Contrast polarity, chromaticity, and stereoscopic depth modulate contextual interactions in vernier acuity

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Vernier alignment thresholds are strongly compromised when the vernier is embedded in an array of equal-length flanking lines. Here, we show that these contextual interactions can be diminished by giving the flanks the opposite contrast polarity, e.g., white flanks surrounding a black vernier. Similar results are obtained for red verniers and equiluminant green flanks and when vernier and flanks have different binocular disparity. Using special flank configurations, we can eliminate location uncertainty as an important factor for this kind of contextual interactions. We interpret these results as evidence that perceptual grouping of the vernier and the flanks plays an important role in the vernier threshold elevation caused by contextual flanks.

Introduction

The processing of a target stimulus can be prominently influenced by contextual stimuli. For example, Westheimer and Hauske (1975) showed that vernier offset discrimination strongly deteriorates when the vernier is flanked by single neighboring lines (see also Levi, Klein, & Aitsebaomo, 1985). Explanations offered include that the lines activate the inhibitory region of neurons dedicated to vernier offset discrimination and thereby decrease the neural activity corresponding to the vernier. Other explanations draw on the integration of information from the target and the flanking lines (e.g., Badcock & Westheimer, 1985; Baldassi & Burr, 2000; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli, Palomares, & Majaj, 2004; Wilkinson, Wilson, & Ellemberg, 1997). Such pooling mechanisms are supposed to deteriorate performance because irrelevant information from the flanking elements interferes with the processing of the target. For example, it is supposed that vernier offset discrimination deteriorates in the presence of flanks because the signals of the vernier lines are pooled with the signals of the flanks.

It was recently demonstrated that when the flanks are either shorter or longer than the vernier target, performance improves compared to when flanks have the same length as the vernier (Figure 1; Malania, Herzog, & Westheimer, 2007). Particularly, the longer flank condition renders explanations based on lateral inhibition and pooling insufficient because the same-length lines are part of the longer lines. Hence, lateral inhibition and pooling of irrelevant information are at least not lower for longer flanks compared to same-length flanks.

On a descriptive level of perceptual organization, we proposed that performance increases when the vernier stands out from the flank configuration, as it is the case when the flanking lines are longer or shorter than the vernier. Performance deteriorates when the target is grouped within the flanking lines and does not stand out from the flank configuration. In the present experiments, we investigated whether differences in contrast polarity, color, and perceived depth between vernier and flanks can modulate contextual interactions.

Materials and methods

We measured vernier acuity thresholds. A vernier target consists of two lines that are slightly offset to the left or to the right. Observers have to indicate the direction of the offset.

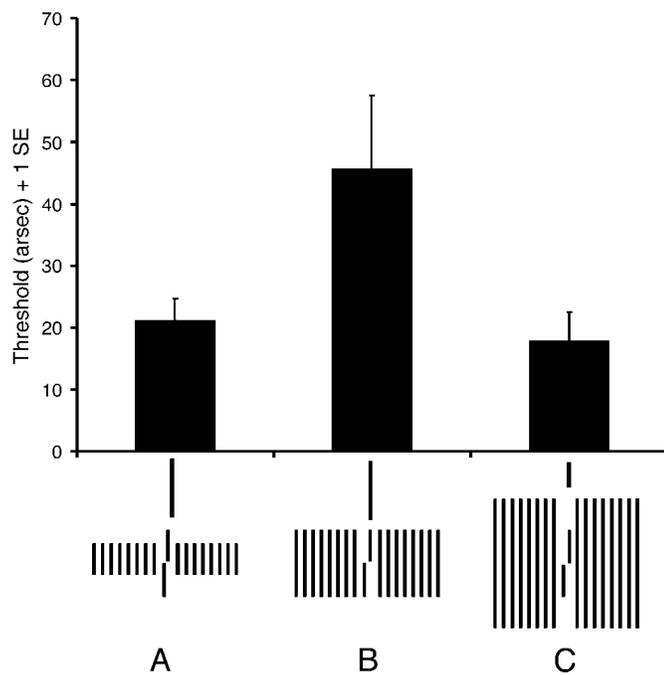Received December 14, 2007; published June 30, 2008

Figure 1. A vernier flanked by 8 short lines on each side (A) yields lower thresholds compared to a vernier flanked by 8 lines of the same length as the vernier (B). Interestingly, also lines that are longer than the vernier improve performance compared to same-length flanks (C) (replotted from Malania et al., 2007).

Stimuli in Experiments 1 and 2 were presented on a PHILIPS 201B4 CRT monitor driven by a standard accelerated graphics card. The screen resolution of the CRT was set to 1024 by 768 pixels. The monitors white point was adjusted to D65. Color space was computationally linearized by applying individual gamma corrections to each color channel (8 bits per channel). A Minolta CA-210 display color analyzer was used for calibration measurements. In Experiment 3, stimuli appeared on two Tektronix 608 analogue monitors. Luminance measurements have been performed using a Minolta Luminance meter LS-100.

Stimuli were presented in the fovea. The vernier target consisted of two vertical (horizontal in Experiment 3) 10′ long lines separated by a vertical (horizontal) gap of 1′. The vernier was either presented alone or flanked by 1 or 10 (8 in Experiment 3) vertical (horizontal) lines on each side.

If not stated otherwise, flanks were 21′ long, having the same length as the vernier target. The two flanks in immediate proximity to the vernier were located at a distance of 1.33′ from the vernier. The distance between each two flanking lines on each side of the vernier was also 1.33′. Flank configurations were symmetrical and centered on the vernier stimulus.

In each trial, the vernier target was randomly offset either to the left or to the right (up or down in Experiment 3). A block consisted of 80 trials and each block had a different pseudorandom sequence of left and right (up and down)

offsets. The number of left and right (up and down) offsets was balanced within each block. Maximally four subsequent offsets in one direction were presented. The observers' task was to indicate the direction of the horizontal (vertical) offset by button press. After each trial, the screen remained blank for a maximum period of 3000 ms during which the observer was required to make a response. After the response, the screen remained blank for 500 ms until the next trial. Errors and omissions were indicated by auditory feedback.

Observers viewed the monitor from a distance of 5 meters in Experiments 1 and 2 and the analogue monitors from a distance of 2 meters in Experiment 3. In all experiments, the room was dimly illuminated (0.5 lux).

The order of conditions within experiments was randomized individually for each observer. All conditions where measured twice. To compensate for possible learning effects, the order of conditions was reversed after each condition had been measured once. In all experiments, thresholds for verniers without flanks were measured as a baseline condition.

An adaptive staircase procedure was used to determine the threshold for which an observer reached 75% correct responses (PEST; Taylor & Creelman, 1967). The starting offset was 150″ in Experiments 1 and 2 and 75″ in Experiment 3. A cumulative Gaussian was fitted to the data and thresholds were determined by using probit and likelihood analyses.

Subjects were between 20 and 35 years of age and were students at the EPFL or the Université de Lausanne (UNIL). Subjects were paid 20 CHF per hour for their participation. In Experiments 2 and 3, one of the authors participated. Before the experiments, subjects were informed about the general purpose of the experiment and gave their written consent. Participants were told that they could quit the experiment at any time. Experiments were approved by the local ethics committee.

The Freiburg visual acuity test was used to determine observers' visual acuity (Bach, 1996). To participate in the experiments, subjects had to reach a value of 1.0 (corresponding to 20/20) for at least one eye. All subjects had normal or corrected-to-normal visual acuity. The Ishihara pseudoisochromatic color plates were used to test for red-green color vision deficiencies; no color deficiencies were observed in any subject.

Experiment 1: Contrast polarity

In the first experiment, contrast polarity was investigated as a potential grouping cue. Verniers and flanking lines were presented on a gray background and were either incremental (white) or decremental (black). The actual luminance of the background, the flanks, and the target vernier was adapted individually for each observer using the following method. Subjects were presented with two conditions, a black vernier flanked by 10 black lines on

each side or a white vernier flanked by 10 white lines on each side. In these initial conditions, black was set to 11 cd/m^2, white to 80 cd/m^2, and the gray background to 46 cd/m^2. Thresholds between the two conditions were compared. If performance substantially differed, the luminance of the stimuli and the background was adapted until the performance of the particular observer was similar in the two conditions. For example, if an observer showed superior performance in the white condition than in the black condition, luminance of the white stimuli was decreased to make this condition more difficult. Luminance of the background ranged between 41 and 51 cd/m^2, that of the white flanks and verniers between 66 and 100 cd/m^2, and that of the black flanks between 2 and 11 cd/m^2.

Using the individually determined luminance, observers were first presented with black verniers flanked by either 10 black or 10 white lines on each side and white verniers also flanked by either 10 black or 10 white lines. Second, stimuli consisted of black verniers flanked by one white line on each side, alternating white and black lines, alternating "butterflies," or black verniers presented without flanks. In the alternating white and black lines condition again 10 lines flanked the vernier on both sides. On each side, the first line next to vernier was white, the second line black, the third line white, and so forth. The alternating "butterflies" were similar to the alternating condition with the only difference that the length of the flanks increased linearly from the innermost flanks (23′) to the outermost (41′). Presentation time was 100 msec. Six observers (three females) participated, all naïve to the purpose of the experiment.

Experiment 2: Color

In the second experiment, instead of black and white stimuli against a gray background, verniers and flanks consisted of isoluminant red and green lines presented on a black background. The luminance of the vernier target and the flanks was set to 2.2 cd/m^2. To assure that the effects found were due to color and not brightness differences, control experiments were performed in which the luminance of the flanking lines was varied (see Appendix A). In the first part of the experiment, a red vernier flanked by 10 red or 10 green lines on each side and a green vernier also flanked by either 10 red or 10 green lines on each side was presented for 100 ms. As in the contrast polarity experiment, flanks and vernier had the same length.

In the second part, stimuli consisted of red verniers flanked by one green line on each side, alternating red and green lines, alternating "butterflies," and red verniers presented without flanks. In the alternating red and green lines condition again 10 lines flanked the vernier on both sides. On each side, the first line next to vernier was green, the second line red, the third line green, and so forth. The

alternating "butterflies" were similar to the alternating condition with the only difference that the length of the flanks increased linearly from the innermost flanks (23′) to the outermost (41′). Presentation time was 100 msec.

In the first part of the experiment, five subjects including one of the authors participated (four females). In the second part of the experiment six observers (four females) participated.

Experiment 3: Stereoscopic depth

In Experiment 3, stereoscopic depth was investigated as a grouping cue. Stimuli were presented on two Tektronix 608 analogue monitors equipped with P31 phosphors and controlled by a PC via fast 16-bit DA converters. The two monitors were placed in a right angle to each other with a beam splitter (ST-SQ-NP40, National Photocolor) in between at an angle of 45°. Linear polarization filters (Polaroid HN32) were used as faceplate for the monitors as well as for the goggles which have been attached to a custom-made chin/head rest. The monitor for the right eye was aligned to the line of sight and had a horizontal polarizing faceplate, while the monitor for the left eye was mirrored by the beam splitter and had a vertical polarizing faceplate. Beams through polarizer and beam splitter were controlled to have the same luminance.

Stimulus line elements were composed of dots drawn with a dot pitch of 200 μm at a dot rate of 1 MHz. Dot pitch was selected to make the dots overlap slightly, so that line width, i.e., the dot size, was of the same magnitude as the dot pitch. Elements were refreshed at 200 Hz, e.g., a presentation time of 20 msec was realized by four refresh cycles. Luminance was set to 80 cd/m^2 and measured with a two-dimensional dot grid using the aforementioned dot pitch and refresh rate. This luminance value includes the effects of all optics, including the interposed optical components. A Minolta LS-100 luminance meter equipped with a close-up lens (Minolta no. 122) was used to measure luminance.

Five different stimuli were used in the experiment. In all conditions, horizontal verniers were presented. In two stimulus conditions, the same configuration was presented to the left and the right eye, that is, no disparity was present in these conditions: In the first condition, a vernier without flanks was presented. In the second condition, the vernier was flanked by eight horizontal lines above and below the vernier. In the third condition, the vernier was presented with 80″ disparity while again 8 flanks above and below the vernier were presented simultaneously without disparity. The vernier was shifted 40″ to the left in the left eye and 40″ to the right in the right eye. In this condition, the vernier appears to be in a depth plane behind the flanks. In the fourth condition, the vernier presented to the left eye was displaced 40″ to the right and the vernier presented to the right eye was displaced 40″ to the left. Again, 8 flanks without disparity were presented

above and below the vernier. Perceptually, the vernier appeared in front of the depth plane of the flanks. In the last condition, the flanks with shifted verniers from conditions 3 and 4 were presented pseudorandomly to only one eye to control for a potential influence of the offset between vernier and flanks alone.

Before the experiment, stereo acuity was assessed using first a stereo test by the Stereo Optical Corporation (Stereo Fly) and, second, the Freiburg Stereo Acuity Test (Bach, Schmitt, Kromeier, & Kommerell, 2001). One subject was excluded because she did not perceive any depth in the Freiburg Stereo Acuity Test. Three other subjects were excluded because of ceiling effects. Six subjects including one of the authors participated in the experiment (3 females). Upon inquiry, all subjects reported to have perceived depth when presented with stimuli incorporating crossed or uncrossed disparity.

Results and discussion

Experiment 1: Contrast polarity

We found that a black vernier flanked by black lines yields higher thresholds compared to a black vernier flanked by white lines. We propose that the vernier stands out from the flanks in the second but not the first condition. Similar results were found for the white vernier conditions (Figure 2). Performance is clearly better in the conditions where contrast polarity differs between the vernier and the flanks compared to the corresponding conditions with the same contrast polarity.

Having established the equivalence between both black vernier and white vernier conditions, we limited the further investigation to black verniers. When the vernier was flanked by two neighboring white lines, thresholds were similar to the condition with 10 white lines on each side (Figure 3). When adding alternating white and black lines on each side of the vernier, performance strongly deteriorated.

This result challenges explanations drawing on purely local interactions between the vernier and the flanks. For example, in the alternating condition and the condition with a black vernier flanked by 10 white lines on each side, the first line to the left and right of the vernier was white. As the two conditions were locally the same, thresholds depended on the additional lines more distant from the vernier.

An alternative explanation for the results is that they are due to subjects' location uncertainty about the target, i.e., low performance could be the consequence of subjects' inability to exactly localize the vernier in the array of presented flanks when they had the same contrast polarity as the vernier. To control for location uncertainty, a flank configuration was used in which an indirect pointer indicates the position of the vernier (Figure 3, alternating "butterfly,"
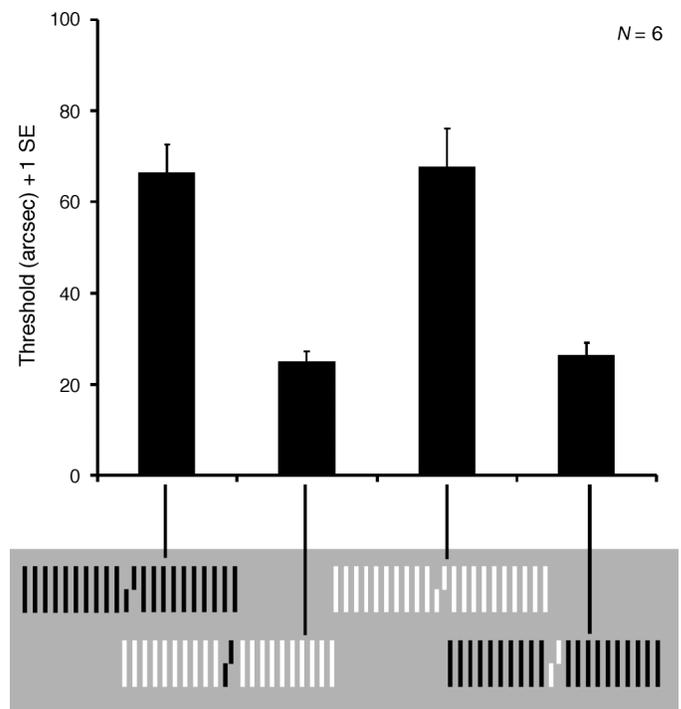

Figure 2. A black vernier yields higher offset discrimination thresholds when flanked by black lines in comparison to being flanked by white lines. Similarly, a white vernier yields higher thresholds when flanked by white lines in comparison to black lines.

see also Duangudom, Francis, & Herzog, 2007; Malania et al., 2007). As can be seen in Figure 3, in the alternating butterfly condition, performance is still worse than when the black vernier is flanked by white lines of the same size. Hence, location uncertainty is not the cause of deteriorated performance in the alternating flanks condition compared to the condition with only white flanks.

Experiment 2: Color

A red vernier flanked by green lines yields lower thresholds in comparison to when flanked by red lines. Similarly, a green vernier flanked by red lines yields lower thresholds in comparison to when flanked by green lines (Figure 4).

Our interpretation of this result is that in configurations with different colors of vernier and flanks, the vernier stands out from the flanks. However, it might be argued that it is not the color difference but a brightness difference that leads to these results. Although the luminance for the red and green stimuli was the same, there might have been brightness differences between the colors for different observers. For example, if green was perceived as brighter than red, it could be argued that this brightness difference causes higher thresholds in the condition in which the green vernier is flanked by green
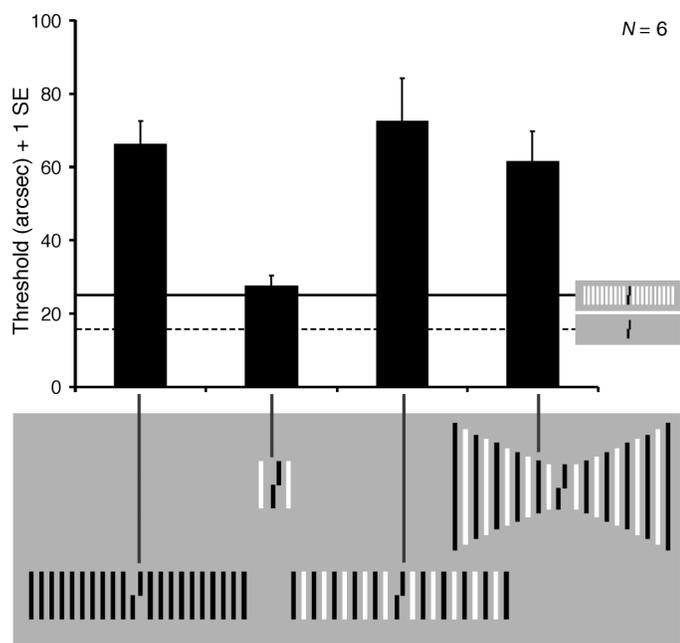
Figure 3. For comparison, the black in black condition from Figure 2 is replotted here. A black vernier flanked by two white lines yields lower thresholds compared to when alternating white and black lines are presented with the vernier although the two lines next to the vernier are the same in both conditions. An indirect pointer to the position of the vernier (alternating "butterfly") does not improve performance. The dashed black line indicates performance for an unflanked black vernier, the black line performance when the black vernier is flanked by white lines (replotted from Figure 2).

lines compared to when it is flanked by red lines. The darker appearing red flanks would interfere less with the processing of the vernier. It could be further argued that the high thresholds of the red in red condition compared to the green in red condition are also due to the lower brightness of red. So far, brightness differences could explain the results. However, the low thresholds in the red in green condition compared to the red in red condition could not be easily explained because the brightness of the green flanks would have been higher than the brightness of the vernier in this condition. Hence, if it was brightness alone leading to the results at hand, flanks of higher as well as lower brightness than the vernier would decrease thresholds compared to conditions in which vernier and flanks have the same brightness. Although this could be possible, we ruled out such an explanation by additional experiments (see Appendix A).

Having established the equivalence of red and green verniers, we limited the control conditions to red verniers flanked by different configurations (Figure 5).

We presented observers with a red vernier flanked by one green line on each side. In this condition, thresholds were similar to the condition with 10 green lines on each side (Figure 5). When presenting the vernier with

10 alternating green and red lines on each side of the vernier, performance strongly deteriorated.

As with contrast polarity, these results question explanations drawing on purely local interactions between the vernier target and the flanks. In the alternating conditions as well as the condition with a red vernier flanked by 10 green lines on each side, the first flank to the left and right of the vernier was green. The thresholds, however, depended on the additional lines more distant from the vernier.

The possible influence of location uncertainty was controlled by using a butterfly-like stimulus consisting of a red vernier flanked by alternating green and red lines (Figure 5, alternating "butterfly"). The performance of observers does not increase when the position of the vernier target is clearly indicated. The butterfly condition rules out that location uncertainty is the cause of the high thresholds in the alternating-flanks condition.

Experiment 3: Stereoscopic presentation

The rationale behind this experiment was that if the flanking lines can be perceptually separated in depth from the vernier target, the vernier would stand out from the configuration of flanks. We hypothesized that such an ungrouping of flanks and vernier increases the performance of observers compared to conditions in which the vernier and the flanks are not separated in depth.
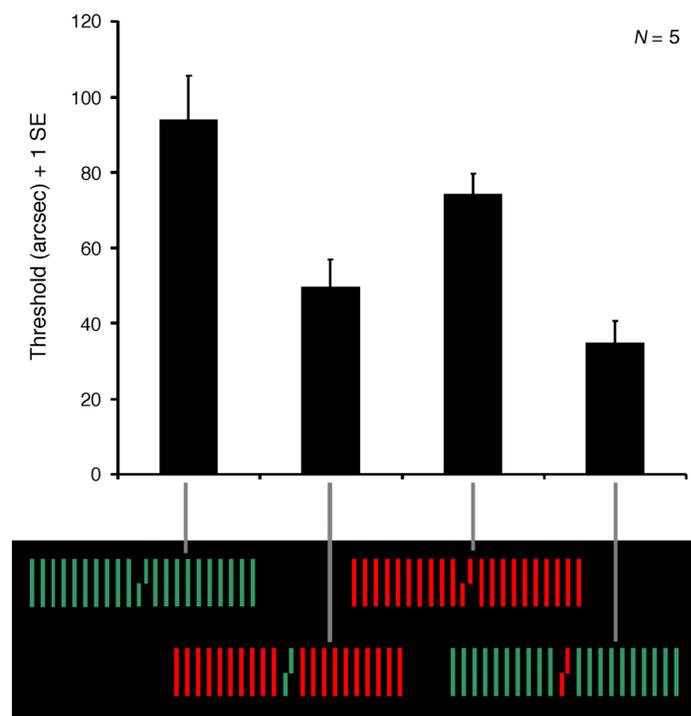

Figure 4. Thresholds are high for a green vernier flanked by green lines and a red vernier flanked by red lines. In comparison, thresholds are lower when a green vernier is flanked by red lines and a red vernier is flanked by green lines.
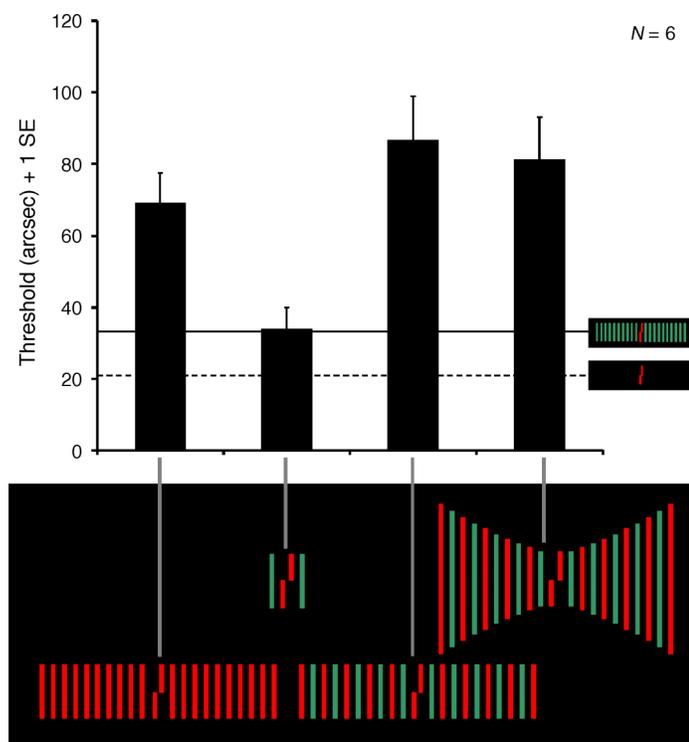
Figure 5. The red in red condition from Figure 4 is replotted here. A red vernier flanked by two green lines yields low thresholds compared to the condition when alternating green and red lines are presented with the vernier. An indirect pointer to the position of the vernier (alternating "butterfly") does not improve performance. The dashed line indicates unflanked vernier performance; the black line indicates performance when the red vernier is flanked by green lines (replotted from Figure 4).

As shown in Figure 6, thresholds are lowest when presenting the vernier without flanking lines (Figure 6, dashed line). Performance in the two conditions where the vernier is perceptually either in front of or behind the 16 flanking lines is better compared to the condition where it appears in the same depth plane as the flanking lines (Figure 6). When presenting only one eye with the shifted vernier and flanks, performance deteriorates even compared to the same depth plane.

Discussion

The perception of a target stimulus can strongly be influenced by neighboring elements. For example, vernier discrimination thresholds increase if a vernier is presented together with single neighboring lines (e.g., Westheimer & Hauske, 1975). Usually, local neural mechanisms such as lateral inhibition or pooling mechanisms are proposed as explanations. However, it was recently shown that such local interactions are not sufficient to explain the influence of flanks on vernier discrimination (Malania et al., 2007).

Global aspects of the spatial layout of the flanks play an important role that was attributed to grouping: The more the flanks group with the vernier, the worse is performance; the more the vernier stands out from the flanks, the better is performance (Figure 1; Malania et al., 2007). In Malania et al. (2007), only spatial aspects such as the length of the flanks were used for the grouping or ungrouping of the vernier and the flanks.

Here, we asked the questions whether color, contrast polarity, and stereoscopic depth can be used to induce analog grouping effects. In all three cases, the answer is positive. When the vernier is different in contrast polarity, color, or depth, performance is better than if not (for analog results in peripheral vision see, e.g., Kooi, Toet, Tripathy, & Levi, 1994; Põder & Wagemans, 2007). For example, a red vernier flanked by green lines yields lower thresholds than when flanked by red lines. A red vernier flanked by green lines yields also lower threshold than a red vernier flanked by alternating lines of which the innermost line is green as well. In these conditions, the
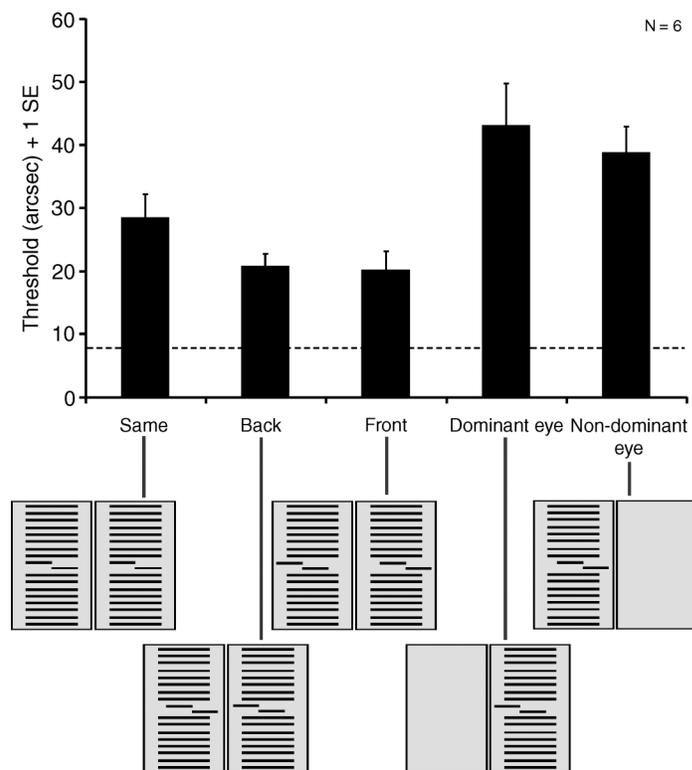

Figure 6. Verniers flanked by 8 lines above and below. The dashed line indicates the unflanked vernier threshold. Each two fields represent the stimuli presented to the left eye and right eye, respectively. In the first condition, "same", both eyes were presented with a vernier and 16 flanking lines without disparity. In the "back" and "front" conditions, the vernier had 40″ crossed or uncrossed disparity. If the vernier appears in front or behind the flanking lines, performance improves compared to when it appears in the same depth plane. Performance decreases when only one eye is presented with one part of the stimulus of the disparity condition.
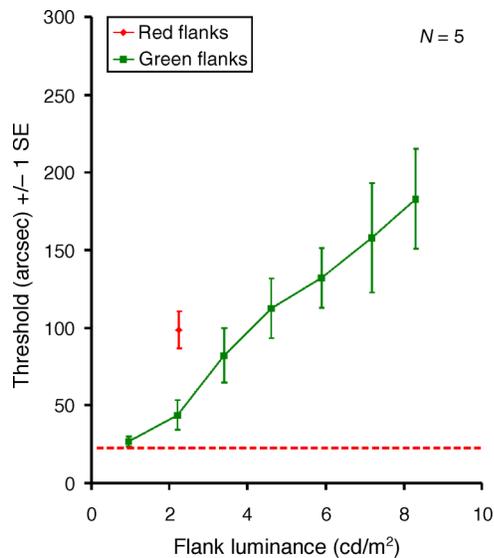
Figure 7. A red vernier flanked by either red lines of the same luminance (red diamond) or green lines of different luminance (green squares). Isoluminance of the vernier and flanks was at 2.2 cd/m². The dashed red line indicates the unflanked vernier threshold. At physical isoluminance of the red and green flanks, the threshold for a red vernier flanked by green lines is lower. Further increasing the luminance of the green flanks increases thresholds.

stimuli do not differ locally (vernier and first line to the left and right of the vernier) but performance differs strongly. As with spatial manipulations, these findings challenge explanations in terms of local interactions.

We can only speculate about the underlying neural substrates. The color manipulations show that features processed primarily in the parvo-cellular system could support grouping without the involvement of the magno-cellular system. We did not determine the exact isoluminance point with standard methods of isoluminance determination (red square on green background) because both the vernier and the flanks were presented on a black background. However, we determined performance for a large range of luminance values of the flanks making it very likely that also the isoluminance point was included in our measurements (see Appendix A). When using a red vernier of 20.5 cd/m², performance for green flanks of various luminance was always better than for red flanks (Figure 9).

Similarly, it can be argued that complex cells do not play a major role in our contrast polarity results. As complex cells respond independently of the contrast polarity of the stimulus (Hubel & Wiesel, 1962), the difference between, e.g., the black vernier flanked by white lines and the condition where it was flanked by black lines, cannot be explained by a mechanism operating within the receptive field of single complex cells. On the other hand, the results support the contention (Westheimer, 2007) that contrast polarity is conserved in the passage of signals through the primary visual cortex. Moreover, it seems that

grouping occurs at least partly after binocular fusion because ungrouping the vernier from the flanks by using stereoscopic depth decreases thresholds (for a review see Palmer, Brooks, & Nelson, 2003).

On a descriptive level of perceptual organization, we postulate that grouping is crucial to understand the effects flanks exert on target processing. This leaves open the question on which level of the neural machinery this grouping takes place. It may be that Gestalt processing already occurs within circuits in the primary visual cortex (e.g., Caputo, 1996; Hermens, Luksys, Gerstner, Herzog, & Ernst, 2008; Herzog, Ernst, Etzold, & Eurich, 2003; Li, 1999, 2002; Sugita, 1999; Wolfson & Landy, 1999; Li, 2003).

Appendix A

In Experiment 2, it could be argued that observers perceived the red flanks as brighter than the green flanks or vice versa.

Better performance in the conditions with different vernier and flank color could thus possibly be attributed to the grouping of the flanks because of their perceptual difference to the vernier based solely on brightness. To rule out such an interpretation, we conducted control studies in which the luminance of the vernier was kept constant while varying the luminance of the flanks. This was done first with the same vernier luminance as in Experiment 2 and second in a higher luminance regime. In the first part, flank luminance was varied between 0.6 and
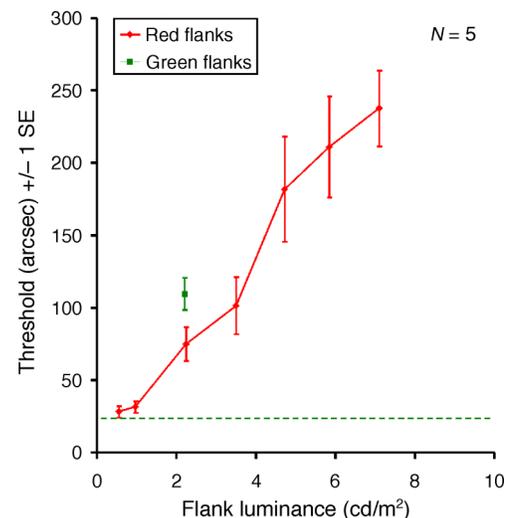

Figure 8. A green vernier flanked by either green lines of the same luminance (green square) or red lines of different luminance (red diamonds). Isoluminance of vernier and flanks was at 2.2 cd/m². The dashed green line indicates the unflanked vernier threshold. At physical isoluminance of the red and green flanks, thresholds for a green vernier flanked by red lines are lower. Further increasing the luminance of the red flanks deteriorates performance.

7.1 cd/m^2. In the experiment, five subjects including one of the authors participated (2 females).

The results show that at isoluminance of the vernier and the flanks, performance is better when the flanks have different colors than the verniers replicating the results of Experiment 2 (Figures 7 and 8). Only when the luminance of the differently colored flanks is almost doubled, the performance is roughly the same as in the same color cases. Therefore, brightness differences as an explanation of the results in Experiment 2 can be rejected: If color did not play a role for the results, performance would have to be the same when vernier and flanks have the same brightness. When using the red vernier at 2.2 cd/m^2, this would be the case at about 4 cd/m^2 for the green flanks (Figure 7). When using the green vernier, however, the red flanks would have to have a luminance of about 4 cd/m^2. This is a contradiction. Hence, color plays a role in the results at hand.

In a further experiment, we increased the luminance of the stimuli. A red vernier of higher luminance (20.5 cd/m^2) flanked by either isoluminant red lines (20.5 cd/m^2) or green lines of different luminance was presented. For each observer individually, we chose one luminance level for the green flanks which appeared clearly darker than the red vernier and one which appeared clearly brighter. The luminance of the "clearly darker" flanks ranged between 13.8 and 34.3 cd/m^2, the luminance of the "clearly brighter" flanks between 20.5 and 47.7 cd/m^2.

Three observers including one of the authors participated (1 female). Figure 9 shows data of the 3 subjects
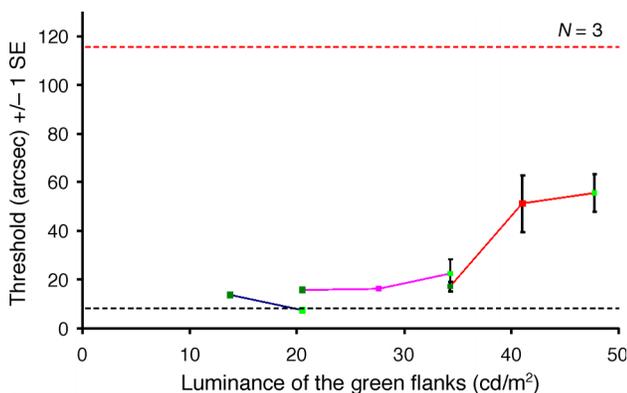

Figure 9. A red vernier (20.5 cd/m^2) was flanked by isoluminant red lines (dashed red line) or green lines of different luminance (blue, pink, and red line; each line corresponding to one observer). The dashed black line indicates unflanked vernier threshold. The green squares on the left side of connecting lines indicate subjects' performance when the green flanks were perceived as "clearly darker" compared to the red vernier. The green squares on the right side of connecting lines indicate subjects' performance when the green flanks were perceived as "clearly brighter" compared to the red vernier. For two observers, additional luminance values of the green flanks in between the clearly darker and brighter were measured (pink and red square, respectively) (standard errors can be smaller than symbol size).

(RT, BS, and ET). In all cases, performance is superior when the flanks are green compared to when the flanks are red. This is further evidence that color plays a major role in the reported results.

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