved direction discrimination performance. It seems reasonable to expect that the performance is thus related to the size of these clusters. In Experiment 2a we will examine the influence of the size of equal polarity clusters on direction discrimination thresholds. In Experiment 2b, we elaborate on another finding from Experiment 1. When clusters of opposite polarity, which on their own lead to very low direction discrimination thresholds, are adjacent to one another in the direction of motion, they lead to a decrease in performance. By separating these two columns in Experiment 2b, we seek to define the area over which negative interactions between those opposite contrast polarity clusters occur.

4.1. Vertical periodicity

Only single columns were used, containing checks that were either vertically contiguous (one segment) or separated by two pixels (64 segments). Cluster-sizes were varied between one (alternation) and 64 (all checks dark[2]). The direction discrimination thresholds were compared to those of stimuli with a random distribution of dark and bright. For an example see Fig. 4 (only the 64 segment condition is shown).
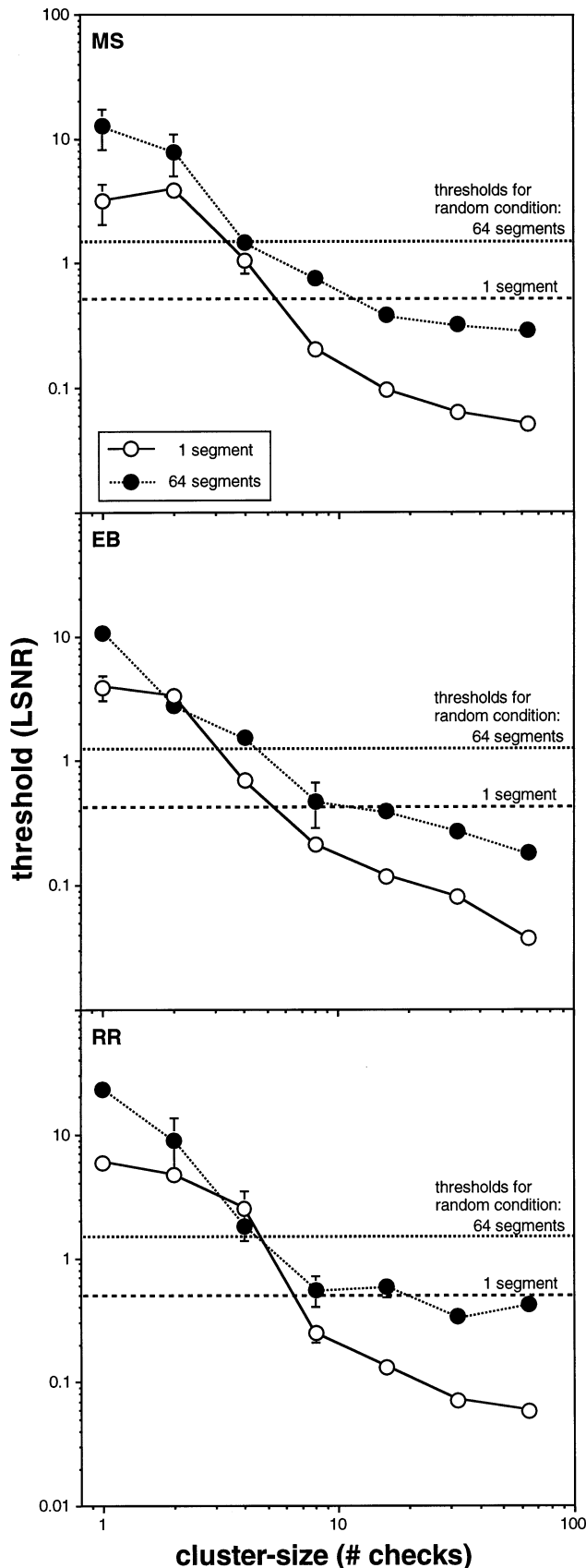
Fig. 5.

4.1.1. Results

Fig. 5 shows a gradual transformation from the vertical periodicity condition (cluster size 1) to the dark only condition (cluster size 64) of Experiment 1, for both one segment (open circles) and 64 segments (filled circles). In between these extremes, the contrast polarities are distributed across the checks in clusters of increasing size (see Fig. 4). The dashed and dotted lines represent the thresholds for the random distribution of contrast polarity, for the one and 64 segments, respectively.

Thresholds for both the one segment and the 64 segments conditions drop as a function of the cluster-size. The thresholds for the 64 segments condition are generally higher than those for the one segment condition, which would be expected from the difference in the number of checks per area in the two conditions. The thresholds for the random polarity distribution lie between those for cluster-sizes of four and eight (one segment condition) or at about the threshold for cluster-size 4 (64 segments condition). This is surprising in two ways: (1) the thresholds for the random distribution relative to those for the clustered conditions, differ for the one segment and the 64 segments conditions and (2) thresholds for the random distribution in both conditions are relatively low, compared to those for the clustered conditions. These results cannot be explained solely on the basis of the probable occurrence of large clusters of equal contrast polarity in the random distribution. As can be seen in Table 1 the probability of a cluster of four checks of equal contrast polarity, occurring in the random distribution is about half the probability of a cluster of the same size occurring in the clustered condition (cluster-size 4). Only about one in two random configurations has an equal polarity cluster of eight checks. Even if one looks at the total number of available clusters across spatial scales one would expect the thresholds for the random distribution to lie between those for cluster-sizes of two and four. An interpretation of these results will be presented in the discussion.

4.2. Horizontal periodicity

In this experiment, the influence of column separation on direction discrimination thresholds is examined.

Fig. 5. The results of Experiment 2a (vertical periodicity) for three subjects. The direction discrimination thresholds (LSNR) as a function of the size of clusters of checks with equal contrast polarity. Error bars show the SEM. Open symbols represent the condition where all checks were vertically adjacent to one another (one segment), closed symbols represent the 64 segment condition (all checks were vertically separated by two pixels from one another). The dotted line represents the threshold for the random 64 segments condition, the dashed line the threshold for the one segment condition with a random distribution of contrast polarity across the checks.

The stimuli consisted of two columns of 64 checks, where the checks were all vertically separated by two pixels. The two columns were horizontally adjacent, or separated by a number of pixels (32 at maximum). The contrast polarity was either distributed randomly across all the checks, or all the checks of one column would be dark while all of the other column would be bright (horizontal periodicity) (see Fig. 6). In the latter condition, the 'dark' cluster would always come first in the direction of motion (i.e. when the stimulus moved to the left, the column containing only dark checks was the left column; when it moved to the right, the right column contained the dark checks).

4.2.1. Results

Fig. 7 shows that the threshold for the random distribution of contrast polarity across the two columns of 64 checks (grey squares), increases gradually when the horizontal distance between the columns increases from one (adjacent) to 32 pixels. This increase can be explained by a decreasing temporal integration efficiency (see results of Experiment 1). An additional
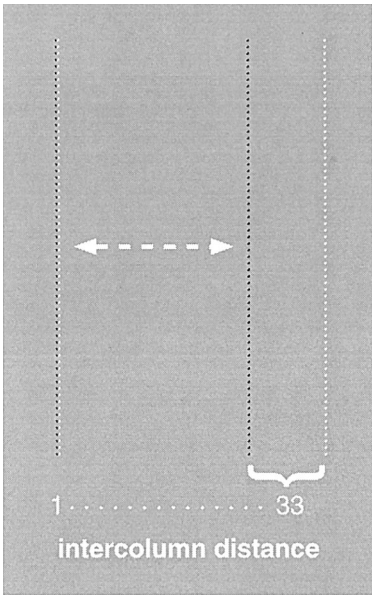

Fig. 6. An example of the stimuli of Experiment 2b (horizontal periodicity). This example is for stimuli moving to the left. If the stimulus moved to the right, the dark column was on the right-hand side. The intercolumn distance could be one (adjacent) to 33 (32 pixels horizontal interval between columns). Only the horizontal periodicity condition is shown. This condition is compared to a condition where the contrast polarity is distributed randomly across the checks of both columns.

factor might be that the movement of the checks starts further and further away from the fixation dot (on both sides). Although the centre of the moving stimulus is still the fixation dot, the check-columns start at a certain distance from the dot. Since the observers know the stimulus starts around the fixation dot, their attention is probably focused on the dot and thus the initial motion of the columns might lie further from their focus of attention (Treisman, 1977).

It is also clear from Fig. 7, that the dark and bright columns (black and white squares), show a sharp decrease in thresholds for the initial increase in inter column distance. The highest sensitivity to these stimuli (lowest thresholds), is found around 5–8 pixels (4.7–7.5 min arc) inter column distance, after which thresholds rise again, in a way which is similar to the threshold increase for the random columns. The lowest threshold is lower than the threshold for a single dark column in Experiment 1, which would be expected from spatial signal summation and temporal integration (see above).

A control condition (two dark only columns) was added later and tested only by observer MS. The thresholds for this condition (black squares) are the lowest for the small intercolumn distances and show a similar gradual increase with intercolumn distance to the random condition and the horizontal periodicity condition beyond five pixels intercolumn distance.

Table 1

Cluster size	Stimulus configuration (see Fig. 3)							
	Random	1	2	4	8	16	32	64
1	64	64	64	64	64	64	64	64
2	31.506	0	32	48	48	60	62	63
3	15.504	0	0	32	48	56	60	62
4	7.630	0	0	16	40	52	58	61
5	3.750	0	0	0	32	48	56	60
6	1.844	0	0	0	24	44	54	59
7	0.906	0	0	0	16	40	52	58
8	0.447	0	0	0	8	36	50	57
16	0.002	0	0	0	0	4	34	49
32	< 0.001	0	0	0	0	0	2	33
64	< 0.001	0	0	0	0	0	0	1
Total	< 126	64	96	160	280	404	492	567

The number of clusters of checks of equal contrast-sign that can be found in random and vertical periodicity configuration per cluster-size (vertical). Horizontal: the stimulus configuration (see Fig. 4 for the appearance of the configurations). Values for the random condition were obtained by averaging 10^6 random stimuli. Total gives the total number of clusters of different sizes.

Fig. 7.

5. Discussion

We have shown that opposite contrast polarities are processed separately in some stage(s) of motion extraction (Schiller, 1982; Sherk & Horton, 1984; Shechter & Hochstein, 1990; Mather, Moulden & O' Halloran, 1991; Wehrhahn & Rapf, 1992; Edwards & Badcock, 1994; Croner & Albright, 1997) but that the ON and OFF systems also interact when extracting global object motion. Furthermore, our results show that the spatial distribution of opposite contrast polarities is a cardinal determinant in detecting an object and its motion.

In Experiment 1 we show that a moving column of exclusively dark checks is much easier to detect than the same-size column, consisting of checks with a random contrast polarity distribution. The same holds for a column of exclusively bright checks (van der Smagt & van de Grind, 1996). This finding appears to contrast with data from Edwards & Badcock (1994). They found in their Experiment 2 that direction discrimination thresholds did not differ between the condition where the signal consisted of only bright dots and the condition where the signal was carried by both contrast polarities. However there are considerable differences in the stimulus paradigm between their study and ours. The LSNR-method differs from their 'spatial'-SNR method, in that our SNR does not contain specific spatial cues (see Appendix 2 of Fredericksen, Verstraten & van de Grind (1993)). Still, in the past, the two methods have yielded results which were qualitatively similar (Todd & Norman, 1995).

Moreover, Croner & Albright (1997), using a similar stimulus to the one used by Edwards & Badcock (1994), found—like we do—lower thresholds for signal dots of one contrast polarity. They attributed this discrepancy to differences in dot contrast. Croner & Albright (1997) used Michelson contrast, which results in dark dots with a smaller luminance difference relative to the background, than bright dots. Edwards & Badcock (1994) used Weber contrast giving both polarities an equal luminance difference relative to the background. In our study, however, the luminance of the checks relative to the (mean luminance of the) background was equal for both polarities like in the Edwards & Badcock (1994) study. Yet our results are more in line with those from Croner & Albright (1997).

Fig. 7. The results of Experiment 2b (horizontal periodicity) for three subjects. The direction discrimination thresholds (LSNR) as a function of the distance between the two columns. Error bars show the SEM. Grey squares represent the random contrast polarity distribution, black and white symbols represent the horizontal periodicity condition where the first column in the direction of motion is always dark, while the second is always bright. A control condition (128 dark dots in the same spatial configuration) was tested only by observer MS. This condition is represented by the black squares.
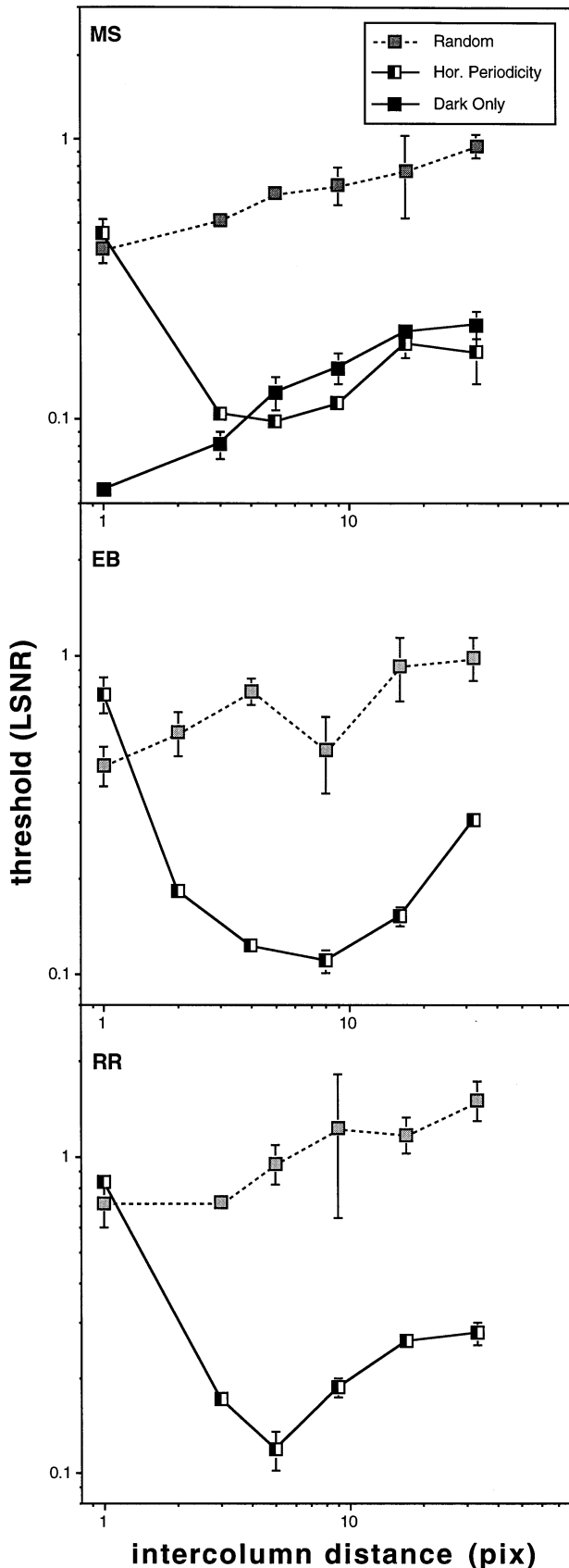
How can the differences between our results and those of Edwards & Badcock (1994) be explained? The size of the stimulus window (12° in their study, to 4° in ours), or speed (6° s^{-1} in their study, to 1.41° s^{-1} in ours) might be significant factors, although pilot studies have shown that our dark and random columns have similar velocity tuning curves. We think the key difference is the difference in individual dot (check) size. Edwards and Badcock used dots of 12 min arc in size, while our checks only subtended 0.94 min arc (on the order of one acuity unit). Van der Smagt and van de Grind (in preparation) show that contrast sign specific integration of our stimulus is confined to about 15 min arc orthogonal to the motion direction, which agrees with the 'co-operative neighbourhood' found by Chang & Julesz (1984). Contrast sign specific integration of this form can hardly occur with the 12 min arc dot size, used by Edwards and Badcock, while it might with the 6 min arc dot size that Croner and Albright used.

An important result of our study is that even when there are as many bright as dark checks in the moving stimulus, their spatial configuration is essential in determining the discriminability of the motion direction. The vertical periodicity condition, where the dark and bright checks are interleaved in our Experiment 1, proves much harder to detect than the random condition. It might be argued that this is merely a matter of spatial scale, since in the vertical periodicity condition, contrast polarity is evenly distributed, so there will never be two moving checks of the same polarity next to one another. The lower spatial frequencies that can thus occur in the random and especially in the dark only condition, could stimulate sensors with large(r) receptive fields. However, Smith, Snowden & Milne (1994), using random dot stimuli, showed that global motion detection did not depend on the presence of low spatial frequencies and must involve integration of local motion signals across space. Furthermore, Brady, Bex & Fredericksen (1997) showed that in stimuli like ours (white noise) information of the high spatial frequencies is more salient and dominates performance in a direction discrimination task.

Experiment 2a (vertical periodicity) also shows that our results cannot be explained by enhanced sensitivity to lower spatial frequencies. Compared to the moving columns where contrast polarity was distributed in clusters of variable size, subjects performed remarkably well in the random contrast polarity distribution condition. As pointed out in the results section, this low threshold is not a result of large clusters of same polarity checks (thus of low spatial frequencies) occurring in the random condition. An explanation that seems plausible is that the ON and OFF systems show inhibitory interactions that can enhance the visual segregation of moving objects (like dark and bright edges). Compared to the random condition, the observer's sensitivity to the stimuli with larger clusters is relatively low because the mutual inhibition of the ON and OFF systems is relatively strong in the vicinity of transitions between positive and negative polarity clusters.

In our Experiment 2b (horizontal periodicity) we specifically looked at interactions between ON and OFF pools of motion sensors. Alone, the moving columns of opposite contrast polarity prove to be much easier to detect than a column with a random polarity distribution. When the columns of opposite contrast are moving adjacent to one another, thresholds are similar to two adjacent, moving columns with a random polarity distribution. Increasing the distance between the two columns results in a steep threshold decrease for the opposite contrast columns up to a distance of about 5–8 min arc, after which thresholds rise again with a further increase in intercolumn distance. This 5–8 min arc distance might well represent the region (along the motion axis) in which inhibitory interactions between the ON and OFF systems occur. Of course, the data from Experiment 2b (horizontal periodicity) give no direct insight in whether this inhibition occurs before or after contrast-sign-specific pooling of local motion signals, but in the light of the above it would be more likely to occur after the pooling stage.

We propose an explanation of our findings in terms of integration within, and interaction between the ON and the OFF motion system, based on the following premises: (1) Information from local motion sensors, that are tuned to either positive or negative contrast polarity only, is pooled separately within regions of limited size. (2) These separate ON and OFF pools engage in mutually inhibitory interactions.

The response of such an organisation to our stimuli would vary with cluster-size. Small cluster-sizes would result in equally active ON and OFF pools, which will inhibit each others output. Mutual inhibition will be most effective if the ON and OFF pools in a certain region respond with equal strength to the stimulus. With increasing cluster-size, mutual inhibition will occur only around the transitions between the clusters, thus leaving an increasing area where inhibition is less strong, or even absent. In certain areas, ON pools will have a strong response, while that of OFF pools is almost zero, and vice versa. The condition with a random contrast polarity distribution results in local imbalances in the strength of the two polarity-specific motion pools. In some region of the stimulus the ON system will be excited more, in other regions the OFF system. This imbalance will result in a less effective inhibition in those regions, and thus in relatively low thresholds for these stimuli. Separating the regions of opposite contrast polarity altogether, like in Experiment 2b (horizontal periodicity), will of course reduce the possibility of mutual inhibition, and will thus result in a better performance by the observers.

An alternative explanation in terms of emerging form cues (one or two vertical lines in our experiments) that facilitate the motion detection of an object, has been described by Stoner & Albright (1993). They propose that form cues, such as luminance, colour, temporal texture and spatial texture differences between object and background, can all lead to an enhanced perception of object motion, relative to the case where motion is the only cue. Neurophysiological support for this conception comes from a study by Albright (1992) who recorded responses to moving objects (defined by different form cues) from directionally selective MT cells in the macaque monkey. At least one psychophysical study supports this notion as well. Mather & Anstis (1995) showed that in an ambiguous apparent motion stimulus, of two squares moving in opposite directions, the square with the larger textural difference to the surround determines the directional judgement by the subjects.

If we apply this notion to our data, however, we would expect our conditions with very small clusters to be different from the background, just like our conditions with larger clusters, since the background has a broad spatial frequency spectrum. Hence, it follows that the thresholds for our small cluster stimuli should also be lower than those for the random distribution condition (in which case the spatial properties of the texture are equal to those of the background), or even that cluster-size would have no influence at all. Yet, our data clearly show that the motion of small clusters is far more difficult to detect than the motion of large clusters or a random polarity distribution.

Therefore, the particular spatial organisation of dark and bright checks appears to be the significant factor affecting the salience of the perceived motion. The specific structure of our stimuli distinguishes them from the sparse and randomly located signal dots, used by most others. As Lorenceau (1996) showed, dots positioned in such a way that they resemble (part of) an object's contour, result in an improved direction discriminability of the moving pattern. Our conditions with large clusters will probably give rise to an improved contour-from-motion perception, which in turn improves direction discrimination performance. The proposed contrast sign specific integration of local motion signals and the mutual inhibition of pools of motion sensors tuned to opposite contrast polarity, might thus induce a 'pre-attentive popout' (Treisman & Gelade, 1980; Bergen & Julesz, 1983), from which the global motion system benefits (Croner & Albright, 1997).

6. Conclusions

We tested two related questions in this paper: (1) does the ON versus OFF distinction remain at least partly intact during the integration of local motion signals? And (2) are there at the same time interactions between the ON and OFF system at some stage in this integration process, in order to allow for object segregation? Our data suggest that both questions can be answered affirmatively and show that the interactions between the two systems are highly correlated with the spatial structure of the stimulus. From an ecological point of view, this would make sense, since for the identification of an object and its direction and velocity it is essential to identify which structures belong to the object and which do not. In nature most moving objects do not have a random distribution of contrast polarities along their edges.

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