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Latency effects in orientation popout

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Abstract

A target that differs in orientation from neighboring lines and "pops out" has been found to evoke larger responses in cortical V1 cells than lines in the uniform texture surround which do not popout (e.g., *Journal of Neurophysiology* 67 (1992) 961). If this is more than a coincidence of observations, physiological properties of contextual modulation should be reflected in the perception of salience. In particular, as the differential suppression from texture surround has been reported to be delayed, target salience may be affected by the history of surrounding lines, i.e. by their orientation before the target was presented. This was tested using a feature flicker paradigm in which target and background lines changed their orientations (Experiment 2). All subjects ($N = 4$) indicated a benefit in target detection when target orientation was not previously present in the surround. A control experiment showed that this effect was not caused by the purely temporal aspects of asynchronous stimulus presentation (Experiment 3). To distinguish this effect from other sources of delayed processing, Experiment 1 compared the performance in target detection and target identification tasks, for single-lines and popout targets. All subjects required longer stimulus presentation time to identify the orientation of a single line than to detect the line itself, indicating that orientation coding needs longer processing than encoding stimulus onset. However, most subjects needed even longer presentations to detect popout, suggesting that the processing of orientation contrast adds to this delay. In an appendix, putative response variations of V1 cells to asynchronous flicker are computed.

Keywords: Salience; Orientation contrast; Contextual modulation; Flicker; SOA; Psychophysics

1. Introduction

A line that differs in orientation from neighboring lines is salient and pops out (Foster & Ward, 1991; Nothdurft, 1992; Treisman & Gormican, 1988). The neural mechanism of this striking perceptual phenomenon has not yet been identified, but response variations consistent with this effect have been observed in single cells of area V1 (Kastner, Nothdurft, & Pigarev, 1997, 1999; Knierim & Van Essen, 1992; Lamme, 1995; Lee, Mumford, Romero, & Lamme, 1998; Nothdurft, Gallant, & Van Essen, 1999; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Zipser, Lamme, & Schiller, 1996). In many cells, a line in the receptive field surrounded by lines outside the field evoked a larger response when the surrounding lines were orthogonal than when they were parallel to the center line. This is consistent with the salience of an orthogonal line in a homogeneous texture field, and it has been proposed that salience variations associated with orientation contrast may resemble response variation by contextual modulation in V1 (e.g., Kastner et al., 1997; Knierim & Van Essen, 1992; Li, 2002; Nothdurft, 1994a,b; Nothdurft et al., 1999). In order to investigate the proposed link of single-cell responses and visual perception, I have recently studied a number of properties of perceptual popout that are predicted by physiological observations but had not yet been identified perceptually (Nothdurft, 2000a–c). One of these was the dynamics of orientation popout (Nothdurft, 2000b). Recordings in behaving and anesthetized monkeys had shown that response differences due to differential contextual modulation occur with a delay in onset of the population response (Bair, Cavanaugh, & Movshon, 1999; Knierim & Van Essen, 1992; Lamme, 1995; Lee et al., 1998; Nothdurft et al., 1999; Zipser et al., 1996). Therefore, if the salience of an orthogonal line is related to the response modulation in V1, the detection of popout should be delayed against the detection of the line itself. This was indeed found

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(Nothdurft, 2000b); subjects needed longer stimulus presentations to detect a line that popped out from orientation contrast than to detect a single line. A second proposal was also verified. Since contextual modulation is delayed, the dynamics of saliency effects from orientation contrast should be different from those based on the onset of responses, e.g. saliency effects from luminance contrast. Indeed, when target and background line features were rapidly exchanged ("feature flicker"), targets defined by orientation contrast lost their salience at lower frequencies than targets defined by luminance contrast (Nothdurft, 2000b).

Although these observations strengthen the assumption that salience from orientation contrast is encoded by contextual response modulation in V1, the comparison of dynamic properties may go one step further. If the onset of differential responses in single cells is linearly related to the presentation of the different texture surrounds, then the response difference between a line with orthogonal surround (the popout target) and lines with parallel surround (the lines in the uniform texture field around the target) should be larger if the surrounds are presented earlier so that the (delayed) suppression from the surround can modulate the line response right from the beginning. This prediction was tested in the present study.

Note, however, that the longer processing of orientation popout is not necessarily due to the neural mechanisms encoding feature *contrast*. The evaluation of line orientation itself may be slower than the evaluation of the presence of the line, and the observed dynamics may simply reflect this difference (see Motoyoshi & Nishida, 2001, for an elegant investigation of this interdependence). The response of an orientation selective cell in area V1 does not indicate *when* stimulus orientation is optimally encoded in the brain. Indeed, early recordings from orientation selective cells in the cat seemed to suggest that tuning curves sharpen with the ongoing response and hence orientation selectivity may improve with time (cf. Hubel & Wiesel, 1959, Fig. 3), although such a dynamic sharpening of orientation tuning has not always been confirmed (Celebrini, Thorpe, Trotter, & Imbert, 1993; Volgushev, Vidyasagar, & Pei, 1995; but see Ringach, Hawken, & Shapley, 1997). Thus, while the proposal from physiology was that detection of orientation contrast would be delayed against the detection of a single line, and this proposal was confirmed (Nothdurft, 2000b), it would be interesting to know whether or not the detection of an orthogonal line (popout) would be delayed against evaluation of line orientation itself.

The present study addressed these two questions. Experiment 1 compared the dynamics of target detection and target identification both with single lines and with lines that popped out from orientation contrast. It was found that the identification of target orientation indeed required longer stimulus presentations than simple detection of the target. However, the detection of popout from orientation contrast required even longer presentations, although this difference was small for one subject. Experiments 2 and 3 addressed the latency question raised above and investigated whether orientation changes applied to targets and background lines in asynchrony, have an effect on target visibility.

2. General methods

This study is a continuation of Nothdurft (2000b) and is based on similar experimental paradigms. Stimulus patterns were made of line elements at one of two oblique orientations (Fig. 1). There was either a single line or a texture-like arrangement of lines with one line orthogonal (popout target). Subjects performed one of two tasks, (i) a *target detection task* in which they had to indicate the location of the target being displayed on either the left or right half of the screen; (ii) a *target identification task* (not tested in Nothdurft, 2000b) in which subjects had to indicate whether the target line was tilted to the left or to the right. All tasks were performed under fixation of a small dot in the middle of the screen. In Experiment 1, stimulus presentation time was varied and

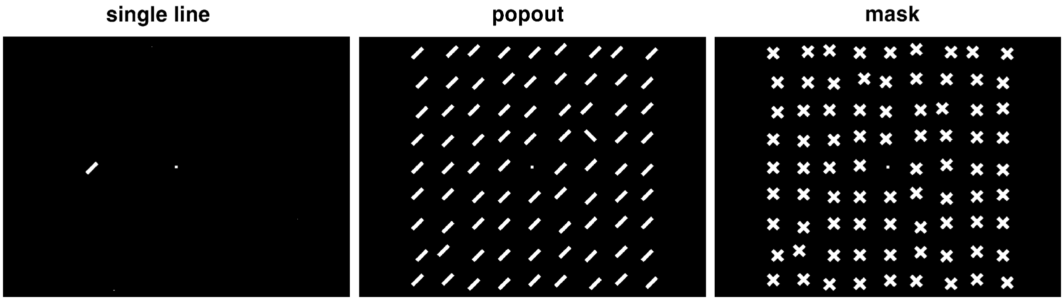

Fig. 1. Stimulus patterns. In Experiment 1, targets were single lines or lines with orientation contrast, which subjects had to detect or to identify. Patterns were masked soon after presentation. In Experiment 2, popout patterns were alternated with complementary pictures, in which all lines were replaced by their orthogonal counterpart. Subjects had to detect the target. In Experiment 3, lines were randomly oriented (Fig. 8) and replaced by orthogonal lines; target and background lines flickered out of phase.

performance accuracy was measured at each of several durations, to reveal the growth of performance with the signal. In Experiments 2 and 3, different popout patterns were presented in sequence so that target and background lines alternated with their orthogonal counterparts (feature flicker). Performance accuracy was measured for different flicker frequencies and for in-phase and out-of-phase target and background flicker.

2.1. Stimuli

Stimuli (cf. Fig. 1) were displayed on a 15″ monitor placed 67 cm in front of the subject. Lines (0.9 deg × 0.25 deg) were arranged in a 9 × 9 texture field (1.8 deg raster width, with random jitter of up to ±0.2 deg at each position). The center element was omitted to avoid interference with the fixation point. Targets were presented at 3.7–5.5 deg eccentricity on the left or right side of the screen and were randomly chosen to display one of the two oblique orientations; the other lines were either blanked (single-line condition) or all orthogonal (popout condition). Masks displayed superimposed line elements at both orientations; even single-line targets were masked with the entire texture field. Monitor refreshing rate was 100 Hz; stimulus durations were synchronized to this rate. Lines (10.5 cd/m^2) and masks (32 cd/m^2) were white on dark background (3 cd/m^2); the fixation point (0.1 deg × 0.1 deg) was green (47 cd/m^2). Stimulus sequences differed between the experiments and will be described below.

2.2. Subjects

Four subjects (21–53 years; two females) including the author participated in experiment; three of them received payment for the time they invested. All subjects had normal or corrected-to-normal visual acuity. Three of them had performed similar tests before; one subject (EB) had carried out target detection and identification tasks but had not been tested with feature flicker. All subjects except the author were unaware of the purpose of the experiments.

2.3. Procedure

Subjects indicated their choice by pressing specified keys on a computer keyboard. Targets located in the left half of the screen and targets tilted to the left were associated with a left-hand key, targets located in the right half or tilted to the right with a right-hand key. There was no time pressure for the response. About half a second after the subject's reaction a new trial started with the 1 s presentation of the fixation point.

The different series of experiments were performed in sequence. At the beginning of each series, subjects were given a test run to familiarize them with the stimulus conditions and with the tasks. Fixation was controlled by means of a video camera focused on the subject's eyes. Since all subjects kept their eyes still right from the beginning of the study, only occasional controls were made in later sessions. Stimulus durations in Experiment 1 were too short to take advantage by shifting the eyes.

Tests were blocked for the task (detection vs. identification) and for target type (single line vs. popout; Experiment 1) or cycle time (Experiments 2 and 3). Blocks contained 30 repetitions of each individual test condition and were repeated in an interleaved fashion so that, finally, each data point resembled measurements from at least 90, but often 120 or more repetitions of the same stimulus condition, for every subject. Performance of a single test block took 10–25 min; subjects could pause whenever they wished. Tests were carried out in sessions of up to 2 h; 7–8 sessions were needed to complete all experiments. Subject HCN performed a number of additional tests.

3. Experiment 1: detection and identification of single-line and popout targets

Nothdurft (2000b) reported that the detection of a target that pops out from orientation contrast requires longer stimulus presentation than the detection of a single line. This was assumed to reflect the delayed manifestation of differential contextual modulation in V1, which generates a larger response to the popout line than to lines in the surrounding uniform texture field (Knierim & Van Essen, 1992; Nothdurft et al., 1999). However, orientation contrast can only be evaluated if line orientation is represented in the brain, and it would be interesting to see whether the longer processing time needed to detect orientation popout is explained by the time needed to encode line orientation, or goes beyond such an effect. A straightforward test would be to compare the dynamics of popout target detection with those of an orientation discrimination task.

3.1. Methods

Four different tests were included in this experiment (cf. Fig. 1). A single-line and a popout target had each to be detected or to be identified. Targets were randomly tilted to the left or right and occurred randomly on either side of the display. Each trial began with a 1 s presentation of the fixation point, then the stimulus pattern was shown for variable duration and subsequently masked. The mask disappeared after 500 ms.

3.2. Results

Performance in these four tests differed considerably (Fig. 2). Subjects could generally detect single lines of

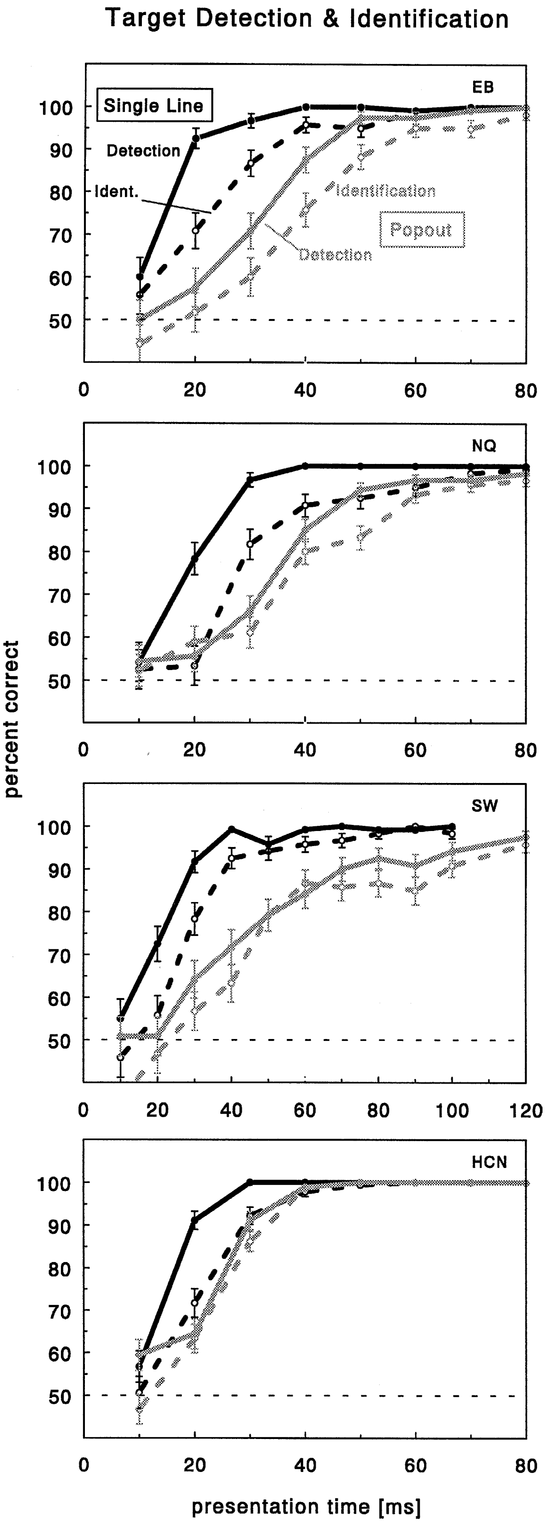

Fig. 2. Detection and identification of single-line and popout targets. Individual data of all four subjects. Error bars give the confidence range of each measurement, corresponding to the standard error of the mean (SEM). With increasing presentation time, performance increases in each task. Targets were generally detected faster than they were identified, and single lines faster than popout targets, irrespective of the different speed at which subjects performed the tasks (note different scales).

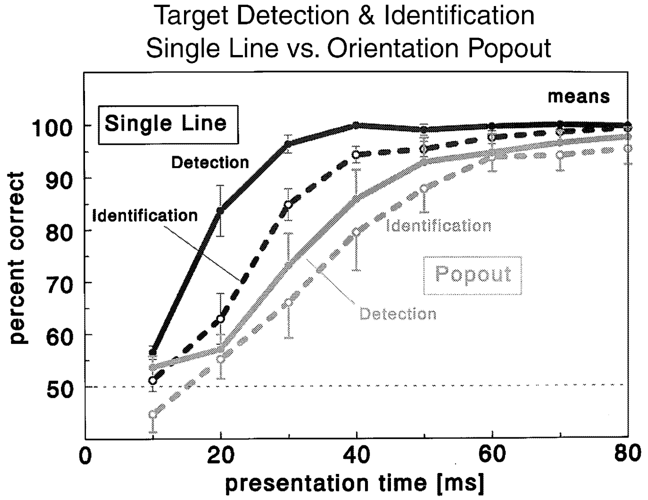

Fig. 3. Mean data and SEM of Fig. 2.

shorter durations than popout targets, and required longer presentation time to identify a target than to detect it. However, these differences were not equally strong for all subjects. Whereas most subjects revealed a considerable shift of performance between the tasks, the curves of one subject fell closer together (HCN). Nevertheless, the ranking of performance was consistent among subjects and was also apparent in the mean data (Fig. 3). Single lines could be identified from shorter presentations than could popout targets be detected, indicating that the evaluation of orientation contrast added to the processing time needed to encode orientation.

A repeated-measures two-factor ANOVA revealed significant differences between the single-line and the popout target detection task [$F(1,3) > 47.8; p < 0.0001$] as was already shown in the previous study (Nothdurft, 2000b), in which three of the four subjects also participated. Popout detection was also significantly delayed relative to single-line identification [$F(1,3) > 7.63$; $p < 0.01$]. In general, the same task for different targets led to significant differences; not only the detection but also the identification of popout targets needed significantly longer presentation times than detection and identification of a single line [$F(1,3) > 24.2$; $p < 0.0001$]. Finally, target identification was significantly delayed compared with target detection both for single lines [$F(1,3) > 35.4$; $p < 0.0001$] and popout targets [$F(1,3) > 4.6$; $p < 0.05$].

3.3. Discussion

There were reliable differences in performance between the different tasks. In particular, single targets were detected faster than popout targets, as found in the previous study (Nothdurft, 2000b).

However, the question behind the experiment was whether or not this difference can be explained by the time needed to encode line orientation in the brain: if representation of line orientation were delayed compared to the representation of line onset, then the detection of orientation popout would necessarily take longer than the detection of a single line. The data do confirm the slow encoding of orientation information, but they do not indicate that the slower detection of orientation contrast is due exclusively to this effect. All subjects needed longer stimulus presentations to identify the orientation of a single line than to detect it (Fig. 2, black continuous vs. dashed curves). But most of them needed even longer presentations to detect the orthogonal popout target (gray, continuous curves). This suggests that encoding of salience from orientation contrast is delayed beyond the (delayed) encoding of orientation. Note, however, that this additional delay was very small for subject HCN.

This is in disagreement with recent observations by Motoyoshi and Nishida (2001), who measured the temporal-frequency limits of local orientation coding and orientation-based texture segregation and found similar cut-off frequencies for both properties. The authors concluded that the temporal limit for orientation-based texture segregation depends *only* on that of local orientation coding. This was not generally confirmed in the present study, but the reason for this discrepancy is not yet clear. On the one hand, there were several methodological differences between the studies. In the present study, local orientation coding was measured explicitly by having subjects identify the orientation of a single line; Motoyoshi and Nishida measured local orientation coding indirectly, with stimulus patterns that were designed to lose orientation information when temporally fused. Another distinction is the usage of different stimuli; Motoyoshi and Nishida used second derivatives of Gaussians rather than bars, and studied texture segregation, not popout. On the other hand, however, the small differences between single-line identification and popout detection for subject HCN suggest that the processing time for detecting orientation contrast is not always above that of orientation coding but may perhaps be reduced with practice. Furthermore, orientation coding and orientation-based popout were measured, in the present study, in different patterns and it is not obvious that this difference did not affect performance. In fact, several studies have shown that the responses of V1 cells to a single line are reduced when the line is presented with texture surround (Kapadia, Westheimer, & Gilbert, 1999; Li, Thier, & Wehrhahn, 2000; Nothdurft et al., 1999). But latency shifts are rather small (Li et al., 2000) and perhaps too small to account for the differences seen in Fig. 3.

Interestingly, single lines were not only *detected* faster than popout targets; they were also *identified* faster. At a first glance, this is astonishing. Whereas the detection of a single line may be based on stimulus properties (e.g., luminance onset) other than the detection of orientation popout, hence the different dynamics in target detection are perhaps not surprising, target identification should always be based on the neural representation of line orientation. Why should it take longer to identify the popout target than to identify the single line? Part of this effect may again be due to the attenuation of neural responses by texture surround (Kapadia et al., 1999; Li et al., 2000; Nothdurft et al., 1999).

Another explanation might be that targets must be localized before their orientation can be identified. Since single lines were detected faster than popout targets, they might also be identified faster. Such a delay between salience detection and target identification would be consistent with observations on the dynamics of attention shifts to salient targets (Nothdurft, 2002).

In conclusion, Experiment 1 has shown that detection of orientation contrast requires longer stimulus processing than detection of a single line. For most subjects, this time exceeded even that for orientation coding. Given the uncertainty of when orientation is encoded in the response of a cell population in V1, the results are consistent with the proposal that popout from orientation contrast manifests with a delay compared to stimulus onset, as it might be associated with (delayed) differential contextual modulation in area V1. The second part of this study will investigate if and how this delay affects the detectability of flickering popout targets.

4. Experiments 2 and 3: the effect of asynchronous target and background flicker on target visibility

Contextual modulation of line responses in V1 manifests in two effects, (i) responses are generally suppressed by texture surround, and (ii) the suppression is stronger when the surrounding lines are parallel. Only this latter, differential effect is delayed and proposed to account for the salience of popout targets as in Fig. 1. If this suppression is linearly related to the onset and offset of parallel texture surround, target salience should depend not only on the actual popout display but also on the history of the lines around the target before that pattern was shown. The aim of Experiment 2 was to test this prediction. Is a popout line more salient when the surround was orthogonal before the target is switched on than when it was parallel to the orientation of the target?

The question was studied using a feature flicker paradigm (Harasawa & Sato, 1999; Motoyoshi & Nishida, 2001; Nothdurft, 1999, 2000b) in which target and background lines frequently change their orientations. By having target and background lines switch in asynchrony, it should be possible to distinguish the dynamics of differential effects from parallel and orthogonal surrounds. However, onset delays themselves are recognized by the visual system (Leonards, Singer, & Fahle, 1996; Theeuwes, 1991; Ziebell & Nothdurft, 1999) and the synchronized flicker of all background elements together may help to detect the target (Lee & Blake, 1999). To exclude the possibility that variations in target detectability were simply due to the asynchronous presentation of target and background lines, irrespective of their orientation contrast, the detectability of pure timing effects also had to be measured (Experiment 3).

4.1. The "C4F" paradigm

One way to study the dynamics of popout from feature contrast is to measure the "critical feature flicker fusion frequency" (C4F; Nothdurft, 2000b). The paradigm is illustrated in Fig. 4A. In a pattern with feature contrast (schematic drawing on the left), target and background features are regularly exchanged (center and right-hand drawings). In each pattern, the target pops out from orientation contrast. However, this popout is not seen if alternation rates are too fast to be resolved by the neural mechanisms encoding feature contrast; the target would then remain undetected even though the feature flicker itself might be observed. In the mean data of five subjects, only flicker rates below 7.7 Hz produced better than 0.5 target detectability for orientation contrast (Nothdurft, 2000b). Targets defined by luminance contrast, for example, were seen up to considerably higher flicker rates (17.5 Hz). The inverse of flicker frequency is cycle duration, T; for the C4F of orientation popout (7.7 Hz) each stimulus pattern must be shown for about 65 ms ($T/2$).

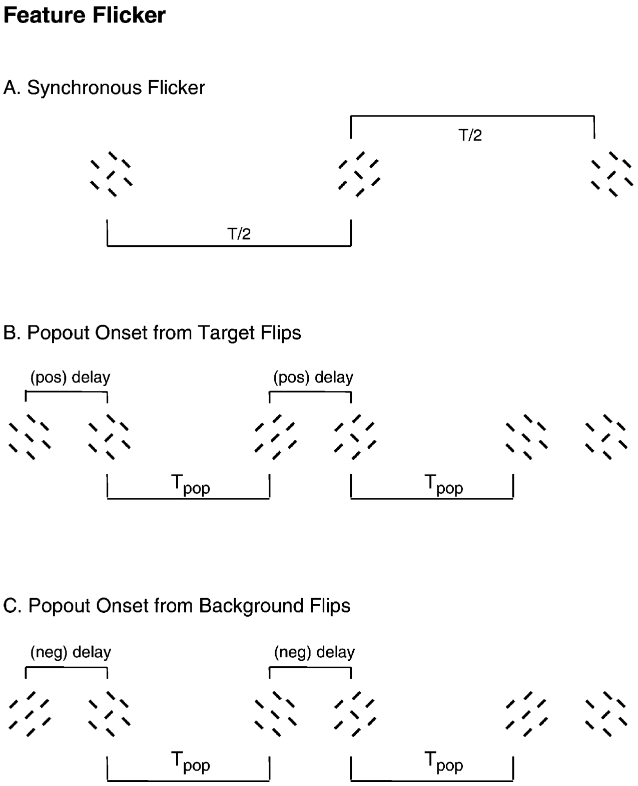

Fig. 4. Paradigm of Experiment 2. In popout patterns like Fig. 1, target and background lines change orientation. For synchronous flicker (A), the popout target is always present but occurs at different orientations. For asynchronous flicker, two sequences are distinguished (B, C) in which popout is either achieved by an orientation change of the target or by orientation changes of background lines.

Fig. 4B and C illustrate the stimulus sequences when target and background elements flicker out of phase; delays indicate the time when target orientation changes relative to the last, or next orientation change of background elements. The sequence of popout patterns is now interrupted by patterns with uniform texture. If cycle duration is held constant, the time during which the target pops out (T_{pop}) is reduced but the frequency at which either target or background elements flip is not affected. The length of the delay plus T_{pop} always add to half a cycle, and longest popout presentations are obtained for zero delays ($T_{\mathrm{pop}} = T/2$), when target and background lines flip in phase (as sketched in Fig. 4A). Vice versa, the maximum delay is $T/2$, which results in uniform texture patterns with no popout at all ($T_{\mathrm{pop}} = 0$). Fig. 4B and C distinguish two cases. In Fig. 4B, the popout condition is reached by an orientation change of the target; the later change of background orientation makes the popout disappear. In Fig. 4C (sketched for the same T_{pop}), the popout condition is achieved by an orientation change of the background lines; the popout effect disappears when the target is changed. If suppression from parallel lines in the surround is delayed, we should expect poorer target visibility in Fig. 4C than in Fig. 4B, for the same T_{pop}, since suppression from background lines parallel to the target might still be effective in Fig. 4C but not in Fig. 4B. Thus, with the nomenclature used here, positive delays should produce better target detectability than negative delays of the same duration.

4.2. Experiment 2: feature flicker

This section presents experimental data obtained with asynchronous feature flicker in a target detection task.

4.2.1. Methods

Stimuli were line patterns as in Fig. 1 (center) with an orthogonal popout target that subjects had to detect. Each line in the pattern alternated with its orthogonal counterpart, so that, in synchronous flicker, the target always differed from the surround (cf. Fig. 4A). In the original experiment (Nothdurft, 2000b), flicker rate was varied to find the frequency at which the target lost its salience and could not be detected. In the present study, not only flicker frequency but also the phase of target and background flips were varied.

Stimulus presentation was synchronized to the frame rate of the monitor (100 Hz). Each trial started with a 1 s presentation of the fixation point; then flicker sequences were shown for 1 s. Subjects were asked to keep their eyes on the central fixation point. To avoid onset and offset effects with medium flicker frequencies, each stimulus period was started and terminated with a 60 ms period (three cycles) of the fastest flicker possible (50 Hz). (In an additional series of experiments with subject HCN, no difference was found when the initial fast flicker period was omitted, provided that flicker sequences started with the uniform stimulus pattern (not possible for zero delay). However, when the stimulus sequence started with the popout display, the target was, at medium durations T_{pop}, sometimes detected from the first pattern even if it was not seen in the later flicker sequence, in close agreement with Beaudot (2002).

Subject HCN performed the most extensive testing in this study. Based on his data, three cycle durations were selected for the experiments which the other subjects were asked to perform.

4.2.2. Results

Fig. 5 shows target detection rates of subject HCN, for a variety of flicker frequencies. The continuous (but flickering) presentation of popout patterns did not always allow the target to be easily detected; except for the longest cycle duration ($T/2 = 200$ ms) performance with synchronous flicker (delay $= 0$ ms) was generally below 100%. With increasing delay, performance increased, both for positive and negative delays and then dropped down to chance when stimuli displayed uniform textures with no popout target at all (delay $= T/2$).

Except for the fastest flicker rates tested, the curves show an obvious asymmetry in performance for delays close to $T/2$. Targets were seen better when popout was obtained from a target change (positive delays; continuous curves) than when obtained from a change of background orientation (negative delays; dashed curves).

There was a similar though less pronounced performance asymmetry at short delays, where preferences were reversed and targets were seen better in negative than in positive delays.

To illustrate the variations with flicker, detection rates for different popout presentations (T_{pop}) were

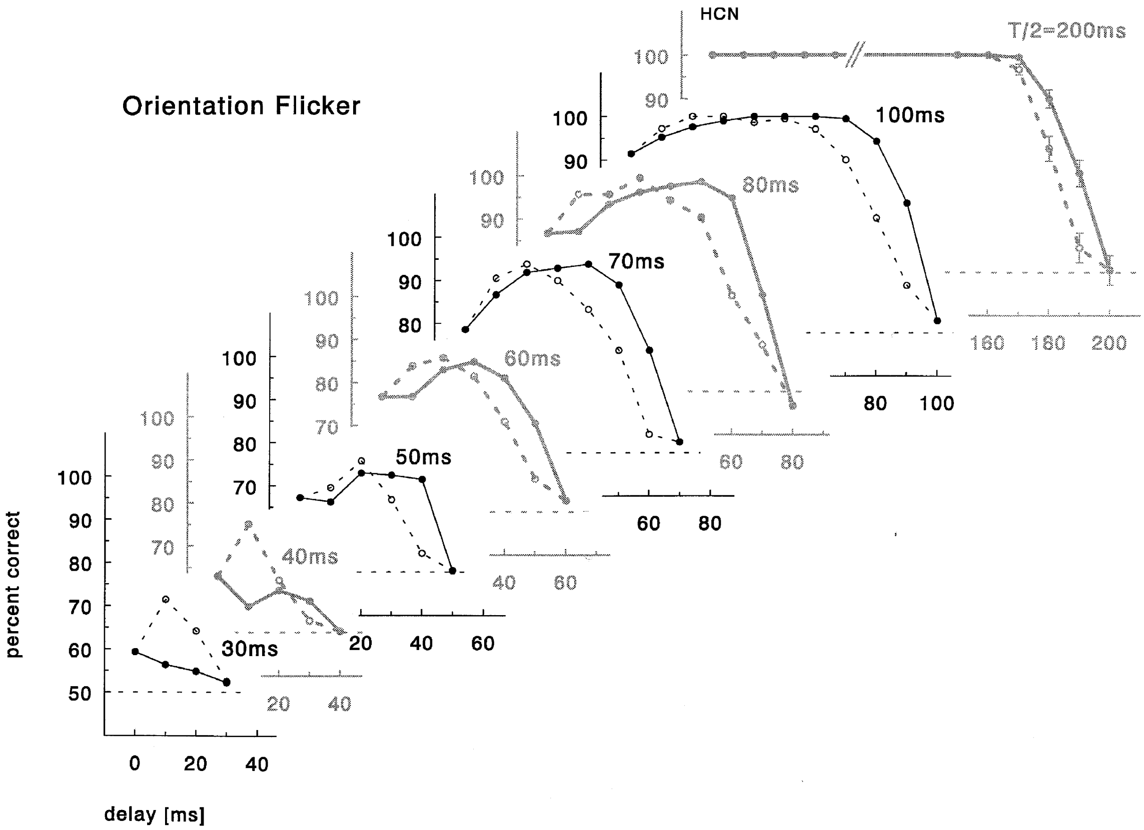

Fig. 5. Data of subject HCN in Experiment 2. Numbers give half cycle time, $T/2$, in milliseconds. Errors bars in $T/2 = 200$ ms indicate the confidence range of each measurement, corresponding to SEM. The value varies with the level of performance; error bars in other flicker rate conditions were similar. Performance in target detection differed between positive (continuous) and negative delays (dashed), as qualitatively predicted from delayed contextual modulation. Targets were generally detected better in asynchronous than in synchronous flicker and were seen best at long positive and short negative delays.

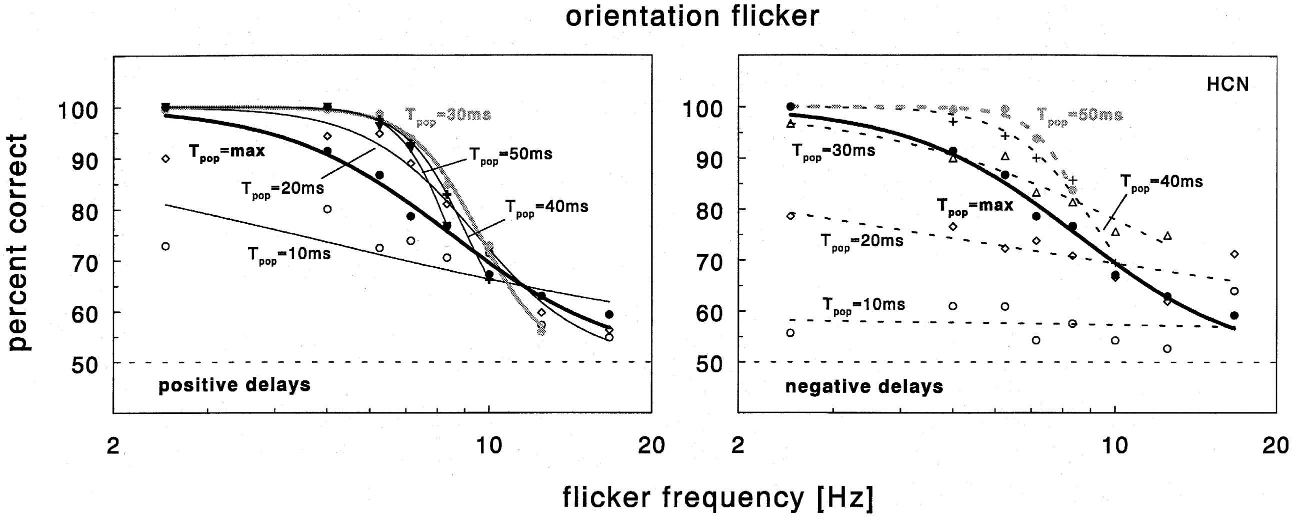

Fig. 6. Performance variations with flicker frequency; data re-plotted from Fig. 5. Target detection generally deteriorated with increasing frequency. Steepest curves, i.e. best performance at medium frequencies, were not obtained for synchronous ($T_{\text{pop}} = \max$; thick line) but for asynchronous flicker. Positive (A) and negative delays (B) produced similar curves except that performance at negative delays was generally diminished and longer popout presentations were needed to reach maximal performance ($T_{\text{pop}} = 30$ vs. 50 ms; gray lines).

plotted against flicker frequency (Fig. 6). With increasing flicker frequency, performance generally decreased, but steepest curves (best performances) were not obtained for the maximal popout duration (thick lines) but for asynchronous flicker with shorter presentations of the popout target (gray lines). For positive delays, presentations of $T_{\text{pop}} \geqslant 30$ ms produced the steepest curves and, hence, the best performance at intermediate flicker frequencies. Only for the shortest popout presentation ($T_{\text{pop}} = 10$ ms) was performance worse than for the synchronous flicker condition, $T_{\text{pop}} = \max$. A similar improvement of performance was seen for negative delays though shifted towards longer presentation times. The steepest curve, i.e. best performance was obtained for $T_{\text{pop}} = 50$ ms; two curves, $T_{\text{pop}} = 10$ and 20 ms, fell below that of the synchronous case.

The asynchronous flicker experiment was repeated, for three cycle durations, by the three other subjects (Fig. 7). The results were consistent and showed the same characteristic properties as those of subject HCN. All subjects revealed strong differences in performance at short popout presentations (delays close to $T/2$), in agreement with the expected differences for positive and negative delays. These asymmetries were seen at all three flicker rates tested. There also were asymmetries, in the opposite direction, at short delays (delays close to 0) but these were generally less pronounced. Popout targets were less easily detected when target and background lines flipped together (delay 0 ms) than when either target or background flicker preceded. Performance generally diminished towards high flicker rates (short $T/2$).

The different strength of asymmetry effects at large vs. short delays is well seen in the mean data of all four subjects (Fig. 7B). Two-factor ANOVA for repeated measures revealed that performance differences at large delays were significant, whereas those at short delays were not. The differences between positive and negative delays in the four shortest T_{pop} conditions were highly significant for $T/2 = 100$ and 200 ms [$F(1,3) > 22.0$; $p < 0.0001$]; they also were significant in the three shortest T_{pop} conditions of $T/2 = 60$ ms [$F(1,3) > 4.85$; $p < 0.05$]. When the same popout durations T_{pop} at different flicker frequencies were looked at, asymmetry effects for $T_{\text{pop}} = 10$ and 20 ms were each highly significant [$F(1,3) > 27.6$; $p < 0.0001$]. For $T_{\text{pop}} = 30$ ms, the strength of asymmetry effects began to diminish [$F(1,3) > 5.31$; $p < 0.05$] because 100% performance was reached in some conditions. In contrast, the differences at short flicker delays generally did not reach significance ($p > 0.26$).

4.2.3. Discussion

Experiment 2 revealed several interesting effects. First, asynchronous flicker indeed produced performance differences beyond the variations associated with the duration of popout presentation. In particular, for short popout presentations (long delays) detectability varied considerably between conditions in which popout was obtained from an orientation change of the target (so that the surround was always orthogonal to the new orientation of the target) and conditions in which popout was generated by changing background lines (so that the surround was previously parallel). This performance asymmetry was seen with all flicker frequencies above $T/2 = 50$ ms (cf. Fig. 5). Second, asynchronous flicker was generally found to improve target visibility over that of synchronous flicker. This effect was

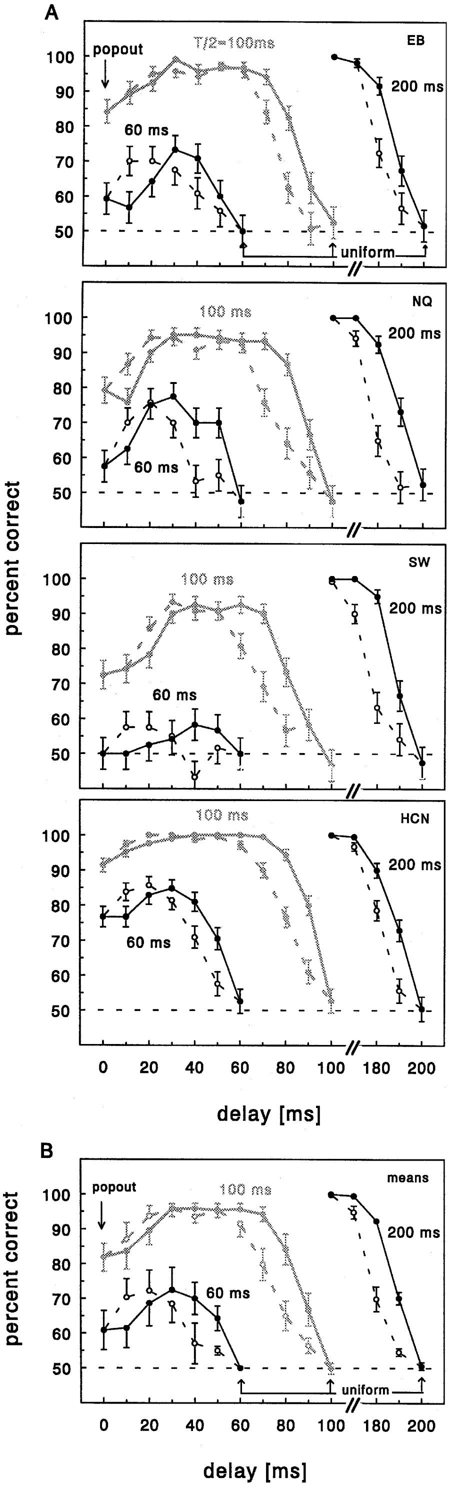

Fig. 7. Replication of Experiment 2 with three additional subjects (data of HCN re-plotted from Fig. 5). Individual data (A) and means (B) show consistent variations in performance and the same asymmetry effects as observed with HCN. Error bars give the confidence range corresponding to SEM (A) and the SEM (B), respectively.

naturally most pronounced at medium and high flicker rates where performance with the synchronous flicker was not yet perfect.

The observed asymmetry at long delays is exactly what is to be expected on the basis of single-cell responses in V1 (see Appendix A). However, two observations are not consistent with a simple model of delayed contextual modulation, the increased performance at short negative delays, and the fact that performance asymmetries are even reversed at these delays. The (presumably delayed) suppression from parallel surround should *always* be stronger, thus target salience always be reduced, for negative than for positive or zero delays (see Appendix A).

Note that targets were salient not only from their (momentary) orientation contrast but also from their different flicker compared to background lines (Leonards et al., 1996). Thus, targets might have been detected because they were flickering out of phase. This would explain why performance increased in asynchronous presentations, even for negative delays. To understand the unexpected performance asymmetry at short delays, it would be helpful to re-consider the underlying stimulus sequence. The *sign of the delay*, positive or negative, indicates in which part of the pattern an orientation flip made the target pop out from orientation contrast; it thus tells about the previous orientation of lines in the surround when the popout target was displayed. It does not indicate, however, the temporal sequence of target and background flicker in these replacements. In fact, a small positive delay (close to 0 ms) corresponds to a target change shortly *after* the background change, whereas a large positive delay (close to $T/2$) corresponds to target switching shortly *before* background. These sequences are reversed for negative delays (see Fig. 4). Thus, if the visual system would detect flicker sequences in which the single line is changed first better, targets should be detected better at short negative and long positive delays, which is exactly the finding of Experiment 2. In order to exclude the possibility that the observed performance asymmetries were due to a particular sensitivity for the sequence of target and background orientation flips, independent of orientation popout, we should compare these data with the performance in a task in which targets had to be detected from flicker asynchrony alone.

4.3. Experiment 3: control for purely temporal effects

In Experiment 3, target detection was measured in asynchronous orientation flicker with no orientation popout. In a first version of this experiment, target and background lines did not change orientation but were blanked for half of the cycle, so that target and background lines were onset and offset with a delay relative to each other. However, the strong luminance flicker associated with this display affected performance and thus rendered the comparison with Experiment 2 difficult. In a second version, which is presented here, all

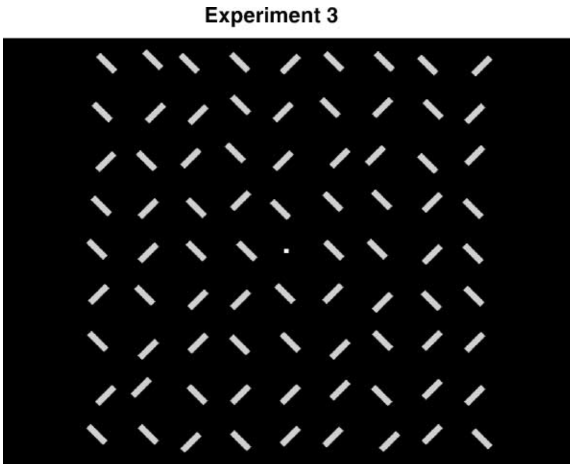

Fig. 8. Stimulus patterns as used in Experiment 3. All lines simultaneously flipped into orthogonal lines, except the "target" line which flipped at a delay. Subjects were asked to indicate on which side of the screen the target was located.

lines regularly changed their orientation, as in Experiment 2, but the distribution of line orientations was random so that no single line popped out (Fig. 8).

4.3.1. Methods

The stimuli of Experiment 3 resembled those of Experiment 2 except that lines were randomly assigned to one of the two oblique orientations (Fig. 8). During presentation, each individual line was regularly replaced by its orthogonal counterpart; as in Experiment 2, "background" lines all flipped in synchrony and at various delays before and after the target line. Subjects were asked to detect the target that "differed" from the rest.

Subject HCN performed Experiment 3 for a variety of flicker frequencies. For all other subjects, testing was restricted to the three flicker rates in Experiment 2.

4.3.2. Results

Fig. 9A illustrates performance of subject HCN in Experiment 3. The larger the delay between target and background orientation flips, the better the target was seen, confirming that flicker asynchrony itself was well detected. The sensitivity varied only slightly with flicker rate; the target was not detected in very fast flicker ($T/2 = 40$ ms) but there were almost no differences for flicker periods above $T/2 = 80$ ms.

Different to Experiment 2, there were no pronounced asymmetry effects in Experiment 3. For $T/2 = 60$ ms, targets were detected slightly better when they flipped before the background lines than when the background lines flipped first, but this asymmetry was reversed at slower flicker rates (e.g., $T/2 = 200$ ms).

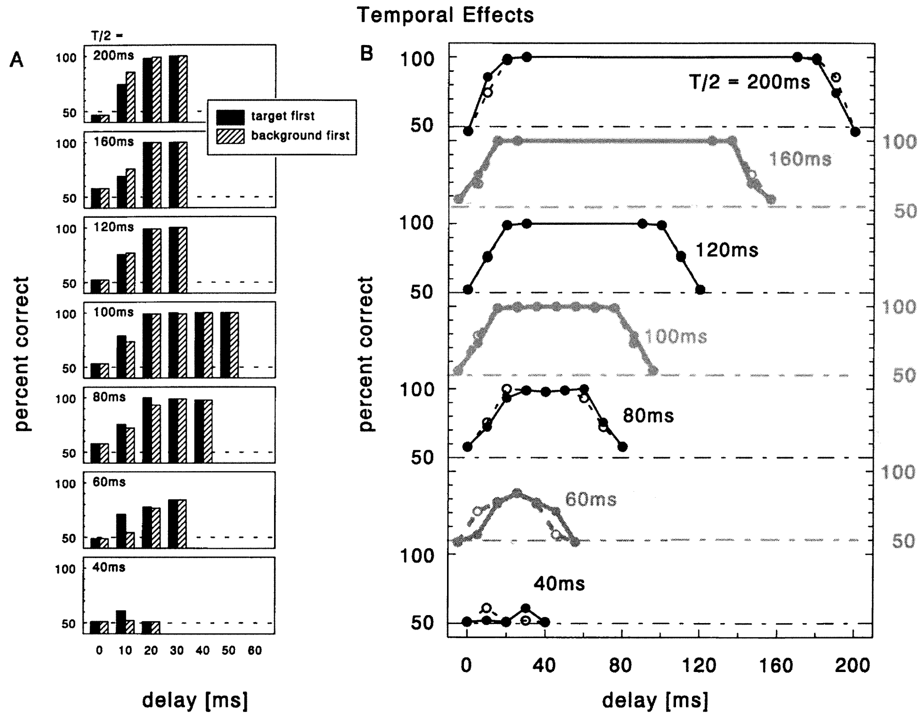

Fig. 9. Performance of subject HCN in Experiment 3; targets could only be seen from asynchronous orientation changes. (A) Performance varied with flicker rate (graphs) and asynchrony ("delay"). For some flicker rates, targets were seen better when their orientation changes preceded that of the background lines; for other flicker rates perferences were reversed. (B) Data re-plotted in the scheme of Fig. 7 to illustrate the contribution of temporal effects upon the asymmetries seen in Experiment 2. Only $T/2 = 60$ ms produced a small asymmetry effect as in Experiment 2; slow flicker rates sometimes produced reversed effects.

In Fig. 9B the data are re-plotted in the format of Figs. 5 and 7 to illustrate the possible effect which pure onset delays might have had on target detection in Experiment 2. Since the same flicker sequences correspond to different values for positive and negative delays, curves are mutually symmetrical. Only for $T/2 = 60$ ms did performance asymmetries occur in the same direction as those in Fig. 5, but the magnitude of this effects was much smaller than in Experiment 2.

Similar results were obtained from the three other subjects (Fig. 10); measurements were restricted to the flicker rates tested in Experiment 2. Except for subject EB, performance asymmetries were generally small and revealed preferences in different directions (continuous vs. dashed arrows), which average out in the means (Fig. 11A). Performance asymmetries, if at all present, show preferences opposite to those seen in Experiment 2 (Fig. 11B). A two-way ANOVA with repeated measures revealed that these differences were, however, not significant ($p > 0.15$).

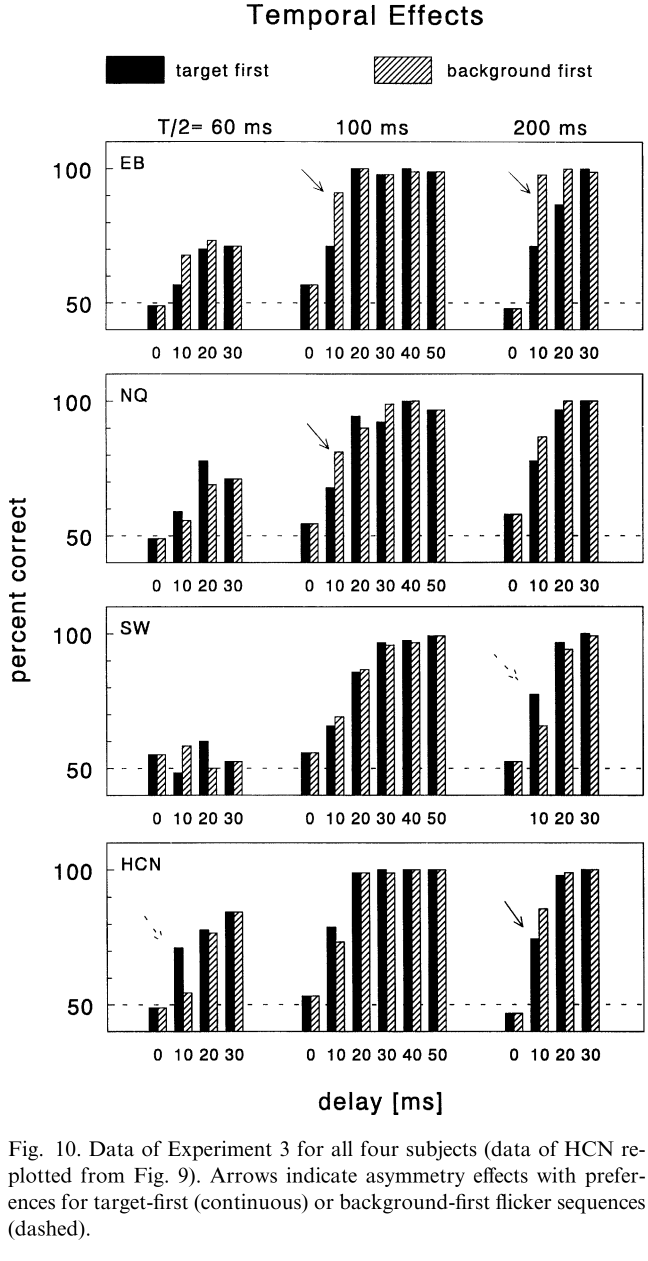

Fig. 10. Data of Experiment 3 for all four subjects (data of HCN re-plotted from Fig. 9). Arrows indicate asymmetry effects with preferences for target-first (continuous) or background-first flicker sequences (dashed).

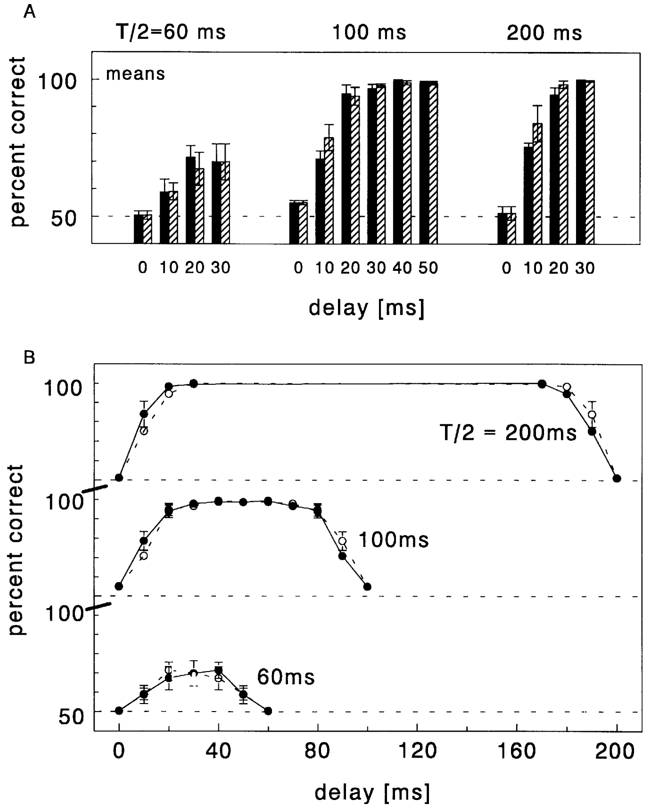

Fig. 11. Mean data of Experiment 3. (A) Histograms show minor, if any, performance differences when target orientation flips either preceded or followed those of background lines. (B) The same data re-plotted in the scheme of Fig. 7 to illustrate the magnitude of asymmetry effects in Experiment 2. Performance differences are small and reveal reversed preferences to those in Experiment 2. Error bars indicate SEM.

4.3.3. Discussion

The comparison of data curves in Figs. 7 and 12 shows that the asymmetric performance of subjects in Experiment 2 is not explained by purely temporal effects associated with the sequence of target and background orientation changes. Without flicker, popout targets are better detected when presented shortly before the surround (background) than when the surround precedes (Ziebell & Nothdurft, 1999). This was also seen in flicker ($T/2 \geqslant 100$ ms), when target and background lines were blanked rather than replaced by orthogonal lines (first version of Experiment 3). For orientation flips, however, performance differences between the two sequences were negligible and targets were seen similarly well whether they flipped before or after the background lines.

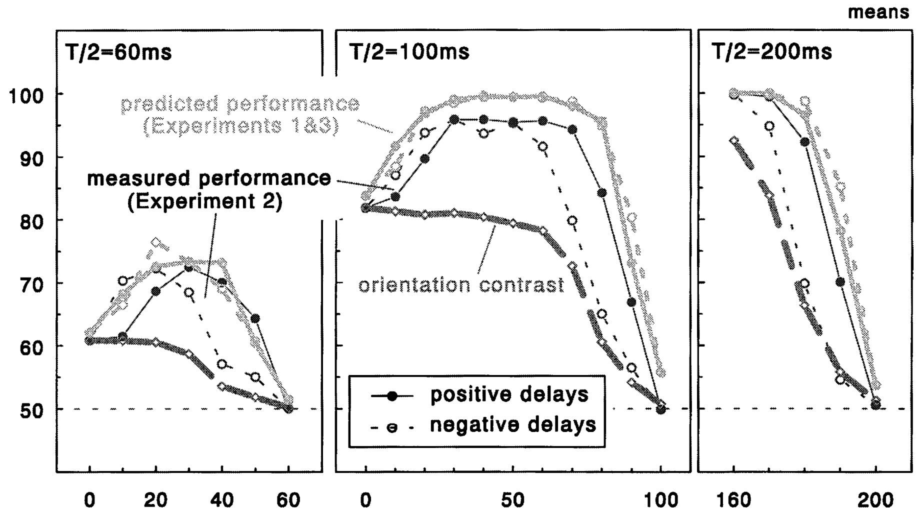

Fig. 12. Comparison of orientation flicker with temporal effects. Mean data from Experiment 2 (black, re-plotted from Fig. 7) are compared with predictions made from Experiments 1 and 3 (gray). Thick-line curves plot the predicted detection of orientation popout if this depended only on popout presentation time (Experiment 1) and flicker frequency (Experiment 2; data for delay = 0 ms). Gray curves were obtained by adding the observed sensitivity to flicker asynchrony (Experiment 3). Predicted performance is often better than measured. In particular, there are large deviations at long negative (dashed curves) and short positive delays (continuous curves), which indicate delayed suppression from parallel surround.

On the other hand, the good performance of all subjects in detecting targets that were only defined by their asynchronous orientation flip suggests that such an effect was also present in Experiment 2. In the next section we will try to separate the two saliency effects.

4.4. Comparison of Experiments 2 and 3

Target salience in Experiment 2 was probably based on two effects, their orientation contrast to neighboring lines and the fact that target and background lines flipped in asynchrony. How do these different effects add to the performance measured in Experiment 2?

4.4.1. Method

Let us assume that the salience from orientation contrast did not depend on the history of target and background lines but was only defined by the duration of the popout stimulus, T_{pop}. Let us further assume that the salience from flicker asynchrony (as measured in Experiment 3) added to this salience.

Salience from orientation contrast increases with presentation time; this was measured, for single stimulus presentations, in Experiment 1 (gray, continuous curves). In flicker, particularly at fast flicker rates, performance is reduced; note that detection rates at maximum presentation times in Experiment 2, $T_{\mathrm{pop}} = T/2$ (delay = 0 ms), were generally smaller than those for similar popout durations in Experiment 1. Thus, to predict salience from orientation contrast in Experiment 2, we must attenuate the curves from Experiment 1 so that they fit the performance at synchronous flicker in Experiment 2. [1] Formally, the predicted salience from orientation contrast, $\mathrm{SAL}^*_{\mathrm{ori}}$, at delay t, is then given by the salience of orientation popout as measured in Experiment 1, $\mathrm{SAL}_{\mathrm{exp1}}$ (which depends on popout presentation time, T_{pop}), normalized to the target salience at delay = 0 ms for a given flicker rate, as measured in Experiment 2, $\mathrm{SAL}_{\mathrm{exp2}}$. Because $T_{\mathrm{pop}} = T/2 - t$,

$$\mathrm{SAL}^*_{\mathrm{ori}}(t) = \mathrm{SAL}_{\mathrm{exp1}}(T/2 - t)\,\mathrm{SAL}_{\mathrm{exp2}}(0)/\mathrm{SAL}_{\mathrm{exp1}}(T/2).$$

This is illustrated in Fig. 12 ("orientation contrast"). Note that salience is assumed to be linearly related to the detection rate, which varies from 0 to 1 for performance levels between 50% (chance) and 100%.

Saliency effects from onset delays should be added to these curves while taking probability summation into account. This can be achieved by multiplying the probabilities of detection failures, i.e. when subjects had to guess,

$$(1 - p_{\text{combined effects}}) = (1 - p_{\text{orientation}})(1 - p_{\text{onset delay}})$$

which is equivalent to

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[1] One could argue that this approach is not exactly true. Popout targets were shown only once per trial in Experiment 1, but were shown repeatedly, and even at two different orientations, in Experiment 2. However, if these repeated presentations would accumulate, targets should have been seen perfectly at zero delays in Experiment 2, where popout was present during the entire flicker sequence (1 s total duration). This was clearly not the case. Therefore, given the variation of performance with flicker frequency (Nothdurft, 2000b) which is also seen in Figs. 5 and 7, we assume that popout is accumulated only over half a flicker period. This assumption has no effect on the further computations, provided data curves from Experiment 1 are normalized to match the performances at zero delays in Experiment 2.

$$p_{\text{combined effects}} = p_{\text{orientation}} + p_{\text{onset delay}} - p_{\text{orientation}} \cdot p_{\text{onset delay}}.$$

4.4.2. Results

The computations were made for each subject and then averaged; the resulting performance curves are shown in Fig. 12 (gray). Comparison with the measured data (black) reveals two major deviations. First, the predicted performance is slightly better than measured. This is obvious for $T/2 = 100$ ms where maximum performance in Experiment 2 did not exceed 96% but was close to 100% in Experiment 3. Also for $T/2 = 200$ ms, but not for $T/2 = 60$ ms, the predicted performance was generally slightly better than measured in Experiment 2. The second and, in fact, more prominent differences are the deviations of certain branches of the curves. For all three flicker rates, true performance at large negative delays was strongly reduced, whereas performance at the corresponding positive delays tended to follow the predicted curves. This difference disappeared at delays 30–40 ms below $T/2$. Similar differences between the measured and the predicted data are seen at short delays but now reversed. For $T/2 = 60$ ms, for example, the performance at negative delays matches the predictions while that at positive delays is reduced.

Two-factor repeated-measures ANOVA revealed partial significance of these two observations. Except for $T/2 = 60$ ms, the predicted data points for positive delays were significantly higher than the measured ones [$F(1,3) > 15.9$; $p < 0.001$], and performance at the three longest negative delays was significantly reduced [$F(1,3) > 65.9$; $p < 0.0001$]. For $T/2 = 60$ ms, however, differences did not reach significance, probably because the threshold-near performance varied too much between subjects.

4.4.3. Discussion

The better performance in the predicted than in the measured data is due to a generally better performance of some subjects in Experiment 3 than in Experiment 2. The reason for this improvement is not clear, but there is evidence that it may reflect long-lasting training effects. The present version of Experiment 3 was carried out several months after Experiment 2, and subjects had participated in other experiments on temporal flicker in the mean time. To compare the actual performance in the two experiments, two subjects repeated the critical measurements of Experiment 2 after they had performed Experiment 3. For one subject (EB), performance in Experiment 2 had indeed improved during that time and data points for long positive delays now fell upon the predicted curves. Nevertheless, her performance at long negative delays was still strongly reduced, as it was in the first series of measurements. The other subject (HCN) had experienced a long time of practice in these tasks even before the measurements began, and in his data there was no significant difference for medium and long positive delays between the predicted curves and the early and late measurements in Experiment 2. The differences at long negative delays (cf. Fig. 5) were, however, replicated. These observations suggest that the general improvement of performance between Experiments 2 and 3 reflects long-lasting training effects.

The second and more dramatic deviation of measured from predicted data is the performance reduction at large negative delays. Target visibility is strongly suppressed when orientation popout is obtained from background flips. In this case (cf. Fig. 4), lines in the surround were parallel to target orientation until they flipped around. Apparently, the stronger suppression from the (previous) parallel surround was delayed and lasted long enough to block even the detection of onset asynchronies, which were, however, well seen when the surround was previously orthogonal to the new target (positive delays). This suppression was effective for 30–40 ms after the parallel surround had been switched off (i.e. changed to orthogonal orientation). Thereafter, i.e., for negative delays shorter than $T/2$ minus 30–40 ms, performance was dominated by the temporal effects and deviations between positive and negative delays were small. Different from the nearly symmetrical performance that would be predicted from flicker asynchrony in Experiment 3, the true performance measured in Experiment 2 was strongly suppressed at (long) negative but not positive delays. This would be consistent with delayed suppression from parallel texture surround.

Interestingly, this suppression was also seen in the first version of Experiment 3, in which (parallel) lines were switched on and off. Targets that preceded the onset of the (parallel) surround were seen better than targets that followed it and hence were suppressed more strongly.

Given these consistent observations, the deviations at long negative delays seem to be well explained by delayed suppression from parallel surround. But why are these effects reversed at short delays, where the predictions tend to match the measurements for negative but not positive delays? Positive delays indicate that orientation popout is obtained from a target orientation change; that is, the surround is, and was before, orthogonal to the new target orientation. However, the history of the previous display might have been rather short. At a delay of +10 ms, for example, the orthogonal surround preceded the target flip by only 10 ms; before that time, the surround was parallel to the (new) popout target (cf. Fig. 4). Accordingly, at short negative delays the surround before the popout presentation was parallel, but only for a short time. Thus, if suppression from parallel surround needs time to establish, and also decays with a delay, the deviations from predicted performances should be reversed at very short delays, exactly as it is seen in Fig. 12.

5. General discussion

The study reports two major findings. First, the slower detection of an orientation popout target compared to a single line is not explained alone by the slow encoding of orientation information in the brain but seems to suffer from an additional delay (Experiment 1). Second, the history of line orientation in the surround was found to affect the detectability of popout in flicker (Experiment 2); the observed performance asymmetries with orientation flicker were not explained by temporal saliency effects from the asynchronous stimulus presentation (Experiment 3). Both findings would be consistent with the observation that differential contextual modulation is delayed.

Delayed contextual modulation has been reported in a number of single-cell studies; the measures varied from 50–60 ms (Knierim & Van Essen, 1992; Nothdurft et al., 1999) to 80 ms (Lamme, 1995; Lee et al., 1998; Zipser et al., 1996) after stimulus onset; this gives a delay of 15–40 ms after the onset of the earliest responses in area V1, after which responses to a center stimulus are differently modulated by different surrounds. While differential contextual modulation itself was putatively related to various perceptual phenomena (see Lamme, Supèr, & Spekreijse, 1998, for a review), the question of whether these perceptual phenomena manifest with a delay was at first not studied.

Meanwhile, a number of studies have investigated the temporal aspects of contextual modulation in perception, with slightly divergent results. Nothdurft (2000b) reported that the detection of orientation popout (salience from orientation contrast) needs longer processing time than the detection of a single line (salience from luminance onset), as would be expected from a delayed onset of differential contextual modulation. The different dynamics of orientation popout and stimulus onset were also confirmed in flicker experiments. Motoyoshi & Nishida (2001) compared the processing time for orientation coding and for orientation contrast, and did not find a significant difference. However, as orientation coding itself is delayed against the detection of line onset (cf. Experiment 1), their results are not in disagreement with the proposed delay.

Vidnyánszky, Papathomas, & Julesz (2001) recently stressed that "contextual modulation of orientation discrimination is independent of stimulus processing time", a conclusion that again seems to be in conflict with the present findings. However, these authors measured variations of orientation discrimination when Gabor (test) patterns were flanked by parallel Gabors (masks). The flanks produced a threshold elevation, which did not vary relative to no-flank measurements for stimulus processing times between 56 and 392 ms. This task is very different from the detection of popout targets. Discrimination thresholds varied between 10° and 2° and were frequently far below 5° even in the flank condition. In contrast, saliency effects from orientation contrast only become visible around 10–15° minimum (Caelli & Jelesz, 1978; Nothdurft, 1992, 1993). Nevertheless, the kind of contextual modulation that affects the orientation discrimination task revealed the same effects on single-cell responses (Li et al., 2000) as modulation studied in the context of popout (Knierim & Van Essen, 1992; Nothdurft et al., 1999) and, therefore, may also manifest with a delay. From our single-cell recordings in anesthetized monkeys, performance asymmetries as seen with orientation flicker in Experiment 2 would be predicted (see Appendix A). However, the range of delays at which these asymmetries would occur is small (cf. Fig. 6) and might have been missed in the study by Vidnyánszky et al. From our data, differential contextual modulation should already be well established in 56 ms processing time. While these authors intended to point out that no (large) delays occur with contextual modulation, I would like to stress the presence of a delay as short as 10–15 ms.

Still, from the flicker tests of the present study there is no direct evidence for the existence of such a delay at stimulus *onset*. Experiment 2 has revealed strong performance asymmetries which indicate that salience of orientation popout is reduced when the parallel surround is shown before. This indicates that suppression effects *disappear* with a delay, but it does not indicate that their onset is delayed as well. I carried out a number of additional tests to measure onset latencies, but none of these was unequivocal and free of possible pitfalls from other effects. The major problem seems to be that stimulus durations of 10–20 ms are too short to let orientation contrast pop out, but at longer durations differential contextual modulation is already activated. While this coincidence suggests that differential contextual modulation in V1 might be essential for the perception of popout, it does not prove it. However, a delayed decay of suppression, as documented in Experiment 2, should produce a strong perceptual effect, as differential contextual modulation has fully developed at this time.

Acknowledgements

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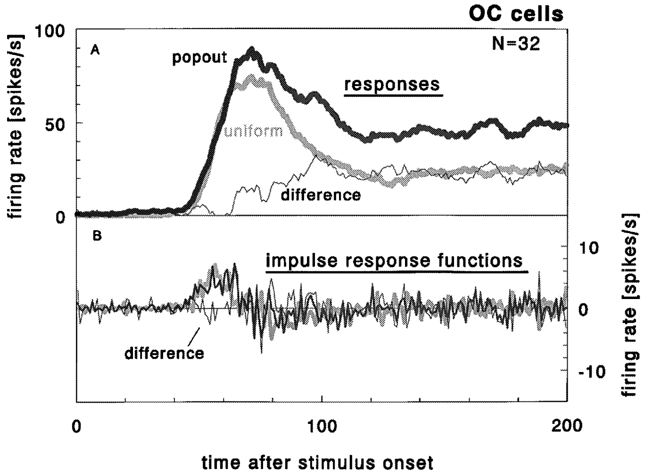

Fig. 13. Population responses of 32 “OC cells” in the anesthetized monkey (from Nothdurft et al., 1999) to lines with parallel (uniform) or orthogonal surround (popout). Response differences reflect differential contextual modulation (difference) which is delayed compared to the onset of responses. From the data in (A) impulse response functions were derived (B) which were used to compute the presumed responses to orientation flicker at various frequencies.

Appendix A. Simulation of saliency effects from single-cell data

To evaluate perceptual performance on the basis of single-cell physiology, a simulation of asynchronous orientation flicker was made on the basis of cell responses obtained in anesthetized monkeys (Nothdurft et al., 1999). The results reflect some of the effects obtained with orientation flicker in Experiment 2; purely temporal flicker effects as studied in Experiment 3 were not investigated.

Fig. 13A shows the mean responses of 32 cells in monkey area V1 that gave a significantly larger response to lines in the popout condition than to the same lines presented in uniform texture. With respect to the stimuli used in Experiment 2 (Fig. 1, center), these two curves would resemble mean responses to the popout target (“popout”) and to lines in the orthogonal texture surround (“uniform”). It was proposed that the larger response to the popout target may correspond to its particular salience (cf. Knierim & Van Essen, 1992; Li, 2002; cf. Nothdurft, 1994a, 1997). Obviously, the presumed responses to target and background lines are first identical and only start to differ after a delay. Given these data from single-cell recordings in anesthetized monkeys, how would response differences vary when target and background lines flicker out of phase?

A.1. Methods

Simulations were made to reflect the C4F paradigm of Experiment 2 as sketched in Fig. 4. They were based on linear combinations of the physiological data in Fig. 13A; the resulting saliency effects were computed from the response differences between target and background lines. The underlying model used only two independent response components, (i) the response to the target in the popout condition and (ii) the additional suppression from parallel surround. General suppression, i.e., suppression similarly evoked from both parallel and orthogonal surround, was not explicitly treated in the model. This is a simplification since both texture surrounds have been reported to suppress the response (Kapadia et al., 1999; Knierim & Van Essen, 1992; Li et al., 2000; Nothdurft et al., 1999). However, this suppression is implicitly implemented in the response to the popout target. Since targets were always presented with one or the other surround, this simplification is likely to be irrelevant for the present study.

In detail, target salience was computed along the following steps, which are described for one of the two line orientations in the pattern.

(1) The extra suppression from parallel texture surround was estimated as the difference between the two measured curves in Fig. 13A (“difference”).

(2) To allow for the computation of response offsets (when line orientation was flipped to the orthogonal orientation) and of new (and, in particular, high) flicker frequencies, linear impulse response functions, $\mathrm{irf}(t)$, were derived from the measured responses (to a 500 ms stimulus), $r(t)$, using the following iteration

$$\mathrm{irf}(t_i) = r(t_i) - r(t_{i-1}) \quad \text{for } 1 < i \leqslant 200$$

and

$$\mathrm{irf}(t_1) = r(t_1).$$

Time resolution was 1 ms. The different data curves in Fig. 13A led to three impulse response functions which are plotted in Fig. 13B. From these, the presumed responses, $r^*(t)$, to a given stimulus duration were computed as a convolution of the stimulus with the impulse response function. For a stimulus that lastet $T/2$ ms,

$$s(t_i) = \begin{cases} 1 & \text{for } 0 \leqslant t_i < T/2, \\ 0 & \text{for } t_i \geqslant T/2, \end{cases}$$

the presumed response would be obtained from an integration (here summation over j),

$$r^*(t_i) = \sum_{j=0}^{i-1} \mathrm{irf}(t_{i-j}) s(t_j),$$

which gives stimulus onset responses identical to the measured ones.

(3) The presumed responses for the different conditions (popout, uniform, and difference) were combined according to the sequence of target and background presentations in each test condition. For background

lines, responses were simply taken from the uniform condition synchronized to background flicker, i.e., possible interactions from the target on background line responses were ignored. For target lines, responses were constructed from the popout condition synchronized to target onset, minus the extra suppression from parallel surround (difference) synchronized to the time when surrounding lines switched to become parallel to the target.

For asynchronous flicker, in which the target changes with the delay k after the background lines, the resulting responses, R, are

$$R_{\text{background}}(t_i) = r^*_{\text{uniform}}(t_i),$$

$$R_{\text{target}}(t_i) = r^*_{\text{popout}}(t_{i-k}) - r^*_{\text{difference}}(t_i - T/2).$$

(4) To avoid negative responses, the resulting responses were clipped, i.e. values below zero were set to zero.

$$R^*(t_i) = \begin{cases} R(t_i) & \text{for } R(t_i) \geqslant 0, \\ 0 & \text{for } R(t_i) < 0. \end{cases}$$

(5) Salience, SAL, was computed as the response difference between target and background lines. For the presentation here, responses were averaged over the entire flicker cycle before the difference was taken.

$$\text{SAL} = \sum_{i=1}^{T} R^*_{\text{target}}(t_i) - \sum_{i=1}^{T} R^*_{\text{background}}(t_i).$$

Given the phase-shifted but otherwise identical responses for orthogonal orientations, the same results would be obtained if responses of all orientation channels were averaged for the computation of salience (cf. Nothdurft, 1994b, 1997). However, slightly different data, but with similar characteristics, were obtained when responses were averaged over a limited (but not too small) time window.

A.2. Results

Fig. 14 shows the predicted responses of neurons with similar orientation preference to slow orientation flicker ($T/2 = 200$ ms); target and background lines flipped either in phase or out of phase, as depicted in Fig. 4. The phase of background flicker was held constant (Fig. 14A); the response reflects the measured cell response in Fig. 13A. Target responses varied with flicker asynchrony (Fig. 14B) and were reduced by additional suppression from the parallel surround (gray curves). Due to its longer latency, this additional suppression was still effective in synchronous flicker (delay = 0 ms; arrow) and disappeared only when background lines were changed before the target (cf. delay = 20 ms; arrow). When either target or background lines were switched long in advance (delays +180 and −180 ms), there was only a short period in which the target was presented

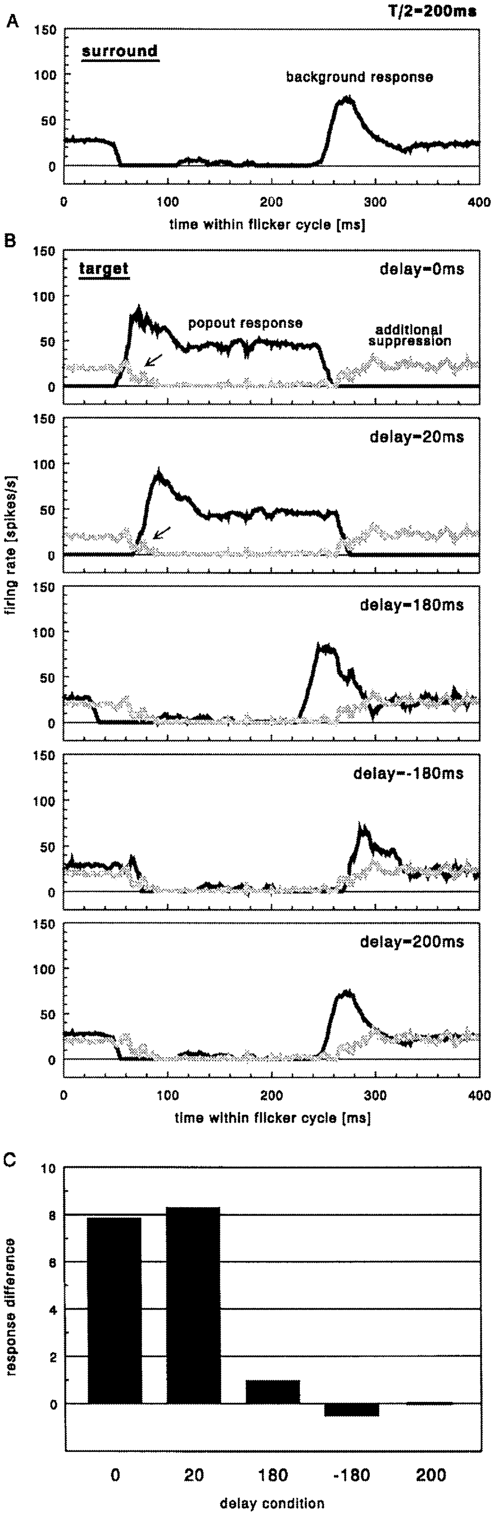

Fig. 14. Simulated responses to an orientation flicker of 2.5 Hz (half cycle duration $T/2 = 200$ ms). (A, B) Responses to different lines in the pattern, at the same orientation. Background line flicker (A) was held constant, while the phase of target flicker (B) was varied between the different graphs. Responses are plotted in black, the additional suppression from parallel surround in gray. (C) Mean response differences between target and background lines for the conditions in B. Positive delays produced larger differences than negative delays.

with orthogonal surround and additional suppression disappeared. However, due to latency differences, these two conditions were not symmetrical but target responses were more strongly suppressed at negative delays, in which suppression from parallel surround was still present. For antiphase flicker (delay = 200 ms), the target was always surrounded by parallel lines and responses of target and background lines became indistinguishable. (Additional suppression was delayed here, too, but this was also the case with the background line responses.)

Fig. 14C plot the differences between target and background responses in the depicted conditions. Stronger responses to the target would help to detect it; response differences may thus be related to the salience of the target in these conditions. Note that target responses could be even smaller than background responses, when the parallel surround was presented shortly before the target.

Similar pictures were obtained for faster flicker rates. Fig. 15 summarizes the predicted saliency effects for different cycle times as a function of the delay. Asynchronous flicker always produced variations in salience and a strong asymmetry between positive and negative delays (continuous vs. dashed curves). The differences were more pronounced for medium and short cycle durations than for $T/2 = 200$ ms. Maximal salience was reduced at short cycles, due to the short presentation of the popout target, and salience maxima were generally obtained for slightly positive delays (20–30 ms) rather than for synchronous flicker.

A.3. Discussion

Given the simple assumptions on which the model was based, the similarity to measurements is likely to be limited. Negative salience is, of course, not meaningful (but may be helpful to illustrate the principle variations with an asynchronous target and background flicker). It can be easily removed by minor modifications of the simulation, e.g., by clipping responses below zero. Another uncertainty of the computation comes from the fact that we do not know how response differences in the simulation would relate to salience. It might be meaningful not only to introduce a threshold below which response differences remain undetected. It also seems plausible to assume saturation, in particular, when salience is measured as percentage of targets detected; even with a very salient target, performance cannot excede 100%. The exact transformation of response

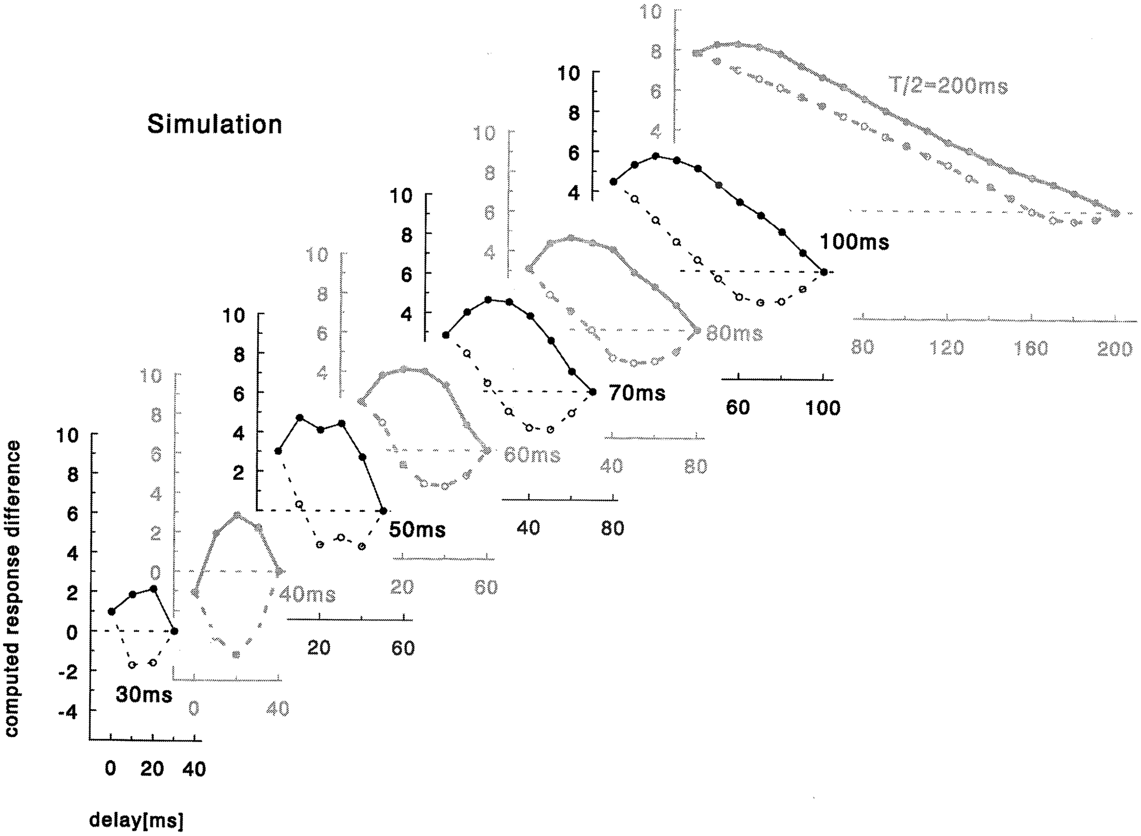

Fig. 15. Summary of the simulation. Response differences indicate strong asymmetries between positive (continuous curves) and negative delays (dashed curves) for various cycle durations. With increasing delays, response differences increase, then remain constant, and finally diminish towards antiphase flicker (delay = $T/2$).

differences into perceived salience for intermediate values is also not known; salience increases nonlinearly with increasing differences in feature space (cf. Nothdurft, 1993). Finally, it should be stressed that the computation of responses to flickering patterns was made, on linear grounds, from the impulse response functions derived from stationary patterns (presented for 500 ms). For higher flicker rates this is likely to be incorrect, since any nonlinearities at faster flicker rates and, in particular, the limited temporal resolution (Kelly, 1961) of the system were ignored. The long averaging of neural activity to compute salience for low flicker rates is also probably not realistic.

Despite these limitations, however, the simulation revealed interesting parallels to the subjects' performance in Experiment 2. First, asynchronous flicker did produce strong performance differences between positive and negative delays. Second, some asynchronous presentations were found to improve target salience over that of synchronous flicker (when popout duration was maximum). This effect was more pronounced for short flicker periods and relatively small at long durations (cf. $T/2 = 60$ vs. 200 ms). Third, beside some differences in detail, the general response patterns for different flicker frequencies were rather similar (except for the shortest cycle times). This was also seen in the experiment.

However, there are also clear deviations from the measurements in Fig. 5. The simulations gave constant performance asymmetry over all delays, whereas the measured differences quickly diminished when the delay decreased. At short delays, preferences were even reversed—opposite to the predictions made from the simulation. As documented in Experiment 3, all these deviations are likely to be due to the fact that, in addition to orientation differences, the purely temporal flicker sequence also generated salience. When these effects were large enough, targets were easily detected and performance was much better than predicted from (asynchronous) orientation popout alone.

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