Quantifying target conspicuity in contextual modulation by visual search

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Contextual elements can strongly modulate visual performance. For example, performance deteriorates when a vernier is flanked by neighboring lines. On a neural level, such contextual modulation is often explained by local spatial interactions such as lateral inhibition or pooling. However, these mechanisms cannot account for a number of recent results which showed that global rather than local factors play a key role in contextual modulation. On a level of perceptual organization, we proposed that contextual modulation increases when the target groups with the flankers and decreases when the target stands out from the flankers. To quantify this "standing out" in foveal vision, here, we performed both a visual search and a vernier offset discrimination task on the same stimulus configurations. Stimulus configurations yielding short reaction times in visual search yielded good vernier discrimination performance. Stimulus configurations yielding long reaction times yielded weaker discrimination. Hence, vernier offset discrimination is superior for targets that are efficiently searched and vice versa.

Introduction

Visual performance can be strongly modulated by contextual elements. For example, in foveal vision, vernier offset discrimination deteriorates when the vernier is flanked by neighboring lines (e.g., Badcock & Westheimer, 1985; Levi, Klein, & Aitsebaomo, 1985; Westheimer & Hauske, 1975; Westheimer, Shimamura, & McKee, 1976; see also Flom, Weymouth, & Kahneman, 1963; Jacobs, 1979; Toet & Levi, 1992). On a neural level, local interactions between a target and its context are often proposed to explain contextual modulation. For example, neurons dedicated to vernier discrimination are thought to be inhibited by the flankers (e.g., Westheimer & Hauske, 1975; see also Bjork & Murray, 1977). In peripheral vision, the deleterious influence of flankers ("crowding") is often explained by spatial pooling: neural activity corresponding to both the target and the flankers is integrated and, thus, feature identification is impaired (e.g., Baldassi & Burr, 2000; Parkes, Lund, Angelucci, Solomon,

& Morgan, 2001; Pelli, Palomares, & Majaj, 2004; Wilkinson, Wilson, & Ellemberg, 1997).

A number of recent findings challenged these explanations. For example, increasing the flanker size reduced foveal (Figure 1A; Malania, Herzog, & Westheimer, 2007) as well as peripheral flanker interference (Saarela, Sayim, Westheimer, & Herzog, 2009; see also Levi & Carney, 2009). Accounts based on lateral inhibition and pooling predict stronger (or similar) interference by longer flankers. We proposed that contextual modulation is reduced when the target "ungroups" from the flankers and stands out from the configuration (Herzog & Fahle, 2002; Malania et al., 2007; Saarela et al., 2009; Sayim, Westheimer, & Herzog, 2008, 2010). This proposition is well in line with a number of studies showing that the overall spatial layout of the stimulus is a key factor of contextual modulation (Banks & Prinzmetal, 1976; Banks & White, 1984; Livne & Sagi, 2007, 2010; Prinzmetal & Banks, 1977). Also when the target stood out from the flankers because of color differences (such as a red target among green flankers), target discrimination improved
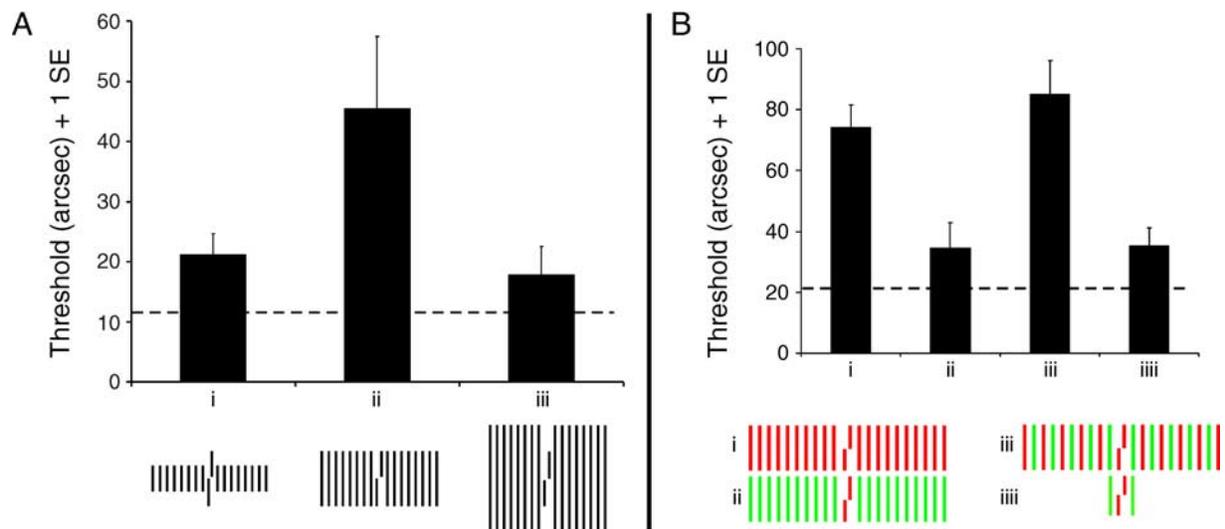
Figure 1. (A) In foveal vision, a vernier flanked on each side by eight short lines (i) yields lower thresholds compared to a vernier flanked by eight lines of the same length (ii). The condition with longer flankers (iii) yields superior performance compared to the condition with same-length flankers (adapted from Malania et al., 2007). (B) A red vernier yields higher offset discrimination thresholds when flanked on each side by ten red lines (i) compared to ten green lines (ii). Thresholds are also higher when the vernier is flanked by alternating green and red lines (iii) but not when the vernier is flanked by single green lines (iiii). In conditions ii, iii, and iiii, the flankers next to the vernier are green but thresholds vary strongly (adapted from Sayim et al., 2008). The dashed lines in A and B indicate unflanked vernier thresholds.

compared to when colors of target and flankers were the same (Figure 1B; in the fovea: Sayim et al., 2008; in the periphery: Kooi, Toet, Tripathy, & Levi, 1994; Põder, 2006, 2007; Scolari, Kohnen, Barton, & Awh, 2007).

To quantify the relationship between "standing out" and vernier discrimination in contextual modulation, we compared performance in visual search with vernier offset discrimination by using similar stimuli in both tasks. Each observer was presented with 1120 different stimulus configurations on which both a visual search task and a vernier offset discrimination task were performed. Displays with red or green color-singleton targets yielded significantly less contextual modulation than displays with conjunction targets (Experiment 1). Moreover, the larger the size difference between the target and the flankers, the better was discrimination performance and the faster were reaction times in visual search (Experiment 2). In both experiments, large target-flanker differences also yielded high ratings of the "standing out" of the target.

Experiment 1: Color

Methods

Observers

Observers were paid students of the Ecole Polytechnique Fédérale de Lausanne (EPFL) or the Université de Lausanne (UNIL). Observers were informed about the general purpose of the experiment and gave written consent. Participants were told that they could quit the experiment at any time. All observers were naive as to the purpose of the experiment. The experiments were approved by the local ethics committee.

The Freiburg visual acuity test (Bach, 1996) was applied to determine observers' visual acuity. All observers had normal or corrected-to-normal visual acuity. The Ishihara pseudo-isochromatic color plates were used to test for red–green color vision deficiencies. All observers had normal color vision. Five observers between 20 and 25 years participated (1 female, 4 males).

Apparatus

Stimuli were presented on a PHILIPS 201B4 CRT monitor driven by a standard accelerated graphics card. The screen resolution was set to 1024 by 768 pixels. The monitors white point was adjusted to be 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. Luminance measurements have been performed using a Minolta Luminance meter LS-100. Observers viewed the monitor from a distance of 5 meters. In all experiments, the room was dimly illuminated (0.5 lux).

Stimuli

Stimuli consisted of an array of 31 vertical red and green lines with a small gap of 1′ in between (Figure 2, in the following called "lines"). One of the lines was the
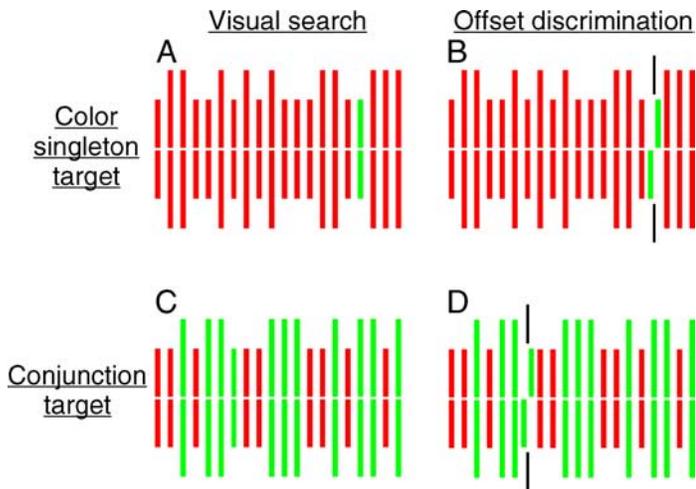
Figure 2. Examples of the stimuli in the visual search task (A & C) and the offset discrimination task (B & D; actual stimulus arrays were composed of 31 elements). Stimuli were exactly the same in both tasks, except that in the offset discrimination task, a positional cue (B & D, black lines) was presented one second before the stimulus, the target had an offset, and presentation time was 150 ms. (A & B) Color-singleton targets. (C & D) Conjunction targets. The target in the four examples is the short green line (vernier). In the search task, observers indicated the presence (shown in the figure) or absence (not shown) of the target. In the offset discrimination task, observers indicated the offset direction (stimuli were presented on a black background, cues were gray).

target and the others were distractors ("flankers"). Lines were equally spaced with a horizontal distance of 3.3′. One subset of the lines had a length of 21′ ("short flankers"), the other subset a length of 31′ ("long flankers"). The target was always 21′ long. In Experiment 1, the target was either a color-singleton ("color singleton" condition), for example, a red target within short and long green flankers, or it was a singleton by a conjunction of color and size ("conjunction" condition), for example, a red target within short green and long red flankers.

In target present trials, the 30 flankers consisted of 15 short and 15 long lines. In target absent trials, an additional long or short flanker was presented instead of the target. In each trial, the positions of target and flankers within the array were randomized with the constraints that, first, at maximum five lines with the same length (independent of color) or the same color (independent of length) were presented next to each other. Second, the target was never presented in the two outermost positions on either side (leaving 27 potential target positions). Each trial was initiated by a white fixation dot (diameter of 1′) that was presented for 800 ms and disappeared with stimulus onset.

Stimulus luminance was individually adjusted for each observer to obtain similar performance for red and green

targets (see Design and procedure). Luminances were 20.7, 25.7, 28.0, 35.9, and 48.1 cd/m^2 for the green elements (the luminance of the red elements was fixed at 18.0 cd/m^2). Stimuli appeared on a black background (0.8 cd/m^2).

These parameters were used for the first part of the experiment (see Design and procedure, visual search). In the second part of the experiment (see Design and procedure, offset discrimination), stimulus presentation was preceded by a cue indicating the position of the target. The cue consisted of two 8′ long gray lines (22.8 cd/m^2), 1.2′ above and below the target. The cue was presented one second before stimulus onset and remained on the screen until the observers' response. In this part of the experiment, the target was randomly offset either to the left or to the right (vernier offset). Flankers were never offset.

Design and procedure

The experiment consisted of two parts, a visual search and an offset discrimination task.

Visual search: In visual search, observers searched for the target, a red (or green) line that was either unique because of its color ("color-singleton" condition) or its conjunction of color and length ("conjunction" condition). Observers fixated on the fixation dot in the center of the screen. After 800 ms, the fixation dot disappeared and the search display was presented. The stimulus remained on the screen until the observers' response but for maximally 5 seconds. Target absence or presence was indicated by pressing one of two buttons. Observers were instructed to respond as fast and accurate as possible. A block consisted of 160 trials of which 80 contained a target. In half of the trials, the target was a color-singleton, in the other half the target was a singleton by a conjunction of color and length (Experiment 1). Target present and target absent trials as well as color-singleton and conjunction trials were randomly intermixed within a block. Maximally four stimuli of the same type (target present or absent; color-singleton or conjunction target) were presented in a row. Note that each single stimulus configuration was presented only once, that is, in a block of 160 trials, 160 different stimulus configurations were presented. Errors were indicated by auditory feedback. When observers did not respond within five seconds after stimulus onset, the trial was aborted (indicated by auditory feedback) and repeated at random within the remaining trials.

Offset discrimination: In the offset discrimination task, the same stimulus configurations as in the search task were presented (in a different random order). Only the subset of target present trials was used. In this task, the target had a vernier offset. Observers indicated the offset direction (left or right) by a button press. Observers were instructed to respond as accurate as possible. Responses were not speeded. The procedure was the same as in the search task except the following. After the fixation dot

disappeared, two lines indicated the position of the target (see Stimuli). These cueing lines were presented 1 second before stimulus onset and remained on the screen until stimulus offset. Observers were instructed to make a saccade to the location where the target was to appear. Presentation time of the stimulus itself was 150 ms. Each block had a different pseudorandom sequence of left and right vernier offsets. The number of left and right offsets was balanced within each block. Maximally four subsequent offsets in one direction were presented.

While it would be desirable to use exactly the same stimuli in both visual search and offset discrimination, the described differences were necessary for the following reasons. First, the position of the target in the offset discrimination task had to be cued in order not to confound search and discrimination. Second, the target in the visual search task did not have any offset because an offset is a cue that may pop out in visual search (Fahle, 1991) thereby reducing the effect of the different flanker conditions.

The cueing lines can potentially improve offset discrimination compared to conditions without cueing lines beyond the intended improvement by indicating the target location (for example, when always presenting the target in the center of the screen). As the upper segment of the vernier is offset relative to the upper cueing line and the lower vernier segment is offset relative to the lower cueing line, observer could use these offsets for target discrimination. Such offsets are only half of the target offset, but they are also less masked by the flankers.

On the other hand, the cueing lines could also reduce performance compared to conditions without cueing lines because they additionally mask the target. While both possibilities cannot be entirely excluded, there are several reasons to assume that it is safe that the cueing lines have no or only weak effects on performance (besides the intended facilitation). First, the cueing lines did not have the same color as the target what usually yields weak contextual interactions (e.g., in foveal vision: Sayim et al., 2008; and peripheral vision: Kooi et al., 1994). Second, the cueing lines were presented one second before stimulus onset. Such preview of flankers has been shown to markedly reduce contextual interactions compared to simultaneous presentation of target and flankers (Huckauf & Heller, 2004; Scolari et al., 2007). Third, in a control experiment, we did not find any difference between the presentation of the vernier alone and the vernier with cueing lines when no flankers were presented (foveal presentation in the center of the screen). Most importantly, any contextual modulation by the cueing lines would have had similar effects in the color-singleton and the conjunction target conditions, and is, hence, only relevant when comparing the visual search task with the offset discrimination task.

The offset of the target, present in the offset discrimination task but not in the visual search task, is the second spatial feature that differs in the two tasks. It creates a region of lower density than the rest of the stimulus and reduces the horizontal regularity of the pattern. Hence, the conspicuity of the vernier region is increased when the vernier has an offset compared to no offset. Again, this difference is relevant only for the comparison between visual search and offset discrimination and not the two conditions, singleton and conjunction targets.

Each observer completed two search and two offset discrimination blocks with each of the two target colors, resulting in a total of 8 blocks. Observers completed the first four blocks with one target color and then the second four blocks with the other target color. Visual search and offset discrimination blocks alternated.

Before the beginning of the main experiment, we adjusted luminance levels and offset sizes of the vernier individually for each observer. Starting with photometric isoluminance of the red and green elements (18 cd/m^2) and an offset size of 30″, observers performed two offset discrimination blocks of 80 trials with green and with red targets, respectively. The target was a color-singleton in half of the trials and a conjunction target in the other half. Stimuli had to meet the following criterion: Performance for both red and green targets, had to be between 75% and 85% correct responses in *at least* one of the two conditions (color-singleton or conjunction target). If this criterion was met, for example, for red targets but not for green targets, the luminance of the green elements was adjusted (luminance of the red elements was fixed at 18 cd/m^2 in all conditions). The luminance was increased if performance in the green target condition was below 75% correct and decreased if it was above 85% correct (the size of the luminance increase or decrease depended on the magnitude of the difference between the two target color conditions and ranged between at least 2.7 cd/m^2 and at most 17.9 cd/m^2). If performance was worse than 75% correct in both target color conditions, the offset size was increased by 15″; if it was above 85% correct the offset size was decreased by 15″. Performance was evaluated after two blocks. If the criterion was not met, the procedure was repeated. Only one offset size per observer was used. This offset size was always the same for red and green targets for each observer. Offset sizes were 15″ for two observers, 30″ for one observer, and 45″ for the remaining two observers.

Data analysis

In the search task, reaction times (RTs) were recorded. Only trials with correct responses were analyzed. Trials with RTs faster than 200 ms or three standard deviations above the mean were discarded from the analysis. In the offset discrimination task, the rate of correctly indicated offset directions (percent correct) was measured. Due to averaging in both measures (RTs in search and percent correct in offset discrimination), information about the unique

trial pairs is lost. Therefore, correlations between RTs and offset discrimination (correct and false) were computed.

Results and discussion

Figure 3A shows the results of the search task. RTs were clearly shorter in the color-singleton compared to the conjunction target condition. The average RT for red targets was 709 ms when presented within green flanker arrays (color-singleton condition), and 1546 ms when presented in flanker arrays containing red and green flankers (conjunction condition; t-test, $p < 0.01$), i.e., more than twice as long. For green targets, the average RT was 743 ms when presented within red flankers, and 1284 ms when presented within red and green flankers (t-test, $p < 0.05$). These results replicate the common RT difference between efficient search for salient color-singletons and inefficient search for less salient conjunction targets. Error rates (misses and false alarms) were low for both target colors in both conditions (red: color-singleton condition: 1.5%, conjunction condition: 7.5%; green: color-singleton condition: 1.5%, conjunction condition: 5.5%).

In Figure 3B, results of the offset discrimination task are shown. For both target colors, the rate of correct responses was higher in the color-singleton compared to the conjunction target condition. Average percent correct responses for red targets were 83.2% in the color-singleton and 59.6% in the conjunction condition (t-test, $p < 0.05$). For green targets, average percent correct was 84.5% in the

color-singleton and 63.6% in the conjunction condition (t-test, $p < 0.05$).

Figure 4 shows individual data points for both red and green target conditions. Trials are plotted as a function of RTs in visual search and offset discrimination accuracy (correct vs. false responses). For both target colors, the correlation between RTs and discrimination performance was significant (t-tests; red target: $r = 0.23$, $p < 0.001$; green target: $r = 0.13$; $p < 0.001$; note that the seemingly low correlations were expected due to the high level of chance performance in the offset discrimination task).

To investigate the subjective "standing out" of the target, three new observers performed twenty trials (ten with color singletons and ten with conjunction targets) with each of the two target colors (individual luminance levels were established as above). Each stimulus was presented for five seconds. Three seconds after stimulus onset, two cueing lines (the same as in the original offset discrimination experiment) indicated the position of the target to indicate that a target was present. Observers were asked to indicate how much the target stood out from the flankers on a scale from 1 (target does not stand out) to 7 (target strongly stands out). On average, color singletons were judged 6.98 and conjunction targets 2.52. Hence, color singletons stood out from the flankers stronger than conjunction targets.

RTs were faster and offset discrimination was better when the target was a color-singleton compared to when it was a conjunction target. A higher salience of one of the two colors as a cause for these results can be excluded as
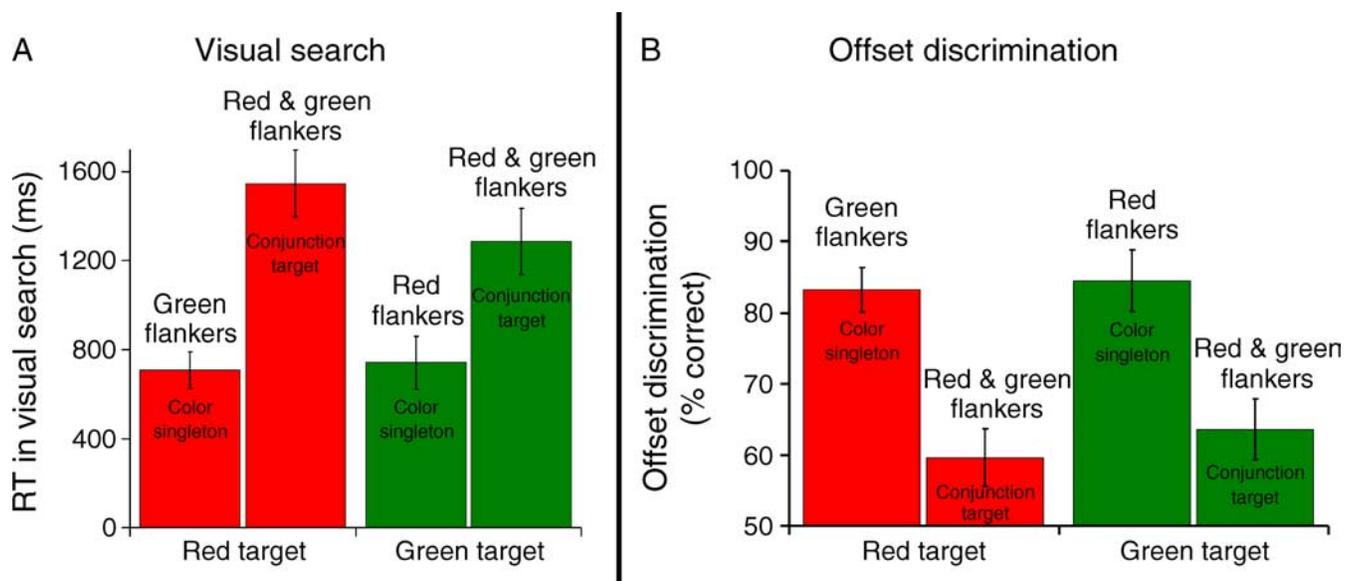

Figure 3. Results of Experiment 1. (A) Average RTs in visual search. RTs for a red target were faster when the flankers were green (color-singleton condition) compared to when the flankers were red and green (conjunction target condition). Similarly, RTs for a green target were faster when the flankers were red compared to when they were red and green. (B) Percent correct in the offset discrimination task. The rate of correct responses was higher for color singletons compared to conjunction targets.
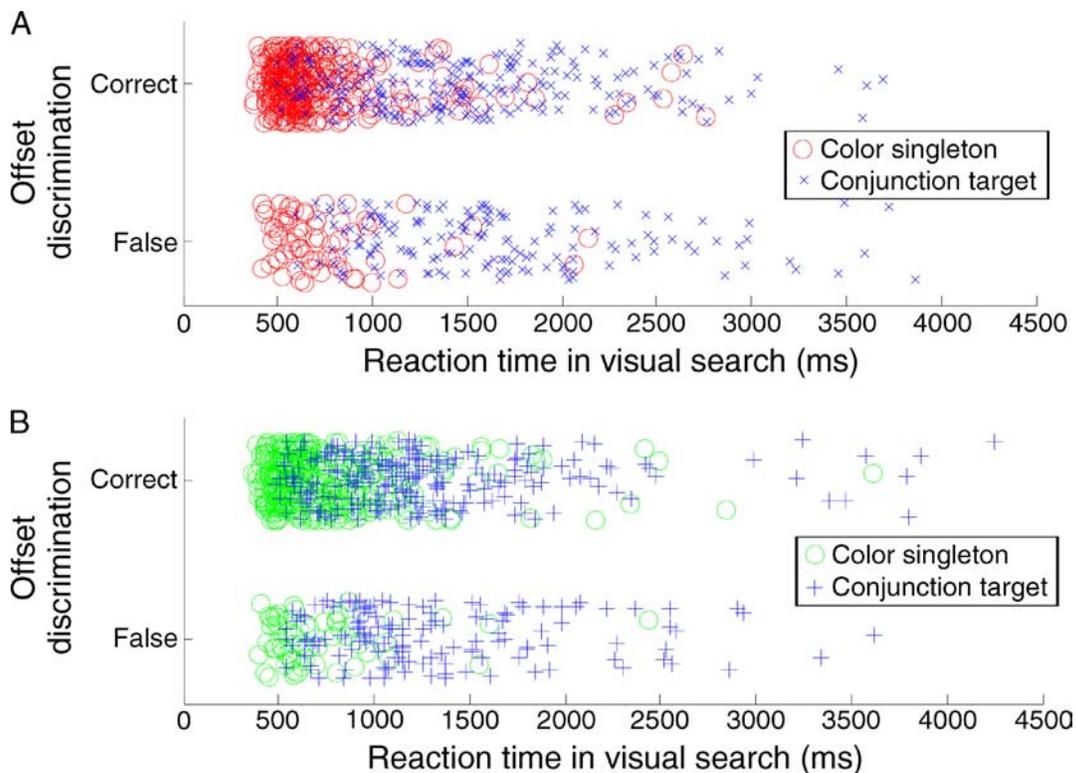
Figure 4. Individual data points for all 800 trial pairs for the red (A) and green (B) target. Trials are plotted as a function of RTs and offset discrimination performance (correct or false). RTs in the color-singleton conditions (indicated in A by red and in B by green circles) strongly cluster around 500 to 1000 ms while RTs in the conjunction target conditions (blue × and + signs) are markedly slower and more variable. In the offset discrimination task, discrimination of color-singleton targets was mostly correct (red and green circles cluster in the upper left corners of the graphs) in contrast to the conjunction target conditions. Correlations between RT and offset discrimination were significant for both target colors.

each of the two colors was used as target color. Target location uncertainty in the offset discrimination task seems unlikely as a cause for the inferior performance in the conjunction condition as the target location was cued. A control experiment with large offsets (150″) yielded ceiling performance in both the color-singleton and the conjunction condition (percent correct over 92.5 for both target colors). Moreover, the presentation time was too short (150 ms) to make corrective saccades. Therefore systematic fixation differences between the two conditions do not cause the present results.

In contrast to the discrimination task, eye movements were allowed after stimulus onset in the visual search task. Hence, observers detected targets either in the periphery or in the fovea. While peripheral target detection seems unlikely in the conjunction target condition because of the long RTs, it is possible that color-singletons were—at least occasionally—detected in the periphery. However, also RTs around 700 ms in the color-singleton conditions allow for a number of saccades and hence fixation of the target before the decision. The possibility of peripheral target detection might call into question in how far the search task can be compared with the (foveal) discrimination task. In particular, RT differences between color singletons

and conjunction targets might vanish (ceiling effects) when presented foveally (i.e., when using a discrimination instead of a search task). In Experiment 2, we use only conjunction targets and reduce the possibility of peripheral target detection.

Experiment 2: Size

The results of Experiment 1 showed reduced interference when the target and the flankers had different colors, i.e. the target was a color-singleton. In Experiment 2, the target was always a conjunction target. To investigate whether different degrees of target conspicuity in contextual modulation can be quantified by visual search performance, we parametrically varied the size of the flankers and hence target-flanker similarity.

Methods

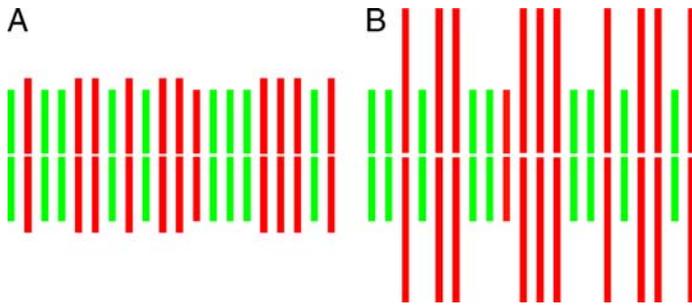The same observers participated as in Experiment 1. Stimuli were the same as in Experiment 1 with the

Figure 5. Stimuli in Experiment 2. Examples (not to scale) of the shortest (A) and longest red flankers conditions (B). The target was always a short red line. Only target present examples for the visual search task are shown. In the offset discrimination task, the position of the offset target was cued (see Figure 2). In visual search, observers indicated the presence or absence of the target; in offset discrimination they indicated the offset direction. Actual stimuli were composed of 31 elements and presented on a black background.

following exceptions (Figure 5). Only conjunction targets were used, i.e., the target was never a color-singleton. The target was always red (as the results for both target colors were similar in Experiment 1). Red flanker lengths were 25′, 31′, 38′, 45′, and 51′. The green flankers were always as long as the target (21′).

The design and procedure was similar to that of Experiment 1, with the following exceptions. As only conjunction targets were used, the individual offset size of the target in the offset discrimination task had to be increased compared to that in Experiment 1 to avoid floor effects. Offset sizes were doubled compared to Experiment 1,

except for two observers who showed ceiling performance with doubled offset sizes (we used 1.7 times the offset size for these two observers; offset sizes were 30″ for two observers, 60″ for one observer, and 75″ for the remaining two observers). The order of the five flanker length conditions was randomized with the constraint that visual search and offset discrimination blocks alternated. As in Experiment 1, all conditions were measured twice. The order of conditions was reversed after each condition had been measured once. Each observer was presented with 800 different stimulus configurations.

Results and discussion

Figure 6 shows the results of Experiment 2. In the search task, RTs decreased with increasing flanker length. The average RT was 1964 ms in the condition with the shortest flankers (25′) and 1046 ms in the condition with the longest flankers (51′), that is, RTs were almost twice as long with short compared to long flankers. This finding was expected as target-distractor similarity is known to influence search efficiency: the more target and distractors resemble each other, the less efficient is search for the target. Note, however, that the same degree to which target and flankers differ can yield quite different performance when switching target and flanker features (search asymmetries, e.g., Treisman & Gormican, 1988; Wolfe, 2001). Error rates were higher in the condition with the shortest flankers (17%) compared to the other conditions (error rates below 6%).

In the offset discrimination task, the average percent of correct responses was smallest (75.9%) in the condition with the shortest flankers (25′) and performance improved
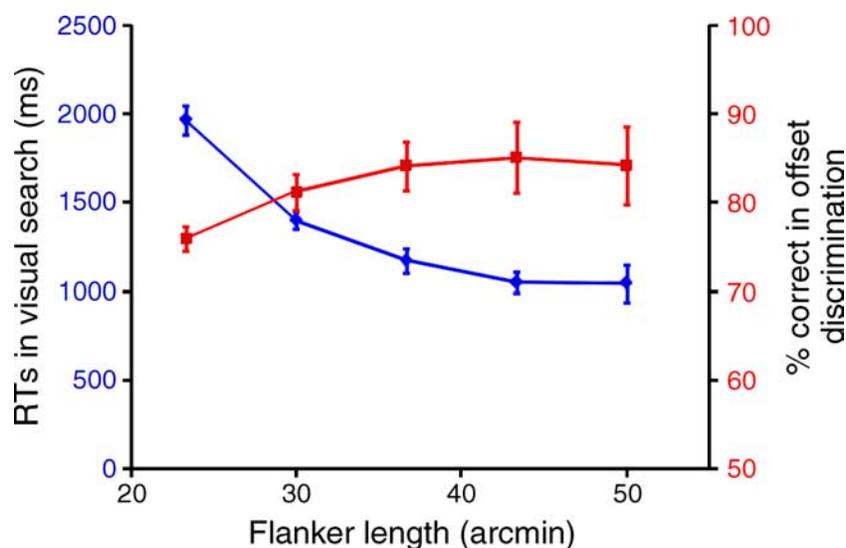

Figure 6. Results of Experiment 2. RTs in visual search and percent correct responses in offset discrimination are shown as a function of flanker length. RTs in the visual search task decreased with increasing flanker length (blue line, left y-axis). The percentage of correct responses in the offset discrimination task increased with increasing flanker length (red line, right y-axis).

with increasing flanker length (maximum at 45′: 85.1%). While the results of all observers in the visual search task had the same pattern, in the offset discrimination task, performance of one of the five observers did not improve with increasing flanker length.

We measured subjective ratings of the "standing out" of the target using the same three observers and the same methodology as in the subjective ratings of Experiment 1. Observers performed 10 trials with each of the five flanker length conditions. Subjective ratings increased from 1.17 in the shortest flanker condition to 5.37 in the longest flanker condition (results of the three remaining conditions, from short to long: 1.73, 2.80, 4.17). The longer the flankers, the higher was the rating of the target standing out from the flankers.

General discussion

Performance on a target can be strongly modulated when it is flanked by contextual elements. While contextual elements can facilitate performance (lateral facilitation; e.g. Ejima & Miura, 1984; Kapadia, Ito, Gilbert, & Westheimer, 1995; Morgan & Dresp, 1995; Polat & Sagi, 1993; Verghese & Stone, 1997), they usually deteriorate performance in the fovea (e.g. Cannon & Fullenkamp, 1991; Levi et al., 1985; Liu, 2001; Westheimer & Hauske, 1975; Westheimer et al., 1976) and in the periphery (crowding; Andriessen & Bouma, 1976; Bouma, 1970; Greenwood, Bex, & Dakin, 2009; He, Cavanagh, & Intriligator, 1996; Pelli et al., 2004; Strasburger, 2005; Toet & Levi, 1992; Tripathy & Cavanagh, 2002). Common explanations for the deteriorating effects of contextual elements are based on lateral inhibition and pooling (e.g., Chastain, 1983; Parkes et al., 2001; Wilkinson et al., 1997). However, there is growing evidence that these explanations are inadequate. For example, increasing the flanker size decreases thresholds contrary to predictions from pooling models (Saarela et al., 2009).

Based on this and other results, we proposed that contextual modulation and crowding increase when the target groups with the flankers and decrease when the target "stands out" from the flankers either by configural cues (Malania et al., 2007; Saarela et al., 2009; Sayim et al., 2008; see also, Livne & Sagi, 2007, 2010, who put forward the importance of flanker–flanker groupings) or by basic features such as color or contrast polarity (e.g., Kooi et al., 1994; Põder, 2007; Sayim et al., 2008; Scolari et al., 2007).

"Standing out" of the target is usually taken to be evident and is not further quantified (for example, Sayim et al., 2008; see also, Kooi et al., 1994; Põder, 2007; Scolari et al., 2007). To investigate the relation between the standing out of a target and contextual modulation or crowding, it is required to quantify how much a target stands out, either by subjective measures (Malania et al., 2007; Saarela et al., 2009) or by objective measures such

as reaction times in visual search. In peripheral vision, crowding was reduced for targets that stood out (pop-out) in visual search by color or motion direction compared to targets that did not stand out (Gheri, Morgan, & Solomon, 2007). Surprisingly, crowding was not reduced for peripheral targets that popped out by orientation (Felisberti, Solomon, & Morgan, 2005). Our results in foveal vision with color stimuli are in line with the results of Gheri et al. (2007). Moreover, we showed that decreasing the similarity between the flankers and a conjunction target by parametrically increasing the length of the flankers yielded a gradual increase of performance. Subjective ratings of the standing out of the target went hand in hand with performance in both tasks, visual search and offset discrimination.

To what extent the neural mechanisms of visual search and flanked vernier discrimination overlap remains an open question. Clearly, the mechanisms are not identical. First, in visual search, directing of attention is essential because the position of the target is not known. In vernier discrimination, the position of the target vernier is known to the observer. Second, flanker interference in vernier discrimination depends stronger on the spacing between the target and the flankers than in visual search. Increasing the element spacing in the conjunction search displays of the present study to 10 arcmin yields no interference in vernier discrimination; however, in visual search, RTs are still long (results not shown; see also Cohen & Ivry, 1991; Nothdurft, 2000).

When a target differs from the flankers in a basic feature, for example color, diminished flanker interference may be explained by reduced interactions between neurons tuned to these basic features (e.g. Blakemore & Tobin, 1972; Cannon & Fullenkamp, 1991; Cavanaugh, Bair, & Movshon, 2002; Petrov, Carandini, & McKee, 2005). However, such an explanation cannot account for the strong interference in configurations as shown in Figure 1B.iii where the green flankers next to the red vernier strongly deteriorate performance while the very same flankers deteriorate performance much less when presented alone (because of their large distance of 6.7 arcmin to the vernier there is no interference from the red flankers closest to the vernier, results not shown; see also Westheimer & Hauske, 1975). A similar argument can be made in regard to the results shown in Figure 1A.iii: Longer flankers may activate end-stopped cells that do not strongly interfere with neurons dedicated to the shorter vernier. However, recently it was shown that interference is reduced when single flanking lines of the same length as the vernier are made part of a figure (Sayim et al., 2010; see also object superiority effect, e.g., Weisstein & Harris, 1974). In regard to these findings, it seems neither likely that the present results of Experiment 1 are merely due to local color differences, nor that the results of Experiment 2 are due to local size differences.

We propose an explanation on the level of perceptual organization: When the target perceptually groups with the flankers, accessibility of the target is reduced and the

processing of the individual features of the target is degraded. If the target stands out from the flankers—in other words, does not group with the flankers—access to the individual target features is not impaired (for grouping effects in backward masking see Herzog & Fahle, 2002). This kind of perceptual grouping presumably resembles processes involved in texture perception resulting in the inaccessibility to the individual elements of the texture (Parkes et al., 2001). Importantly, the perception of a target as part of a group or texture does not only depend on the proximity between the target and the flankers but on several other factors, such as similarity, regularity, and the global layout of the stimulus. This seems at odds with propositions of flanker interference being caused by fixed-size receptive fields (integration fields; Pelli et al., 2004).

To conclude, grouping of the target with the flankers and the degree to which a target stands out from the flankers are the main determinants of contextual modulation. Importantly, this proposition does not imply claims about the underlying neural mechanisms of contextual modulation. Whether or not dynamic lateral inhibition can explain such effects has to be investigated in future research (Hermens, Luksys, Gerstner, Herzog, & Ernst, 2008; Herzog, Ernst, Etzold, & Eurich, 2003).

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