



Spatial structure, contrast polarity and motion integration

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Received 2 January 1999; received in revised form 19 October 1999

Abstract

It has been shown that in the initial stages of motion processing, the ON and OFF pathways stay more or less separated. There is evidence that this distinction between motion signals from opposite contrast polarities remains at least partly intact in the integration stage of local motion information. At the same time, interactions between the two systems are also apparent. Here we constructed stimuli that contained a constant number of moving checks. The checks were either assigned only one contrast polarity, or contrast polarity was distributed across the checks either randomly or evenly. We investigated how the spatial configuration of the moving stimulus affected direction discrimination thresholds for the different polarity distributions. Our results provide new evidence for contrast-sign-specific integration of local motion signals within areas of limited size, and inhibitory interactions between these separate ON and OFF motion sensor pools. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Motion integration; Motion segregation; Contrast polarity; ON detector; OFF detector

1. Introduction

The human visual system is capable of separating a moving object from its surroundings, even when this object is well camouflaged while stationary. The relative motion of the object is a powerful segregation cue. Often, however, objects are not visible as a whole because they are partially occluded by other objects, or there is an abundance of local irrelevant motion signals which might mask the object's motion. Hence, the visual system must be able to combine spatially (as well as temporally) segregated motion signals and at the same time be able to distinguish them from other interfering local motion signals. One way to do so, is to combine the motion cue with other segmentation cues.

One of the cues our visual system can use to determine whether two separated motion signals originate from the same object, is equal contrast polarity of the two signals. It has been shown, both physiologically (Schiller, 1982; Sherk & Horton, 1984; Schiller, Sandell & Maunsell, 1986) and psychophysically (Shechter &

Hochstein, 1990; Mather, Moulden & O'Halloran, 1991; Wehrhahn & Rapf, 1992; Edwards & Badcock, 1994) that opposite contrast polarities are processed separately in the initial stages of motion processing. The question whether equal contrast polarity of separate motion signals enhances global motion detection, was studied by Edwards and Badcock (1994) and Croner and Albright (1997) with contrasting results. Although they used a similar experimental paradigm (a variant of the one used by Newsome & Paré, 1988), Croner and Albright found that direction discrimination in moving random dot stimuli improved when they changed the contrast polarity of the dots carrying the signal to be opposite to that of the noise dots, whereas Edwards and Badcock did not find such an improvement.

In a previous paper, van der Smagt and van de Grind (1999) also investigated the role of contrast polarity in combining local motion signals. They were interested in object motion and used relatively small moving objects which resembled partially occluded lines or edges. These moving objects contained a constant number of checks of both positive and negative contrast polarity. Van der Smagt and van de Grind showed that the way contrast polarity was distributed across the (aligned) checks largely determined direction discrimination per-

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formance. They proposed a mechanism in which information from local motion sensors, tuned to positive or negative contrast polarity only, is pooled separately within regions of limited size after which these separate ON and OFF pools engage in mutually inhibitory interactions.

An important characteristic of their stimuli was that they resembled an actual form.¹ The spatial organisation of the coherently moving checks remained equal, while the distribution of contrast polarities across these checks was varied. However, contrast polarity distribution across the checks and their spatial arrangement are probably two factors that interact when object motion is extracted. If information from local motion sensors is to be pooled within regions of limited size, the amount of information (i.e. the number of checks that move

within this region) is clearly a key factor in detecting the object's motion. In the present paper, we will thus focus on the interaction between contrast polarity distribution and the spatial configuration of the checks.

Like in the previous study, the basis for our stimuli was a vertical column of checks with one of four contrast polarity distributions: *vertical periodicity*, where the contrast polarities are vertically interleaved; *random*, where the contrast polarities are randomly distributed across the checks; and a *dark only* and *bright only* condition, where all the checks are dark and bright, respectively (see Fig. 1 for an example of the polarity distribution conditions and their respective direction discrimination thresholds as reported in van der Smagt & van de Grind, 1999). In two experiments we will gradually distort the line-like appearance of the stimulus, either in the vertical (orthogonal to the direction of motion) or horizontal direction (along the motion axis). We will show that this distortion causes a decrease in sensitivity to the motion stimuli in most conditions. At the same time, our data show that there are indeed strong interactions between the distribution of contrast polarity across the checks, and the spatial distribution of the checks across the stimulus window. The present results add to previous evidence for contrast-sign-specific integration of local motion signals and provide the spatial boundaries within which such a mechanism might act.

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, 1 pixel subtending 0.55 mm. At a viewing distance of 2 m, this resulted in a display area of 4 deg arc and a pixel size of 0.94 min arc.

The stationary background consisted of a 256×256 random-pixel-array (RPA). Using an RPA rather than a plain (grey) background ensured that the actual stimuli (even the *dark only* and *bright only* conditions, which differ in mean luminance from the others and the background RPA) were well camouflaged when stationary. We tested this in a control experiment, where the stimuli were randomly placed either right or left of the fixation dot, but did not move. Observers performed at chance level in a right–left position discrimination task, for all contrast polarity distributions.

All stimuli moved coherently (velocity = $1.41^\circ/\text{s}$) either to the left or to the right, starting from the centre of the screen. They moved in front of the background,

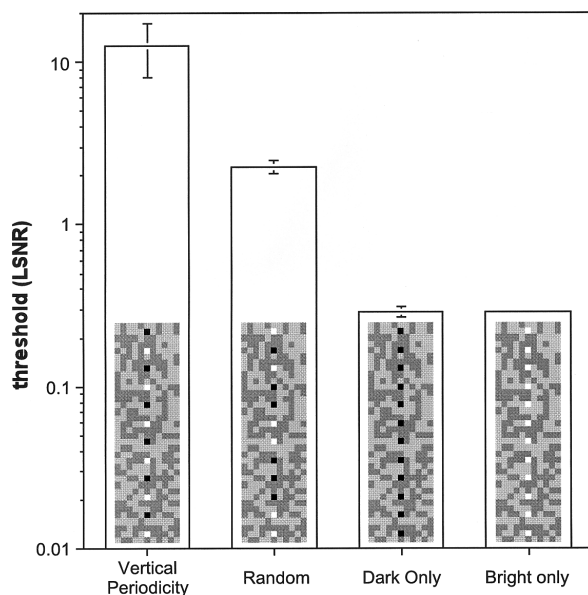


Fig. 1. Example of the basic stimuli and their thresholds. On the abscissa are four contrast polarity distribution conditions: *vertical periodicity*; *random*; *dark only*; and *bright only*. In the *vertical periodicity* condition, the contrast polarity is vertically interleaved. In the *random* condition the contrast polarity is distributed randomly across the stimulus checks, whereas the *dark only* and *bright only* conditions contain only dark or bright checks respectively. The background is a binary random-pixel-array (RPA). For illustration purposes, the background pixels are made grey, while under experimental conditions the dark and bright pixels of the background had the same luminance as the moving dark and bright checks. Only a horizontal slice of the moving stimuli is depicted. The direction discrimination thresholds are for horizontally moving columns of 64 checks, each separated vertically from its nearest neighbours by 2 pixels. High thresholds mean low sensitivity. Error bars depict the SEM. Data (pooled) from van der Smagt and van de Grind (1996) for the *bright only* condition and van der Smagt and van de Grind (1999) for the other conditions.

¹ Note, that in most cases the form of the stimulus (a vertical line or edge) was not perceived as a result of 'static' form cues. The stimuli were well camouflaged when stationary.

thus sequentially occluding pixels of the background random-pixel-array. The moving stimuli consisted of either 16 or 64 1×1 pixel ‘checks’. Each check was identical in shape and luminance to either the dark or bright background pixels. We use the term checks, to distinguish them from these background pixels and the multi-pixel dots used in other studies. The position of each individual check with regard to neighbouring checks, as well as its contrast polarity (dark or bright) could be manipulated.

An uncorrelated dynamic ‘noise’ RPA was superimposed on both the background and the stimuli, meaning that the luminance of each pixel/check was increased or decreased by a noise value (depending on the polarity of the superimposed noise pixel). 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. An LSNR-increase means that the contrast of the noise pattern is decreased while that of the stimulus (and background) pattern is increased by the same amount. As a consequence, the stimulus motion will be perceived more easily, while an LSNR-decrease will have the inverse effect. One of the advantages of the LSNR method in this study over other noise paradigms, such as that used by Newsome and Paré (1988), is that the noise does not contain any spatial information (such as local dot density differences) within and between frames, since each pixel of both the background and stimulus is affected equally by the noise RPA each frame. For a more detailed description of the LSNR method, see van de Grind, Koenderink and van Doorn (1987), Fredericksen, Verstraten and van de Grind (1993) or van der Smagt and van de Grind (1999).

2.2. Procedure

Directional motion detection thresholds were measured in a two-alternative forced-choice (2AFC) horizontal (left–right) motion discrimination task. The thresholds were determined using a staircase procedure that pursued the 79% correct level; three correct direction-discriminations in a row 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 turning-points, 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, the 95% confidence interval of the calculated average had to be within $\pm 5\%$ of this value. In order to decrease the required 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, the three threshold-values were averaged and the SEM was calculated.

The experiments were performed in a darkened room, where the only light came from the monitor. Observers used a chin and head rest and viewed the stimuli binocularly. They were instructed to fixate on a black dot (diameter 3.76 min arc) in the centre of the screen and to keep 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. Observers were two of the authors and two naive observers, who were unaware of the aim of this study. All had normal or corrected to normal vision.

3. Experiment 1

In this experiment, the line-like appearance of the stimulus was distorted by ‘stretching’ the vertical line, but keeping the number of signal checks the same. We started with a basic configuration of 16 vertically aligned checks. The vertical interval between two nearest neighbour checks varied from 2 to 16 pixels. The four above mentioned contrast polarity distributions were used: *dark only* and *bright only*, where all the checks are either dark or bright; *random*, where contrast polarity is randomly distributed across the checks;

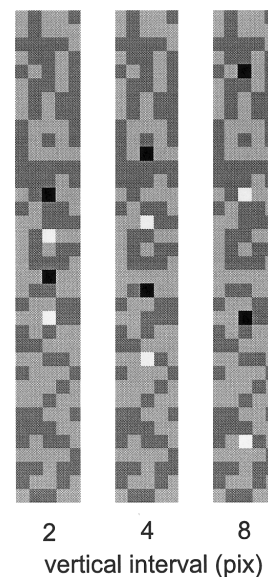


Fig. 2. Example of the stimuli used in Experiment 1. Depicted are four of the 16 checks of the *vertical periodicity* condition. The pixels of the background RPA are made grey for illustration purposes only. Three vertical separation conditions are shown: 2, 4 and 8 pixels. The 16 checks in the column moved coherently left or rightward.

and *vertical periodicity*, where contrast polarity is interleaved between the nearest neighbour checks (see Fig. 2 for an example of this condition). In the *random* condition, the contrast polarity was redistributed randomly across the checks each trial. Only three of the observers performed the experiment for the *bright only* condition.

Based on the previous results one would expect the different conditions to yield different thresholds at the small distances between nearest neighbour checks (since the 2 pixel interval condition is comparable to the stimuli used before as shown in Fig. 1) and thresholds are expected to rise as the interval between nearest neighbour checks increases. Eventually the curves for the different polarity distribution conditions are expected to converge, if one assumes the integration of the local motion signals is contrast-sign-specific and confined to a limited area. This point of convergence might thus indicate the size (orthogonal to the motion axis) of this integration area.

3.1. Results

From Fig. 3, it is clear that in the initial condition (2 pixel vertical interval between nearest neighbour checks) the pattern of results for our 16 vertically aligned checks is similar to that obtained with 64 checks by van der Smagt and van de Grind (1999) as given in Fig. 1, although thresholds are generally higher due to the decreased signal strength in the stimulus (16 vs. 64 signal checks). The *dark only* and *bright only* conditions yield similar low thresholds. The threshold for the *random* condition is significantly higher, while the *vertical periodicity* condition yields the highest threshold. All observers reported considerable difficulty with the latter condition, even at relatively high LSNR values. Observer EB reported not perceiving any coherent motion in most of the trials, which corresponds with the high thresholds (LSNR > 100). LSNR values > 100 mean that very little noise is added to the

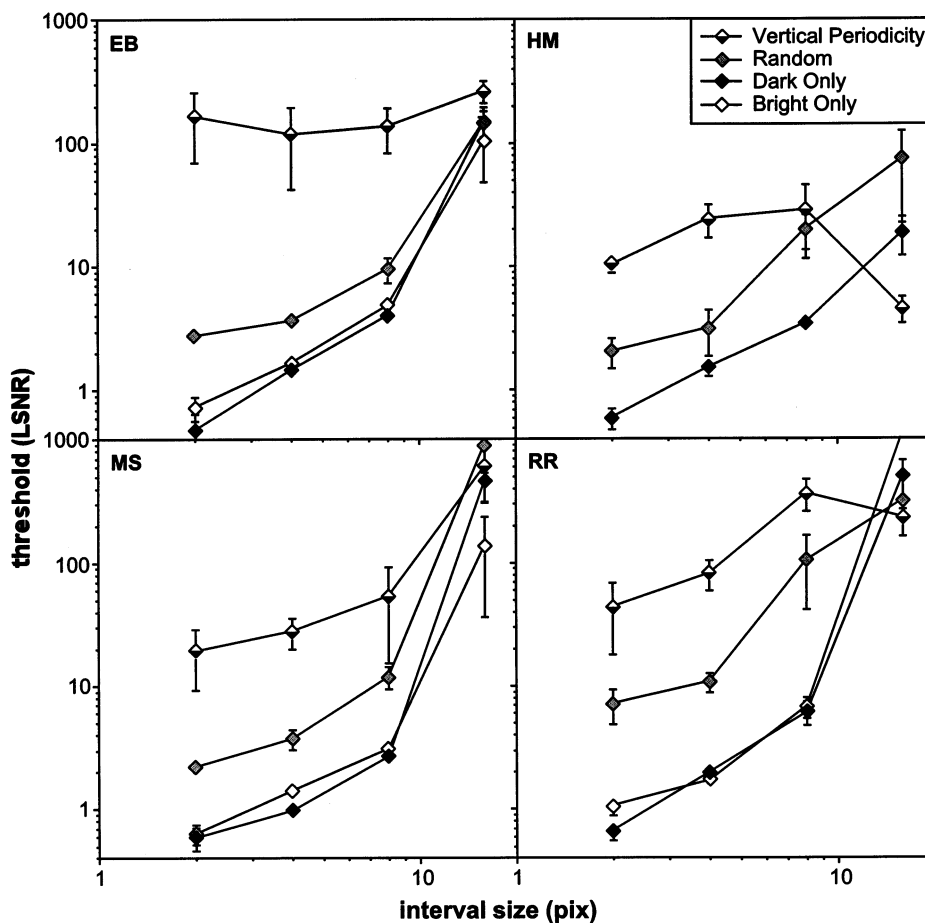


Fig. 3. Results of Experiment 1 for four observers. Direction discrimination thresholds as a function of vertical interval between the nearest neighbour checks. Black diamonds and white diamonds represent the *dark only* and *bright only* conditions, grey diamonds represent the *random* condition, while the black-and-white diamonds represent the *vertical periodicity* condition. The *dark only* and *bright only* conditions yield similar low thresholds, the *random* condition yields higher thresholds, while the *vertical periodicity* condition results in the highest thresholds (for observer EB, very difficult to perceive, even at the smallest interval between nearest neighbour checks). Thresholds increase gradually with increasing separation between the checks. Between a separation of 8 and 16 pixels thresholds show a steeper rise and the stimuli become hardly visible, even without adding noise. When the LSNR is 100 or higher, hardly any noise is apparent in the stimulus.

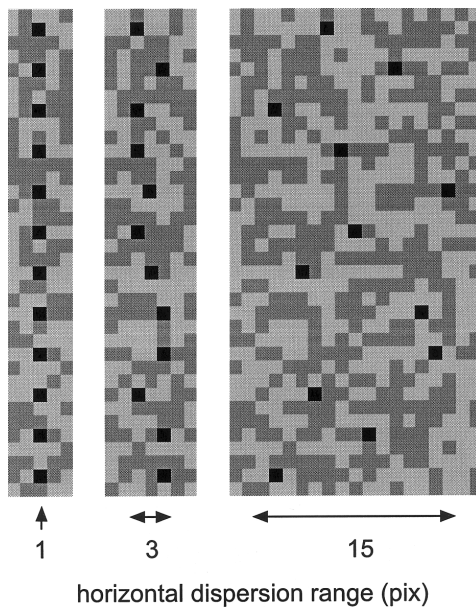


Fig. 4. Example of the stimuli used in Experiment 2. Twelve of the 64 checks of the *dark only* condition are depicted, when the horizontal range within which the checks were dispersed is either 1, 3 or 15 pixels. This means that the actual (horizontal) position of the checks is randomised over 1, 3 or 15 possible positions. Under experimental conditions the bright and dark background pixels (here depicted in grey) equalled the luminance of the bright and dark stimulus checks.

moving stimulus and background. Thresholds become increasingly unreliable above this value.

For increasing vertical intervals between the moving checks, direction discrimination thresholds increase. Between an interval size of 8 and 16 pixels, a sharp threshold increase can be observed for most conditions. Direction discrimination became almost impossible for all conditions, and all observers reported very poor visibility of the moving stimuli with a 16 pixel interval. All thresholds for this interval, with one exception, have an LSNR-value > 100 . The one exception (HM, right most data point) is probably an artefact, since she verbally reported that hardly any motion was perceived for this condition. Many of the staircases (often with higher averages) for this condition had to be discarded for HM, due to lack of convergence.

The results of Fig. 3 not only mean that integration of the motion signals orthogonal to the direction of motion in this stimulus can only occur within an orthogonal area of less than 16 pixels. They also imply that without this integration (as in the 16 pixel interval condition), no moving object (nor a moving single check) can be detected at all. Although an interesting result in itself (see Section 5), this also limits the comparison of the curves for the different polarity distribution conditions. The curves do converge, but only at the point where all conditions are very hard to perceive. In Experiment 2 we thus used a 64 pixel

stimulus (which in Experiment 1 was not possible) to examine this convergence more closely.

4. Experiment 2

In Experiment 2 we distorted the line-like appearance of the stimulus by randomly shifting each check horizontally. This horizontal shift allows us to examine two related issues: how do the contrast polarity distribution and the form of the stimulus (or the position of the moving checks relative to each other) interact; and can we specify the area along the motion axis over which integration of local motion signals occurs?

The basis of our stimulus was the column of 64 vertically aligned checks, with three polarity distribution conditions: *dark only*; *random*; and *vertical periodicity* (see Fig. 1; because thresholds for the *bright only* condition were similar to those of the *dark only* condition the former was not tested). Each check was vertically separated from its nearest neighbour, by a 2 pixel interval through which the background RPA is seen. Within a predefined horizontal dispersion range, each check was assigned a random shift, left or right from its original position (see Fig. 4). The dispersion range was varied between 1 (the original width of the vertical column of checks) and 63 (a stimulus that looks more like a cloud of dots). The resulting stimuli moved from the centre of the display either left- or rightward. Three observers performed this experiment.

Two predictions are initially clear for this experiment: increasing the dispersion range leads to an increase in thresholds if the integration of local motion signals only occur over a limited area (along the motion axis). In addition one expects this increase to be larger for the *dark only* condition, if the integration mechanism is contrast-sign specific, while the *vertical periodicity* condition is expected to show the smallest, or even no threshold increase with increasing dispersion area.

4.1. Results

Fig. 5 shows the results for each separate observer as well as the data pooled across observers (right-bottom panel). Small horizontal dispersion ranges yield very different thresholds for the three contrast distribution conditions. As in Fig. 1, thresholds are initially the highest for the *vertical periodicity* condition, intermediate for the *random* condition and lowest for the *dark only* condition. When the horizontal range over which the individual checks are dispersed is increased, thresholds rise for the *random* and the *dark only* condition, the latter of which shows the steeper increase. Interestingly, the *vertical periodicity* condition first shows a threshold decrease, until at a dispersion range of about 15–31 pixels thresholds start to rise again.

Statistical analysis of the pooled data (one-way ANOVA, Scheffé post-hoc test with significance level of 0.05) shows that for a dispersion range of up to 7 pixels, the thresholds for the three polarity distribution conditions differ significantly. For a dispersion range of 15 pixels, the *dark only* condition is still significantly lower than the other two conditions, while for larger ranges thresholds for the three conditions are not significantly different anymore, and show a similar threshold increase with increasing dispersion range.

5. Discussion

The aim of the presented experiments was to investigate the interaction between contrast-sign specific integration of local motion signals and their spatial configuration. The experiments confirm earlier results that show that opposite contrast polarities are proc-

essed separately in the early (local) stages of motion detection (Schiller, 1982; Sherk & Horton, 1984; Schiller et al., 1986; Shechter & Hochstein, 1990; Mather et al., 1991; Wehrhahn & Rapf, 1992; Edwards & Badcock, 1994; van der Smagt & van de Grind, 1999), since our *bright only* and *dark only* conditions yield much lower thresholds than the conditions in which both contrast polarities were present. In addition, the differences between the *random* and *vertical periodicity* conditions show that interactions between motion signals from opposite contrast polarities are apparent as well. We will elaborate on this below.

5.1. Separate processing of positive and negative contrast polarity

In Experiment 1 we varied the distance between moving checks that were vertically aligned for four different contrast polarity distributions across the

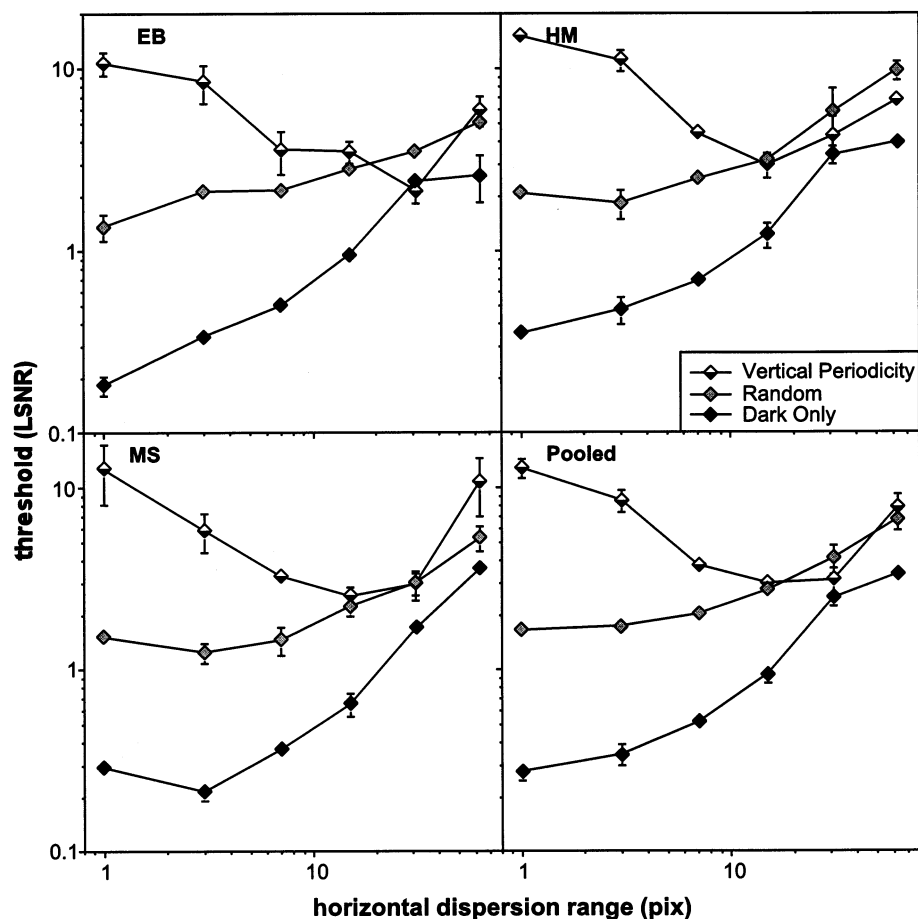


Fig. 5. Results of Experiment 2 for three observers. The data, as pooled over all observers is shown as well (right-bottom panel). The curves represent the direction discrimination thresholds as a function of the size of the horizontal range within which the checks were dispersed. Black diamonds represent the *dark only* condition, grey diamonds represent the *random* condition, while the black-and-white diamonds represent the *vertical periodicity* condition. Thresholds for the *dark only* and (to a lesser extent) the *random* condition, increase with increasing dispersion range. For the *vertical periodicity* condition, however thresholds drop initially until a dispersion range of about 15 pixels after which they also increase with increasing dispersion range. For dispersion ranges of 31 and 63 pixels, no significant difference between the contrast polarity distributions is apparent.

checks. Although the *bright only* and *dark only* conditions yielded similar thresholds, the conditions that contained both contrast polarities proved more difficult for the observers. Especially the *vertical periodicity* yielded very high thresholds. Thresholds for all conditions increased with increasing separation between nearest neighbour checks.

The fact that our *random* and especially the *vertical periodicity* condition yielded much higher thresholds than the equal polarity conditions, leads us to suggest that motion information of positive and negative contrast polarity is processed separately. On first sight, the threshold differences between the polarity distribution conditions in Experiment 1 might seem to be explicable by spatial frequency differences alone. The *dark only* and *bright only* conditions contain clusters of checks with the same contrast polarity and motion sensors tuned to lower spatial frequencies will be able to detect those. In the *random* condition, there are still clusters of equal polarity checks, which might explain the difference between its threshold and that for the *vertical periodicity* condition. However, there are a number of counter-arguments to this view. First of all, it seems unlikely that motion sensors with large receptive fields could signal the motion at nearest neighbour check separations of, say 8 pixels, since this would imply a very high contrast sensitivity even when no noise is added to the stimulus and background. Yet, the differences between the conditions are still very much apparent for this separation. Moreover, Brady, Bex and Fredericksen (1997) showed that in moving whole-field white noise stimuli (comparable at least to our *random* condition) the information of the high spatial frequencies is more salient, and dominates performance in a direction discrimination task. Smith, Snowden and Milne (1994), using random dot stimuli, showed that global motion detection did not depend on the presence of low spatial frequencies, but must involve integration of local motion signals over space. Finally van der Smagt and van de Grind (1999) showed that thresholds for check-columns similar to those used in the present experiments, with *random* polarity distribution are in fact *lower* than might be expected from the appearance of larger equal-polarity clusters in this condition, and can be explained by the mechanism described below.

5.2. Interaction between motion signals of opposite polarity

Van der Smagt and van de Grind (1999) proposed a mechanism in which information from local motion sensors, tuned to either positive or negative contrast polarity only, is pooled separately within regions of limited size. These separate ON and OFF pools then engage in mutually inhibitory interactions. In Experiment 1 we have roughly established the limit of this

contrast-sign-specific pooling, orthogonal to the direction of motion. Between a separation of 8 and 16 pixels (7.5 and 15 min arc) direction discrimination becomes virtually impossible for all conditions, indicating that integration, orthogonal to the direction of motion is only effective within this (15 min arc) area. Apparently, information from at least two moving (equal polarity) checks must be available within this area, in order for our visual system to be able to perform the direction discrimination task. Interestingly, up to that separation, the thresholds for the different polarity conditions stay very different and thus the area over which inhibitory interactions between pools of local, opposite contrast sign motion sensors occurs, seems to be of the same size or possibly larger. If one compares the equal polarity, 8 pixel interval stimuli, with the *vertical periodicity*, 2 pixel interval stimulus, thresholds are still much lower for the equal polarity stimuli (Fig. 3). Yet the distance between equal polarity checks is less in the latter condition.

In Experiment 2, we kept the vertical separation of the 64 checks constant at two pixels while varying the horizontal dispersion range within which the check positions were randomised. Increasing this area leads to an increase in thresholds for the *dark only* condition and (to a lesser extent) the *random* condition. This seems logical, since fewer and fewer equal polarity checks move in the limited area, within which local motion signals are integrated. In contrast, thresholds for the *vertical periodicity* condition initially decrease, until at a dispersion range of between 15 and 31 pixels they are similar to those of the other conditions. For larger dispersion ranges the thresholds increase again. We think this threshold decrease for the *vertical periodicity* condition reflects a decrease in inhibition between the ON and OFF motion sensor pools. Since the position of the individual checks is randomised within the dispersion range, imbalances in contrast polarity distribution will occur. Because the strength of the mutual inhibition decreases, due to this imbalance, this will favour direction discrimination (van der Smagt & van de Grind, 1999). When mutually inhibitory ON and OFF motion sensor pools covering the same retinal location are equal in strength (as is the case when the polarity distribution is balanced across the stimulus, e.g. in the basic *vertical periodicity* condition), the inhibition will be strong. If there is an imbalance in the polarity distribution, then at one retinal location only the OFF pool will give a strong signal (and inhibit the output of the ON pool), while the inverse is true at another retinal location. The overall motion signal is thus stronger in this case, hence the lower threshold for the *vertical periodicity* condition.

It seems logical to assume that the same concept of a decrease in inhibition should hold for the *vertical periodicity* condition in Experiment 1 as well. However,

increasing the vertical interval between nearest neighbour checks does also decrease the possibility of contrast-sign-specific motion integration in these stimuli, while this is not necessarily true for the stimuli in Experiment 2, due to the random nature of that stimulus. In Experiment 1, the contrast polarity distribution stays balanced, as opposed to the distribution in Experiment 2. It is this imbalance which causes the decrease in inhibition (see above).

5.3. Limits to contrast-sign-specific motion integration and inhibition

The size of the integration area orthogonal to the motion direction (Experiment 1), is in agreement with a study by Chang and Julesz (1984), who found a ‘cooperative neighbourhood’ of about 15 min arc, orthogonal to the direction of motion, irrespective of viewing distance. They used two-frame random dot cinematograms, of which stripes of variable width contained either movement or noise. Nawrot and Sekuler (1990) found such an area about three times larger. However, their stimuli differed substantially in dot density (only 22 dots/deg²). They attributed the difference in results to the number of mismatches (or false correlations) that can occur in dense random dot stimuli. Although our moving stimulus consisted of rather sparse aligned dots, our background was not plain, but contained pixels of the same size and luminance as the moving checks. Here too a large number of false correlations are possible, even without added noise. However, there is also a different explanation. When sparse dots on a plain background are used, motion sensors with larger receptive fields (i.e. much larger than the size of the dot) can respond to the moving (high contrast) dots. This means that elementary motion sensors tuned to either high or low spatial frequencies can respond, whereas in our case (and also in the study by Chang and Julesz) mostly motion sensors tuned to high(er) spatial frequencies will respond (see also Brady et al., 1997). Our moving checks, when separated by 16 pixels (15 min arc) are well visible when presented on a plain background with mean luminance, while they were virtually impossible to detect with our RPA background.

At a dispersion range of 31 pixels (about 29 min arc) in Experiment 2 the mean distance between nearest neighbour checks is just under 14 min arc (which is not necessarily a horizontal distance). Note that this is a mean value, and smaller distances do occur. For this stimulus all moving stimuli were still well visible, when no noise was added. It would be interesting to see what happens when the minimum distance between nearest neighbour checks is 15 min arc or more. Are the stimuli then hardly visible, like in the case of Experiment 1? To test this, however, we would need the dispersion range

to be increased to such an extent that other parameters, like presentation duration or speed, would have to be changed considerably also for the stimulus to be visible during the trials. Since at a dispersion range of 31 pixels all conditions yield the same threshold, one could say that the 14 min arc distance is the limit within which inhibition of ON and OFF pools can occur. However, smaller distances between the pixels do occur, and van der Smagt and van de Grind (1999) showed that the area in the direction of motion, within which this inhibition occurs, is presumably smaller (about 8 min arc).

5.4. The form of the stimulus

We have discussed the form of the stimuli and their respective direction discrimination thresholds in the light of contrast-sign-specific motion integration. When in our second experiment the form of the moving stimulus changed from a vertical column to some cloud-like form, it changed gradually into a stimulus which is more like the ones used by others (e.g. Edwards & Badcock, 1994; Croner & Albright, 1997), although the moving checks still covered less than 20% of the stimulus area.

Lorenceau (1996) also used aligned columns (and rows) of dots, and compared those with randomly positioned dots. His paradigm, however, was very different from ours. He positioned dots either on the outline of a square, or randomly within this square. He moved the rows and columns in such a way, that a rotating square could be perceived. In the random position condition he had 50% of the dots move as the rows, and the other 50% move as the columns. Lorenceau used bright dots on a darker background and thus his data are comparable to our *bright only* (and also with our *dark only*) condition. He found that he had to add more noise to the outline configuration than to the random position configuration, in order to induce the percept of a rotating square. The motion information of the ‘components’ (i.e. rows and columns) in the outline configuration thus was much more salient. These data are in accordance with our increase in threshold for the *dark only* stimuli when the horizontal area over which the pixels can be dispersed is increased. It would be interesting to see whether changing the contrast polarity distribution in Lorenceau’s experiments would yield effects similar to ours.

Our results are compatible with a number of studies that show that small distances between motion signals in space-time increase the likelihood that they stem from the same object (Snowden & Braddick, 1990; Stoner & Albright, 1993; Fredericksen, Verstraten & van de Grind, 1994; Ben-Av & Shiffrar, 1995; Shiffrar

& Lorenceau, 1996), as does a spatial arrangement that resembles a form or an edge (e.g. Koffka, 1935; Kovacs, 1996). That similar colour or contrast polarity can bind local motion signals has also been shown by Croner and Albright (1997). To our knowledge not many researchers have investigated the interaction between contrast polarity, motion and form. Shipley and Kellman (1994, 1997) investigated these interactions, but from a different perspective. They sought to find the mechanism that underlies the formation of boundaries by information that is fragmentary in space as well as time. They found that shapes could be identified as a result of local motion signals by a mechanism they called edge orientation from motion, and concluded that in their experiments (like in ours) motion processing precedes form processing. Interestingly performance in the shape identification task was better in the case when the local motion signals came from dots with only a single contrast polarity. When the motion signals originated from both contrast polarities (like in our *random* or *vertical periodicity* conditions) observers performed worse in this task.

Acknowledgements

We thank Dr Richard van Wezel for his valuable comments on an earlier draft of this manuscript. MS was supported by the Council of Earth and Life Sciences (ALW) of the Netherlands Organization for Scientific Research (NWO).

References

- Ben-Av, M. B., & Shiffrar, M. (1995). Disambiguating velocity estimates across image space. *Vision Research*, 35, 2889–2895.
- Brady, N., Bex, P. J., & Fredericksen, R. E. (1997). Independent coding across spatial scales in moving fractal images. *Vision Research*, 37, 1873–1883.
- Chang, J. J., & Julesz, B. (1984). Cooperative phenomena in apparent movement perception of random-dot cinematograms. *Vision Research*, 24, 1781–1788.
- Croner, L. J., & Albright, T. D. (1997). Image segmentation enhances discrimination of motion in visual noise. *Vision Research*, 37, 1415–1427.
- Edwards, M., & Badcock, D. R. (1994). Global motion perception: Interaction of the ON and OFF pathways. *Vision Research*, 34, 2849–2858.
- Fredericksen, R. E., Verstraten, F. A. J., & van de Grind, W. A. (1993). Spatio-temporal characteristics of human motion perception. *Vision Research*, 33, 1192–1205.
- Fredericksen, R. E., Verstraten, F. A. J., & van de Grind, W. A. (1994). Spatial summation and its interaction with the temporal integration mechanism in human motion perception. *Vision Research*, 34, 3171–3188.
- Koffka, K. (1935). *Principles of Gestalt psychology*. New York: Harcourt, Brace & Company.
- Kovacs, I. (1996). Gestalten of today: early processing of visual contours and surfaces. *Behavioural Brain Research*, 82, 1–11.
- Lorenceau, J. (1996). Motion integration with dot patterns-effects of motion noise and structural information. *Vision Research*, 36, 3415–3427.
- Mather, G., Moulden, B., & O'Halloran, A. (1991). Polarity specific adaptation to motion in the human visual system. *Vision Research*, 31, 1013–1019.
- Nawrot, M., & Sekuler, R. (1990). Assimilation and contrast in motion perception: explorations in cooperativity. *Vision Research*, 30, 1439–1451.
- Newsome, W. T., & Paré, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, 8, 2201–2211.
- Schiller, P. H. (1982). Central connections of the retinal ON and OFF pathways. *Nature*, 297, 580–583.
- Schiller, P. H., Sandell, J. H., & Maunsell, J. H. R. (1986). Functions of the on and off channels of the visual system. *Nature*, 322, 824–825.
- Shechter, S., & Hochstein, S. (1990). On and off pathway contributions to apparent motion perception. *Vision Research*, 30, 1189–1204.
- Sherk, H., & Horton, J. (1984). Receptive field properties in the cat's area 17 in the absence of on-centre geniculate input. *Journal of Neuroscience*, 4, 381–393.
- Shiffrar, M., & Lorenceau, J. (1996). Increased motion linking across edges with decreased luminance contrast, edge width and duration. *Vision Research*, 36, 2061–2067.
- Shipley, T. F., & Kellman, P. J. (1994). Spatiotemporal boundary formation: boundary, form, and motion perception from transformations of surface elements. *Journal of Experimental Psychology, General*, 123, 3–20.
- Shipley, T. F., & Kellman, P. J. (1997). Spatio-temporal boundary formation: the role of local motion signals in boundary perception. *Vision Research*, 37, 1281–1293.
- Smith, A. T., Snowden, R. J., & Milne, A. B. (1994). Is global motion really based on spatial integration of local motion signals? *Vision Research*, 34, 2425–2430.
- Snowden, R. J., & Braddick, O. J. (1990). Differences in the processing of short-range apparent motion at small and large displacements. *Vision Research*, 30, 1211–1222.
- Stoner, G. R., & Albright, T. D. (1993). Image segmentation cues in motion processing-implications for modularity in vision. *Journal of Cognitive Neuroscience*, 5, 129–149.
- van de Grind, W. A., Koenderink, J. J., & van Doorn, A. J. (1987). Influence of contrast on foveal and peripheral detection of coherent motion in moving random-dot patterns. *Journal of the Optical Society of America A*, 4, 1643–1652.
- van der Smagt, M. J., & van de Grind, W. A. (1999). Integration and segregation of local motion signals: the role of contrast polarity. *Vision Research*, 39, 811–822.
- van der Smagt, M. J., & van de Grind, W. A. (1996). Signal pooling across on- and off- motion detectors. *Perception*, 25, 7b (Suppl).
- Wehrhahn, C., & Rapf, D. (1992). ON- and OFF-pathways form separate neural substrates for motion perception: psychophysical evidence. *Journal of Neuroscience*, 12, 2247–2250.