Lateral effects in pattern vision

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There is a large literature on lateral effects in pattern vision but no consensus about them or comprehensive model of them. This paper reviews the literature with a focus on the effects of parallel context in the central fovea. It describes seven experiments that measure detection and discrimination thresholds in annular and Gabor-pattern contexts at different separations. It presents a model of these effects, which is an elaboration of Foley's (1994) model. The model describes the results well, and it shows that lateral context affects the response to the target by both multiplicative excitation and additive inhibition. Both lateral effects extend for several wavelengths beyond the target. They vary in relative strength, producing near suppression and far enhancement of the response to the target. The model describes the detection and discrimination results well, and it also describes the results of experiments on lateral effects on perceived contrast. The model is consistent with the physiology of V1 cells.

Introduction

Lateral inhibition in vision has long been known, much studied, and incorporated in models of vision. Lateral excitation or disinhibition has been known for at least 50 years and has also been studied, particularly in pattern vision, but it has not been incorporated into mainstream vision models. One of the reasons for this is that there is not a coherent body of knowledge on these effects. In this paper, I first review the literature on lateral effects produced in the fovea by parallel context on contrast perception, detection, and discrimination. This literature shows that both excitatory and inhibitory effects are produced by lateral context at separations of six wavelengths or more from a foveal target. These effects occur early in the visual pathway and affect later processing. Unfortunately, there are large inconsistencies in experimental results. I then describe seven experiments designed to measure the effects of two configurations of lateral context on the detection and discrimination of contrast. The two configurations are a Gabor target with collinear Gabor flankers and a disk grating with a parallel annular grating surround.

Effects of superimposed context are much better understood than lateral effects, and it is natural to ask whether a model of superimposed context effects (Foley, 1994) can be extended to lateral context. The answer is that it can be if the sensitivity to the target is allowed to depend on the lateral context. This elaboration was proposed by Chen and Tyler (2000, 2001) and is incorporated into the models fitted here. The model for close context combines signals in a different way than the model for more remote context. The principal implication of the models is that stimuli in regions around the target both excite and inhibit the mechanism that detects the target and that the balance between these two effects varies with distance with inhibition dominating at short distances and excitation at longer distances.

Terms

Some terms related to lateral effects have not been used consistently in the literature. The effects have been called "masking effects," but they might better be called "context effects" because some of them are facilitatory. In experiments on context effects, there is a "target" or "test" pattern. These terms are essentially synonymous. They refer to the stimulus element about which judgments are made. In studies of perceived contrast, "test" is often used; in detection, "target" is more common. There are also context patterns whose effects on the perception of the target are measured. The context patterns may be superimposed on the target and added to it, they may be presented in different places or at different times, or they may both be superimposed and extend beyond the target in space and time. I use "pedestal" for a pattern that is spatially identical to the target and coincident with it in time. I refer to other context patterns as "masks" if they are superimposed and as lateral context if not. Flankers and annular surrounds are specific types of lateral context.

When the lateral context consists of a pair of Gabor patterns (flankers), their relative positions are described by their center-to-center separation from the target. When the center stimulus has a sharp edge and the lateral context is an annulus, their separation is often specified as the gap between the outer edge of the center and the inner edge of the surround. However, to facilitate comparisons with Gabor flankers, I have specified the annuli in terms of the radius of the midpoint of the annulus (mid-radius). Both types of lateral context can differ on several other dimensions.

Some terms that describe phenomena are also somewhat ambiguous. Target thresholds may be increased (masking) or decreased (facilitation). Perceived contrast may be decreased (suppression) or increased (enhancement). Psychophysical mechanism responses, which are often assumed to be closely related to perceived contrast, may also be suppressed or enhanced. Sometimes response enhancement is referred to as facilitation, especially in the physiological literature, but that leads to confusion because thresholds often change in the opposite direction to response magnitude because they depend on the steepness of the response function, not its magnitude. As I show, facilitation and enhancement are mediated by different processes, and facilitation may increase over a contrast range in which the response is suppressed. The term "dipper function" is often used to describe a particular relation between the target contrast threshold and pedestal contrast or the lateral context. It refers to a function that decreases and then increases as the contrast increases. I distinguish between a "facilitation dipper" that does not rise above the detection threshold and a "full dipper" that does. I use the following symbols: C_p, pedestal contrast; C_c, context contrast; C_m, mask contrast; C_t, target contrast; and T, target contrast threshold. Contrasts are often expressed in decibels, and dB = 20 $\log_{10}$ (contrast), so 1 dB is one 20th of a log unit.

Review of the literature on lateral context effects

Lateral inhibition in vision has long been known and widely studied. A gray spot appears darker when surrounded by a region of higher luminance. Less well known is lateral enhancement; a gray spot appears brighter when surrounded by a region of lower luminance (Heinemann, 1955). The enhancement effect is much smaller than the suppression effect. More recently, lateral effects on perceived contrast have been found. A gray-level pattern, such as a grating, often appears lower in contrast when surrounded by a higher contrast pattern (suppression), and it sometimes appears higher in contrast when surrounded by a lower contrast pattern (enhancement) (Ejima & Takahashi, 1985; Xing & Heeger, 2001). Suppression is a larger effect than enhancement. Some studies have found only suppression effects even when the lateral contrast was lower than the center contrast (Cannon & Fullenkamp, 1991; Olzak & Laurinen, 1999; Solomon, Sperling, & Chubb, 1993).

Lateral effects have been studied with a variety of stimuli. Sine wave gratings of various shapes and sizes, Gabor patterns, and D6 patterns (sixth derivative of a Gaussian) have commonly been used. Because these patterns can vary on more than a half dozen dimensions and many effects depend on the relation between the target pattern and the lateral patterns, there are a large number of variables to consider. There are not only many interactions among these variables, but also nonlinear and non-monotonic functions. Although there have been many studies of lateral pattern effects, they do not come close to examining all the combinations of even the most basic variables.

Researchers have sought to measure the effects of those variables that have seemed most important. Some of the results do not agree, and we often do not know whether this is a failure to replicate or whether some difference in the stimuli or conditions is responsible for the difference. Among the most salient variables whose effects are complex and which interact strongly are target and context separation and the contrasts of target and context. These variables are the focus of the present study.

When we consider how to describe these effects, we immediately encounter a problem. Each of the dependent variables is a function of at least 10 independent variables, most of which are continuous variables. So the data points correspond to points on a surface in an *n*-dimensional space. As one explores this space, it rapidly becomes awkward and practically impossible to describe this surface in words or images. There is also the fact that results of different studies sometimes appear to be inconsistent although it is almost never the case that all the variables are matched, so what appears to be an inconsistency may be a consequence of unmatched variables. Even if all the physical variables are matched, there are large observer differences. In my experience, within-observer variance tends to be larger when the context is lateral than when it is superimposed.

What follows is an attempt to describe some of the main results found in the literature. I do not attempt to be exhaustive. It is organized by variables that have been shown to have effects with some attempt to show how those effects depend on other variables.

Lateral effects on perceived contrast

Method

Lateral effects on perceived contrast have been studied by having human observers match the contrast of an isolated comparison pattern that has a uniform background to a spatially identical test pattern with a lateral pattern context. The two stimuli are usually presented successively in time, but they are sometimes presented side by side. Either the isolated pattern or the pattern in context is fixed in contrast, and the other is adjusted to match it in perceived contrast. The matching contrast is usually determined by varying one of the contrasts from trial to trial and having the observer judge which contrast appears higher (two-alternative forced choice). There is no feedback. A staircase algorithm is often used to determine the contrast that is judged higher on 50% of the trials.

Results

Lateral patterns can produce a perceived contrast pattern in a uniform field. McCourt (1982) showed that, when low spatial frequency vertical gratings are presented above and below a narrow, orthogonal uniform field, an out-of-phase grating appears in that field. The effect only appears when the spatial frequency is low and the field is narrow, and the higher the spatial frequency, the narrower the uniform field must be to produce the effect (Foley & McCourt, 1985). The effect has been studied extensively by Blakeslee and McCourt (e.g., Blakeslee, Cope, & McCourt, 2016; Blakeslee & McCourt, 1999; Blakeslee, Reetz, & McCourt, 2008).

There are more than a dozen papers that report experiments on lateral effects on the perceived contrast of gray-level patterns. The only way to describe fully what has been found is to describe each of these experiments. It seems more important to single out some of the variables that have been shown to have substantial effects in some contexts. There appear to be inconsistencies in some of the most basic effects.

Grating flankers, annular grating surrounds, and contrast noise surrounds all affect the perceived contrast of a pattern viewed in central vision. They have both suppressive and enhancing effects depending on stimulus parameters. In the periphery, lateral effects are almost entirely suppressive (Petrov & McKee, 2009; Williams & Hess, 1998) although Zenger-Landolt & Koch (2001) found facilitation from orthogonal context in the periphery. This review focuses on central vision.

Substantial lateral effects on perceived contrast occur for spatial frequencies over a range of at least 1 to 8 c/°. Effects are similar for different spatial frequencies when distances are measured in wavelengths (Cannon & Fullenkamp, 1991). However, there is evidence that perceived contrast suppression is greater at very low spatial frequencies (Meese & Hess, 2004; Meese, Hess, & Williams, 2005). The center stimulus can be small or large, at least up to seven cycles of the grating (Xing & Heeger, 2001). If the contrast of the center stimulus is constant over its extent, it usually appears constant, so the effects are not local to the edge.

There are large individual differences. In the extremes, some observers show only suppression even when the lateral contrast is lower than the center contrast (Cannon & Fullenkamp, 1991); other observers show primarily enhancement (Cannon & Fullenkamp, 1993). The relation between the center stimulus features and the lateral stimulus features has large and sometimes complex effects on the perceived contrast of the center.

Relative contrast: The effect of relative contrast depends on the spatial configuration. For close surrounds, when the lateral contrast is greater than the center contrast, the lateral context suppresses the perceived contrast of the center. When the lateral contrast is less than the center contrast, the lateral stimulus often increases the perceived contrast of the center although the transition from suppression to enhancement usually occurs at a test contrast higher than the lateral contrast (Ejima & Takahashi, 1985; Xing & Heeger, 2000, 2001). There are studies in which only suppression was found even when the test contrast was twice the lateral contrast (Cannon & Fullenkamp, 1993, observers MC and SF). Most studies focus on suppression of the center contrast produced by a higher contrast near surround. There is one study that shows effects from very distant contexts. For narrow annular surrounds about 22 wavelengths away from the test field, the perceived contrast of a low contrast test is increased by surround contrasts up to 2.5 times higher, and the perceived contrast of a high-contrast test (0.75) is decreased by all surround contrasts higher than the test contrast (Nurminen, Peromaa, & Laurinen, 2010). The first result is opposite to what Xing and Heeger (2000, 2001) found with a close surround.

Relative position: The lateral stimuli can be above and below or left and right of the center (Ejima & Takahashi, 1985). They can completely surround the center or fill only part of an annulus around the center (Cannon & Fullenkamp, 1991). Suppression is maximum when there is no gap between center and lateral context, but effects occur when there is a gap of up to several wavelengths. Effects weaken as the gap size increases (Cannon & Fullenkamp, 1991). Enhancement of high contrasts by lower contrast surrounds occurs with a very narrow gap (Xing & Heeger, 2000, 2001). When center and surround spatial frequencies are the

same, the effects scale with spatial frequency, at least approximately (Cannon & Fullenkamp, 1991).

Relative size: Effects strengthen as lateral context size is increased either by increasing the outer radius of an annular surround, the angular size of sectors of an annulus, or the number of lateral flankers. As lateral context size increases, the suppression effect increases rapidly at first and then more slowly (Cannon & Fullenkamp, 1991, 1996).

Relative phase: Evidence on the effect of relative spatial phase is inconsistent. Some studies show that an out-of-phase surround has no effect on perceived center contrast (Olzak & Laurinen, 1999). Other studies show that an out-of-phase surround has a different effect than an in-phase surround. For an above–below configuration Ejima and Takahashi (1985) found that an out-of-phase surround enhances regardless of whether the surround contrast is higher or lower than the center. Yu, Klein, and Levi (2001) showed that, when there is no gap between center and surround, an in-phase surround suppresses and an out-of-phase surround enhances. However, when there is a gap, both phases suppress regardless of whether the center contrast is higher or lower than the surround. On the other hand, using stimuli composed of columns of center-surround stimulus elements resembling high spatial frequency gratings, Solomon et al. (1993) found that suppression occurred with no effect of relative phase.

Relative orientation: When the orientation of a grating in the surround is orthogonal to the center grating, some studies have found that the effects are similar to when center and surround are parallel, that is, primarily suppressive, except that the effects of orthogonal context are often smaller in magnitude (Cannon & Fullenkamp, 1991; Ishikawa, Shimegi, & Sato, 2006; Meese & Hess, 2004; Solomon et al., 1993; Xing & Heeger, 2000, 2001). However, Yu et al. (2001) found that parallel annuli suppress perceived contrast whether the center is higher or lower in contrast than the surround, and orthogonal annuli often increase perceived center contrast. The effect increases with center contrast, and there is not a clear dependence on surround contrast.

Shushruth, Ichida, Levitt, and Angelucci (2009) compared the effect of relative orientation on perceived contrast for annuli in the near and the far surrounds. The center contrast was 0.2, and the surround contrast was 0.4, a contrast ratio for which same orientation suppression would be expected. For both near and far annuli, they found that same orientation surrounds suppressed the most and that suppression decreased as orientation difference in-

creased with suppression sometimes replaced by facilitation when the surround was orthogonal. They also measured the responses of single cells in macaque V1 and found them to respond in a similar way. The increased perceived contrast in the Yu et al. (2001) study occurred primarily when the center contrast was high. Another difference between the studies is that Yu et al. (2001) used 8 c/° and Shushruth et al. (2013) used 1 c/°. Meese and Hess (2004) found suppression of perceived contrast from annular surrounds that were oriented at 45° to the center grating and had a spatial frequency that was three times higher than the center grating.

Relative spatial frequency: Cannon and Fullenkamp (1991) found that suppression was greatest when the surround spatial frequency matched the center spatial frequency. As the difference between the surround and center frequencies increased, suppression decreased. Yu et al. (2001) got a different result: Surround frequencies lower than the center frequency produced contrast enhancement; surround frequencies the same as or higher than the center frequency produced roughly equal suppression. They question whether the surround effect on perceived contrast is tuned to spatial frequency.

Summary

Lateral context has predominately suppressive effects on perceived contrast, but it sometimes enhances contrasts that are higher than the surround contrast. There are large individual differences. Effects are largest when the context is close and they gradually decrease with separation. They are largest when the context completely surrounds the test, when the surround is large, and when context and test are the same in orientation and spatial frequency. Effects decrease as orientation difference increases, and orthogonal context sometimes enhances. When there is a gap, relative phase has no effect. When there is no gap, an in-phase context suppresses and an out-of-phase context enhances.

Lateral effects on pattern detection thresholds

Why separate detection and discrimination? They are often studied in separate experiments. The principal relation is different. In detection, threshold as a function of the context contrast (TvCc), is measured for Cp = 0; in discrimination, threshold as a function of pedestal contrast (TvCp), is often measured for Cc constant. We would like to know Tv(Cp, Cc), but very few studies examine this relationship directly.

Method

Detection thresholds are usually measured using a two-alternative, temporal forced-choice task. The lateral context stimulus is presented in both intervals, and the target is randomly presented in one of them. The observer indicates which interval contains the target. Some algorithm, often a staircase or other threshold-seeking algorithm, is used to determine the target contrast that yields a specified proportion of correct responses. The proportion varies somewhat but is usually between 0.75 and 0.82. Error feedback is generally given after each trial. Sometimes the function that relates the detection threshold to the context contrast (TvCc) is measured.

Results

The effects of lateral context patterns on thresholds are different in the fovea and the periphery. In the periphery, the dominant effect is to increase thresholds (Petrov, Carandini, & McKee, 2005). This is consistent with the dominant effect on perceived contrast, which is suppression. The present study is concerned with lateral effects in the central fovea where the phenomena are more complex.

Most of the research has been done with grating-like stimuli, but dots at the ends of a line stimulus affect its threshold in a similar way (Dresp, 1993), so the effects are not limited to grating patterns.

Detection thresholds depend on several properties of the target and the context and the relation between them. TvCc functions are often non-monotonic, so if experiments test at different single values of Cc, they may yield what appear to be inconsistent effects but are really just different points on the TvCc function. There are interactions among several stimulus variables that affect lateral context effects. Effects occur over a large range of spatial frequencies, at least 1 to 13 c/° (Polat & Sagi, 1993).

Context contrast: Lateral context contrast has complex effects on the detection threshold. The relation between the threshold and the context contrast takes on several different forms as the separation between target and context varies. It can be monotonic increasing, a facilitation dipper that does not rise above the detection threshold (Solomon, Watson, & Morgan, 1999) or a full dipper that rises above the detection threshold (Meese & Holmes, 2007; Yu, Klein, & Levi, 2003), the same form that is seen in superimposed masking. Most studies do not use context contrasts greater than 0.5, so functions that are classified as facilitation dippers may become full dippers when the context contrast range is extended, but some functions seem to remain in the facilitation range over the full range of context contrast.

The function relating threshold to lateral contrast also depends on relative orientation. As part of a larger study, Yu et al. (2003) measured detection thresholds in the presence of parallel and orthogonal annuli of different contrasts at one separation. The targets were 8 c/° D6 patterns, and the annuli were close to the target with a small gap and a mid-radius of 2.1 λ. For parallel annuli, the TvCc function was a very shallow full dipper. For orthogonal annuli, the TvCc function was a facilitation dipper with a minimum at a surround contrast of 0.1. Meese, Summers, Holmes, and Wallis (2007) found facilitation dippers with orthogonal surrounding annuli at 7 c/° but shallow full dippers at 1 c/°.

Threshold is a different function of context contrast depending on separation and relative orientation, both of which have large effects. Many of the studies that measure the effects of other variables on detection do not vary context contrast, so they are determining a single point on the TvCc function.

Separation: Gabor flankers affect the detection threshold at center-to-center separations of at least 8 λ, both when the flankers are collinear with the target (Polat & Sagi, 1993, 1994) and when they are parallel and side by side (Adini, Sagi, & Tsodyks, 1997). The form of the TvCc function varies with separation, having, except at the smallest separations, a facilitation dipper shape with facilitation decreasing as separation increases (Polat & Sagi, 1993). Polat and Sagi (1993) varied separation in one-wavelength steps and found a minimum at 3 λ for high spatial frequencies and 2 λ at low spatial frequencies. Woods, Nugent, and Peli, (2002) found that separation effects do not scale with spatial frequency.

Direction: Relative direction interacts strongly with relative orientation, so here I focus on experiments in which target and flankers had the same orientation. Ejima and Miura (1984) showed that in-phase 3 c/° vertical flanking gratings abutting the left and right edges of a vertical target grating decreased the target threshold when they were low contrast and increased the threshold when they were high contrast, a full dipper function.

Polat and Sagi (1994) showed that lateral effects occur for 13.3 c/° Gabor flankers that are above and below, left and right, and on a 45° diagonal through the center stimulus. They used only high-contrast flankers and showed that, when they are close to the target, they mask, and when they are about 2 λ away, they facilitate. This suggests that lateral effects can be produced by symmetrically placed flankers in any direction around the target. However, facilitation is greatest when the target and flankers are collinear.

Yu, Klein, and Levi (2002) compared detection with half and full annulus surrounds. For same-orientation

surrounds, a collinear half annulus (quarter above and quarter below) reduced thresholds the most. A half annulus on the sides or a full annulus reduced thresholds very little. For orthogonal context, all three contexts reduced thresholds substantially.

Chen and Tyler (2008), using vertical Gabor targets and flankers with a separation of 2.8 λ and a flanker contrast of 0.5, found facilitation of detection for azimuths up to 45° from vertical. Facilitation decreased as azimuth increased, and at 90°, masking occurred.

Thus, context patterns in any direction from the target can affect the target detection threshold, but those in the collinear direction have the largest effects.

Relative orientation: Polat and Sagi (1993) measured thresholds for a Gabor pattern with Gabor flankers at the ends of the targets (spatial frequency = 13.33 c/°, Cc = 0.3) in different relative orientations. Collinear flankers at 3 λ separation reduced thresholds. As the flankers were rotated, facilitation decreased for rotations up to 30°. Flankers at 90° had no effect.

Using a 4 c/° vertical Gabor target and annulus flankers of contrast 0.5 above and below the target at 3 λ separation, Chen and Tyler (2002) got inconsistent results for detection. For one observer, all relative flanker orientations reduced the detection threshold; the effect decreased as relative orientation went from collinear to orthogonal. For the other, only collinear flankers produced a clear reduction. However, there is agreement with Polat and Sagi (1993) that collinear flankers produce the largest facilitation effects.

Solomon and Morgan (2006) measured the effect of relative orientation on contrast detection using a Gabor target and a context consisting of eight Gabor patterns arranged in a circle at 4.24 λ from the target. This context had essentially no effect on target detection. They found a small decrease in the steepness of the TvCp function as relative orientation rotated from parallel to orthogonal.

Contrary to the finding of no effect from orthogonal Gabor patterns at the ends of a circular Gabor pattern, Yu et al. (2002) found that at 8 c/° orthogonal Gabor patterns at the ends of a target Gabor pattern with a separation of 2.5 λ reduce thresholds, but only over a narrow range of low flanker contrast. They measured the TvCc function and found that it was a facilitation dipper with a minimum at Cc = 0.1. The earlier studies had used higher flanker contrasts. Yu et al. (2002) also measured effects of half annuli with contrast of 0.1 and a mid-radius of 2.1 λ. They found that orthogonal half annuli at the target ends also reduce thresholds. They also compared the effects of orthogonal and parallel half annuli at the sides of a target. Both reduced thresholds about equally. An orthogonal full annulus reduced thresholds more than the half annuli. Parallel half annuli at the ends, like parallel Gabor patterns,

reduced thresholds to about half, but a parallel full annulus reduced thresholds only slightly. So the effect of relative orientation depends on whether the context is at the ends or sides of the target or extends all the way around it. Parallel context on the sides seems to partially counteract the facilitatory effect of parallel context at the ends even though parallel context on the sides alone has a small facilitatory effect. Yu et al. (2002) further showed that, when the context is only at the sides of the target, relative orientation has an effect opposite to its effects at the ends. On the sides, orthogonal context facilitates more than parallel context. This suggests that collinearity of the context patterns with themselves may contribute to facilitation. However, it is important to be cautious about generalizations because orientation interacts with contrast and separation.

In the same study, Yu et al. (2002) measured thresholds as a function of relative orientation using the full annular surround. Both target and surround were 8 c/°, and the surround contrast was 0.1. When the surround was parallel to the target, there was essentially no decrease in the threshold even though some of the stripes in the annulus were collinear with the target stripes. As the surround orientation rotated away from the target orientation, the threshold decreased for relative orientations up to 45° and then remained approximately constant for orientations up to 90°.

Meese et al. (2007) measured TvCc functions for orthogonal annular surrounds at spatial frequencies of 1 and 7 c/°. At 1 c/°, the annulus produced a shallow dipper TvCc function; at 7 c/°, it produced a facilitation dipper with maximum facilitation of about 5 dB. This shows that orthogonal lateral context effects are highly spatial frequency dependent. Shushruth et al. (2013) rarely found enhancement of perceived contrast by orthogonal surrounds at 1 c/°.

Thus, the relative orientation of target and context has large effects on the target threshold. The effects depend on the direction, separation, shape, spatial frequency, and contrast of the context. For Gabor flankers and half annuli, facilitation is maximum when they are at the ends and collinear with the target. For annular flankers, facilitation is maximum when they are orthogonal to the target.

Relative size: When the area of the context stimuli increases, their effect usually increases. However, there are exceptions to this. When a vertical Gabor target is flanked by a column or a row of identical Gabor patterns, as the number of lateral Gabor patterns increases, the threshold goes down, then up, then down (Adini et al., 1997). As noted above, a pair of collinear Gabor patterns reduces thresholds more than a full circle of eight patterns, all parallel and in-phase with

the target; a pair of collinear half annuli reduces thresholds more than the full annulus.

Solomon and Morgan (2000) measured TvCc functions using a Gabor target and Gabor context patterns on a circle at 2.93 λ separation. There were three conditions in which all patterns were in cosine phase: (a) two collinear flankers at the ends of the target, (b) eight flankers equally spaced in a circle around the target, and (c) the same as b without the collinear flankers. In condition a, they got facilitation dipper functions. In condition b, facilitation was greatly reduced and there was masking at high Cc. In condition c, there was essentially no facilitation, and masking increased non-monotonically. This study shows that, not only do context effects not always increase with context area, but also there are complex interactions between different context elements.

In the same study, Solomon and Morgan (2000) showed that, when the same three context configurations are presented with the context Gabor patterns having opposite polarity to the target, two flankers in the end zones had very little effect, the ring of eight produced a shallow full dipper similar to condition b, and the ring of six without the end zone patterns produced a function something like condition c. Thus, opposite polarity masks that are not in the end zones act like same polarity masks.

When a D6 pattern is flanked by a collinear half annulus, its threshold is reduced to about half; if it is flanked by a full annulus, its threshold is reduced much less. However, if the lateral grating is orthogonal to the target, the threshold is increasingly reduced as the configuration varies from side half annulus to end half annulus to full annulus (Yu et al., 2002). On the other hand, the width of an orthogonal annular surround appears to have essentially no effect (Meese et al., 2007).

So increasing the area of the context may increase or decrease its effect, depending on the way in which area is increased. In some cases, an increase in context area could have the same effect as an increase in context contrast, but most area effects seem to be more complex than this.

Relative phase: The effect of the phase relation between the target and context has been studied in conditions in which the target and context are parallel. The results are complex and not completely consistent. When the flankers are on both sides of the target and abutting it, Ejima and Miura (1984) found that the TvCc function is a full dipper when the flankers are in phase with the target and a monotonic masking function when they are out of phase. When the flankers are collinear with the target, in phase with it, and separated by 2–4 λ, the TvCc function is a facilitation dipper; when they are out of phase, weaker

facilitation and some masking occurs (Zenger & Sagi, 1996). McCourt and Kingdom (1996) found that, at 4 c/°, an in-phase grating abutting the ends of a test grating produces a shallow dipper function, and an out-of-phase abutting grating masks at contrasts up to 0.1. So same-orientation, in-phase context at the ends of a target grating produces full dipper functions when it is close and facilitation dippers when it is farther away. Out-of-phase context has smaller and not completely consistent effects, including masking and facilitation.

When the spatial frequency is less than 1 c/° and the target grating is short, very different results have been found. McCourt and Kingdom (1996) showed that, for these low spatial frequencies, an abutting out-of-phase grating decreased the target threshold when it was low contrast and increased the threshold when it was high contrast, the same effect as a pedestal. As spatial frequency increases, the effect decreases. They explain this effect as being due to the induction of an out-of-phase grating percept in the test field that acts as a pedestal for the real out-of-phase grating, reducing thresholds when it is low contrast and increasing them when it is high contrast. At these low frequencies, an in-phase context pattern masks. They attribute this to the induced grating being subtracted from the target grating. These low-frequency effects are likely due to a different process akin to lateral brightness effects.

A complex interaction between phase, position, and number of context elements (Solomon & Morgan, 2000) is described in the section on relative context size.

Zenger and Sagi (1996) studied the effect of context in which two Gabor flankers had opposite phases to each other. They found that this context produces less facilitation than a context in which all three stimulus elements are in phase.

Relative spatial frequency: Polat and Sagi (1993) found that collinear lateral context effects are tuned to spatial frequency with the maximum threshold reduction occurring when target and context have the same spatial frequency. Yu et al. (2002) got a similar result when the surround was orthogonal to the target.

Summary

As lateral contrast increases, detection thresholds often decrease and then increase, producing a dipper function. At small separations, the function is a full dipper for parallel context and a facilitation dipper for orthogonal context. As separation increases, the magnitude of facilitation decreases, but lateral effects occur out to separations of 8 λ or more. Because the TvCc function is dipper shaped, the maximum facilitatory effect often occurs at low context contrast.
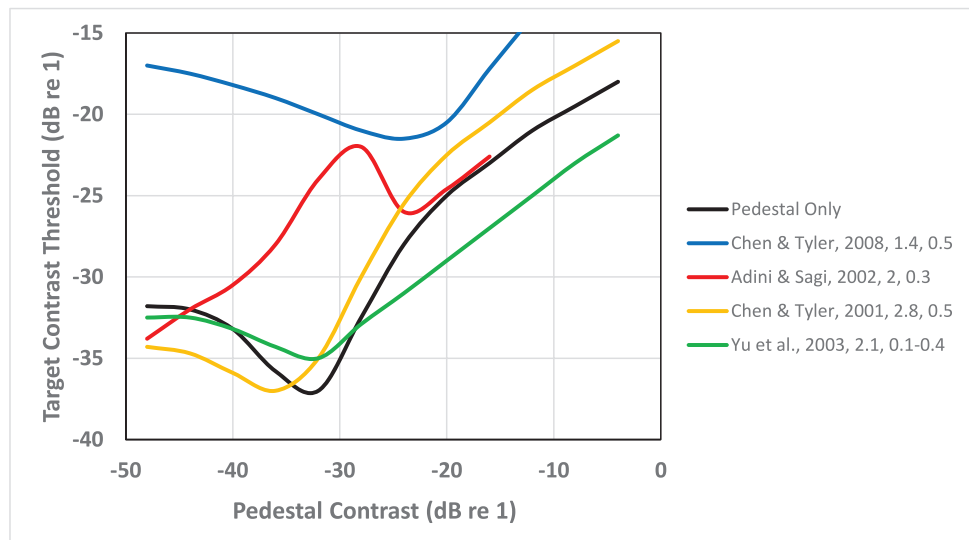
Figure 1. A sketch of some TvCp function types for contrast discrimination, without and with lateral context, found in the literature. All are for the case in which context is parallel to and collinear with the target. The horizontal axis is pedestal contrast, and the vertical axis is target contrast threshold. There are logarithmic decibel scales on both axes. The black curve is the TvCp function when there was no lateral context. The other curves correspond to four different function forms found in the literature. The legend indicates the source, year, center-to-center separation in wavelengths, and context contrast. Other factors, including spatial frequency, vary.

Collinear context at the ends of a target grating (Gabor patterns or half annuli) reduces thresholds more than parallel context of the same contrast on the sides or a full parallel annulus although context stimuli in any direction from the target affect the target threshold. Effects are not simply related to the size of the context, sometimes decreasing as size increases. The effect of relative orientation depends on the shape of the context; when context contrast is low, collinear Gabor flankers reduce thresholds the most, but when the context is an annulus, orthogonal context reduces thresholds the most.

Lateral effects on pattern contrast discrimination thresholds

Method

Contrast discrimination is distinguished from pattern detection by the fact that, in discrimination, a contrast pattern (pedestal or pedestal plus target) is presented in every stimulus interval. Usually the patterns are identical except one has an increment of contrast added to it. The contrast-discrimination threshold is the contrast increment (target contrast) that meets the threshold criterion. In some experiments that are referred to as contrast-discrimination experiments, the lower contrast pattern is a different size than the contrast pattern that is added to it, but they are the same on other dimensions.

Results

Context contrast: In the contrast-discrimination task, both the context contrast, Cc, and the pedestal contrast, Cp, can be varied independently. In most of the studies, Cp has been the primary independent variable, and in some studies, there was only a single value of Cc. When there is no lateral context, the TvCp function has a full dipper form (Legge & Foley, 1980). When there is lateral context, there are several forms that the TvCp function has been found to take. The form depends on the properties of the context patterns, particularly their separation and contrast. The context has complex effects on this function, increasing or decreasing thresholds in different ways depending on the specific context. There are at least four different forms that occur with parallel collinear context. These are illustrated in Figure 1. Most of these forms can be fitted by the models described in the Model section, but with very different parameters.

Most studies of lateral context effects have used separations of 2 λ or more. At a separation of 1.4 λ, using 4 c/° Gabor targets, pedestals, and collinear flankers with a contrast of 0.5, Chen and Tyler (2008) found a TvCp function (blue) that was very different from the others. When there was no pedestal, the flankers increased the threshold by a factor of about two. As pedestal contrast increased, the threshold decreased and then increased, remaining well above the thresholds for the pedestal alone or the other context conditions. Using an annular 1.1 c/° target and a parallel surround (Cc = 1) both inside and outside the

target with only a thin line between them, Zenger-Landolt and Heeger (2003) found that the surround alone increased the detection threshold by a factor of about three. As pedestal contrast increased, the threshold decreased, then increased, then decreased, remaining above the threshold for the pedestal alone at all but the highest pedestal contrast at which the context had essentially no effect. These studies suggest that very close surrounds mask substantially.

Using the same conditions with center-to-center separations of 2.8 and 3 λ (blue), Chen and Tyler (2001, 2002, 2008) found that the context decreased the threshold at and near Cp = 0. At higher pedestal contrasts, the flankers raised the threshold by an approximately constant 2–3 dB. Chen and Tyler measured thresholds for Gabor targets in the presence of Gabor flankers at center-to-center separations of 2.8, 4.2, 5.6, and 8.4 λ. At these separations, they found TvCp functions very similar in form. The magnitude of the context effects decreased as the separation increased.

Adini and Sagi (2001) measured discrimination thresholds for Gabor targets flanked by a pair of collinear Gabor patterns (Cc = 0.3) as a function of pedestal contrast (red). All patterns were 6.67 c/°, and flanker separation was 2 λ. The flankers reduced detection thresholds and increased thresholds for mid-contrast pedestals. When the pedestal was high in contrast, the flankers had essentially no effect. The collinear context produces a substantial increase in the threshold over the mid-pedestal range.

Yu et al. (2003) varied both Cp and Cs using a standard stimulus configuration that they used in several studies (green). Their target was an 8 c/° D6 pattern, which had a Gaussian envelope along the direction of the grating that was cut off at 10 min diameter. It was presented on a disk grating of the same spatial frequency and phase that was 18 min in diameter. The annular surround abutted the disk grating, so there was a small gap between the target and the surround. The midpoint of the context was 2.1 λ from the center of the target. The lateral context was a full annulus containing an 8 c/° grating. Using a full-annulus parallel surround, they measured TvCp functions at five levels of surround contrast. When there was no pedestal, the collinear annulus had very little effect on the detection threshold except to increase it when Cc = 0.8. The lack of an effect on detection is probably a consequence of the separation being at a transition point between near context that masks and far context that facilitates. As Cp was varied, it produced shallow full dipper TvCp functions at all values of Cc. At mid-values of Cp, the threshold was higher than with Cp alone, and at high values of Cp, the threshold was lower than with Cp alone. Thus, at

high pedestal contrasts, the effect of the context was opposite to that found by Chen and Tyler (2002, 2008).

There are very few studies that measured contrast discrimination in the presence of orthogonal context. Yu et al. (2003) did this using their standard stimulus paradigm. When the surround was orthogonal to the target, it decreased thresholds at all values of Cp for all values of Cc. The decrease was usually greatest at the pedestal contrast at which the threshold was lowest. This form is not shown in Figure 1.

Although the stimuli in each of these studies are different, the differences between the four TvCp function forms for parallel context are puzzling. In the Chen and Tyler (2002, 2008) studies, when the pedestal contrast is above threshold, high contrast context never reduces discrimination thresholds. In the Yu et al. (2003) study, context reduces thresholds over a large range of pedestal contrasts. What is responsible for these differences? The Adini and Sagi (2001) form and the Yu et al. (2003) form were found at similar center-to-center separations, 2.0 and 2.1 λ. The Chen and Tyler (2002, 2008) form was found at a range of separations from 2.8 to 8.4 λ. So separation is a factor, but the relationship is not clear. There are other differences in the stimuli that could also influence this function.

Yu and Levi (2000) did a study that provides further evidence that both collinear and orthogonal lateral context reduce discrimination thresholds. Here Cp was fixed at 0.4, and Cc was varied. Using their standard stimulus configuration, they measured the discrimination threshold for a wide range of Cc values. When the surround had the same orientation as the target, as the surround contrast increased, the discrimination threshold decreased to a minimum at the surround contrast that matched the pedestal contrast and then increased to near the threshold with the pedestal alone. When the surround had an orientation orthogonal to the target, the threshold continued to decrease over the full range of surround contrasts (0.1 to 0.8), essentially eliminating the threshold increase produced by the pedestal. So, at high surround contrasts, an orthogonal surround facilitated much more than a collinear surround. They refer to the threshold decrease when there is a lateral context as "unmasking." Unmasking occurs at all relative orientations, but is greatest at 0° and 90°. This result agrees with the Yu et al. (2003) result in that both show that lateral context reduces thresholds when pedestal contrast is high.

Adini and Sagi (2001) varied the number of flanker pairs and showed that this can change the form of the function. This is described under size effects. They also compared collinear and parallel side-by-side arrays. This is described under relative position.

These studies show that both context contrast and pedestal contrast have large effects, as does separation,

and there are strong interactions among these three variables. However, no overall pattern emerges from these results.

Relative position: Adini and Sagi (2001) compared the effects on contrast discrimination of collinear Gabor flankers at the ends of a target Gabor with parallel Gabor flankers to the sides of the target. All the stimuli were 6.67 c/°, the separation was 2 λ, and the flanker contrast was 0.3. Parallel flankers on the sides of the target increased thresholds less than those at the ends at mid-values of Cp and decreased thresholds at high Cp. So positioning the parallel context to the sides of the grating had the general effect of increasing thresholds less than parallel context at the ends.

Chen and Tyler (2008) used 4 c/°, vertical and Gabor targets and flankers with a separation of 2.8 λ ($Cc = 0.5$) to study relative direction more extensively. The flankers were located in different directions (azimuths) from the target, either above or below (collinear, azimuth $= 0$) or in other directions symmetrically placed on a circle centered on the target. When the pedestal contrast was greater than the target detection threshold, flankers in all directions generally increased detection thresholds, and the increase was greatest when the azimuth was zero. So, for parallel target and context with separation 2.8 λ, positioning them so that they are collinear produces the most masking. At low pedestal contrast, the context decreased thresholds, but there was no clear dependence on relative direction.

Distance: As noted above, Chen and Tyler (2008) measured TvCp functions in the presence of lateral flankers at separations of 1.4 to 8.4 λ. For pedestal contrasts above the detection threshold and separations $\geq$ 2.8 λ, the effect of the lateral context was to increase the contrast discrimination threshold by a roughly constant factor of 2–3 dB. This increase was greatest at 2.8 λ and decreased with further separation. At 1.4 λ, on the other hand, thresholds were much higher at all values of Cp, and the TvCp function had a dipper shape.

Relative size: In the Adini and Sagi (2001) condition that produced the form shown in Figure 1, there was a single pair of flankers. In the same study, TvCp functions were measured with additional pairs of flankers arranged in a vertical column or a horizontal row. The predominant effect of adding a second pair was to reduce thresholds. Adini and Sagi also did an experiment (experiment 2) in which they had up to four pairs of flankers but with just two pedestal contrasts. The flankers were separated by 2 λ intervals in a vertical collinear column. The pedestal and the flankers were equal in contrast, either near threshold or 0.3. Because the number of flanker pairs varied, this is

similar to detection on a mask that varies in size. The low-contrast pedestal alone decreased the threshold; the high-contrast pedestal increased it. At both pedestal contrast levels, when one pair of flankers was added, the threshold increased. With two pairs and then three pairs, the threshold decreased. With four pairs, there was little change for the low-contrast stimuli, but for high-contrast stimuli, the threshold increased. With five pairs, the threshold decreased.

Yu and Levi (1997) discovered an effect that is similar to the effect that Adini and Sagi (2001) found when varying the number of pairs of flankers. Instead of flankers, they used a D6 mask of contrast 0.4 that extended under the target and was varied in length. Their target was a D6 pattern. As the length of the mask increased, the threshold increased until the mask was somewhat longer than the target and then decreased. At low spatial frequencies, as the mask gets longer than the target, the threshold goes well below the discrimination threshold when the mask has the same length as the target; at high spatial frequency, it does not go so low, and there is a small increase for the longest masks. Here, the context may be thought of as consisting of a pedestal and an abutting context that is an extension of the same stimulus. Unlike in the other experiments, here Cp and Cc covary and are equal. Yu and Levi (1997) did not get a second increase in most of their conditions, but only at their highest frequencies did the context reach several wavelengths into the periphery, so if the masks are extended further, it may occur. Both of these studies show that, as the context area is extended outward, thresholds increase, then decrease, and sometimes increase again for extended contexts. These effects are not unambiguously size effects because sensitivity varies from region to region in the surround. The threshold may decrease because the context is extending into regions that are more excitatory. The threshold reduction that occurs for larger masks is an instance of the unmasking phenomenon (Yu & Levi, 2000).

Relative phase: Yu and Levi (1997) also examined phase effects. As described above, using D6 patterns for target and mask, they showed that, as a superimposed D6 mask with a contrast of 0.4 was extended beyond the target, the threshold increased and then decreased as mask length increased. They distinguished two zones at the ends of the target. The zone abutting the target on both ends (outer summation zone) acted as if it contained an extension of the receptive field that detected the target. A same phase stimulus in this region increased the target threshold; an opposite phase stimulus decreased the target threshold. This is what we would expect if a linear receptive field extended through this outer summation zone. On the other hand, collinear lateral stimuli

confined to a region beyond the outer summation zone, in what they call the "end zone," reduced thresholds, and in- and out-of-phase stimuli had the same effect. Similar effects of same and opposite phase contexts are consistent with detection studies in which there was a gap between target and lateral contrast (Ejima & Miura, 1984; Zenger & Sagi, 1996).

Relative orientation: Yu and Levi (1998b) showed that, when a grating target is masked by a superimposed grating ($Cp = 0.4$), the facilitation produced by end-zone grating flankers ($Cc = 0.4$) is tuned to orientation with the threshold being lowest when the end-zone context orientation matches the target orientation. The threshold increases with relative orientation and then decreases for larger relative orientations. This effect was found at spatial frequencies of 1.7 to 8 c/°. Yu and Levi, (2000) got a similar result using 8 c/° annular surrounds and pedestals, both with contrast 0.4. They showed that the surround generally facilitated contrast discrimination by lowering the threshold over the full range of surround orientations. The threshold was lowest when the pedestal and surround either had the same orientation or were orthogonal to each other as Yu and Levi (1998b) had found for context at the ends of the target.

This orientation effect is quite different from that found for detection. Yu et al. (2002) showed that, for detection, when the surround is a parallel full annulus with contrast equal to 0.1, it has a very small effect. As relative orientation increases, the threshold decreases up to an orientation difference of 45°, beyond which the threshold is roughly constant. The different effects of context orientation for detection and discrimination imply that, when there is lateral context of varying orientation, the form of the TvCp function must vary with context orientation.

Using Gabor targets and flankers separated by 3 λ, Chen and Tyler (2002) found that orthogonal flankers with contrast 0.5 at 3 λ above and below vertical targets raise thresholds 2–3 dB when the pedestal is above detection threshold, about the same as the effect that they get with parallel flankers. It is not clear why the result is so different from Yu and Levi's (1998b) results.

Chen and Tyler (2002) measured discrimination thresholds for a 4 c/° Gabor pattern in the presence of Gabor flankers with a contrast of 0.5, separated by 3 λ, and varied in relative orientation. For pedestals above the detection threshold, all relative orientations raised discrimination thresholds by 2–3 dB. The increase was roughly equal for all above-threshold pedestal contrasts and all relative orientations. It is puzzling that, at this separation, masking would occur. Polat and Sagi (1993), using Gabor targets and flankers of 13.33 c/°, got no effect of orthogonal Gabor flankers. At other relative orientations, they got effects that varied with

separation. Thresholds were increased at small separations and decreased at larger separations. So the effects of relative orientation on contrast discrimination are complex.

Solomon and Morgan (2006) measured the effect of relative orientation on TvCp functions for contrast discrimination using a Gabor target and a context consisting of eight Gabor patterns arranged in a circle at 4.24 λ from the target. They found a small decrease in the steepness of the TvCp function as relative orientation rotated from parallel to orthogonal.

Relative spatial frequency: Yu and Levi (1998b) showed that the facilitation produced by parallel end-zone context ($Cp = Cc = 0.4$) is tuned to relative spatial frequency with the threshold being lowest when the mask frequency matches the target frequency. Polat and Sagi (1993) also found tuning to relative spatial frequency for both the threshold elevation produced by near context and the threshold reduction produced by farther context.

Duration: Yu and Levi (1999) varied the duration of target and pedestal ($Cp = 0.4$). They found that the threshold decreased as duration increased up to a duration of about 200 ms. When a lateral context grating was added to the stimuli, it had no effect when the duration of the three stimulus components is less than 50 ms. For longer durations, adding the lateral context decreased the threshold further, reaching a minimum at about 200 ms. This indicates that the lateral effect is delayed relative to stimulus onset and reaches a maximum at about 200 ms under their conditions. The facilitating effect of the context is greater at 1.7 c/° than at 8 c/°.

Summary

The literature shows that lateral context has a variety of effects on contrast discrimination. When there is no surround, the TvCp function has a full dipper form. When a context is introduced, it may change this form quite a bit. Lateral context both increases and decreases thresholds, and the same context often does both at different pedestal contrasts, separations, and relative orientations. These effects occur over a wide range of separations and decrease in magnitude as separation increases. There are strong interactions between Cs and Cp. They tend to partially cancel one another's effects.

There are inconsistencies in the literature. Yu and his collaborators (Yu & Levi, 1997, 1998a, 1999, 2000; Yu, Klein, & Levi, 2003) find that collinear lateral context usually decreases contrast discrimination thresholds and the magnitude of the effect depends on the pedestal contrast. Chen and Tyler (2000, 2001, 2002, 2008)

consistently find that collinear lateral context increases contrast discrimination thresholds by approximately a constant factor for all pedestal contrasts above detection threshold. The difference is not due to spatial frequency because Yu and his associates used a range of spatial frequencies. There is a similar discrepancy with orthogonal context. Chen and Tyler found substantial increases in thresholds; Yu et al. found substantial decreases. Although there are differences in their stimuli, none of them suggest an explanation. So the literature leaves uncertainty about this very basic effect of lateral context.

Physiology

Lateral context effects have been studied in the cat and macaque monkey using single-cell recording. Most of the studies have focused on area V1 in the macaque. Cells in single-unit studies are rarely in the central fovea, and it is known that suppression increases away from the fovea, so the cells studied may not be like the cells that mediate central vision in humans. In physiology, an effect is attributed to the receptive field surround if it is produced by a stimulus that is outside the receptive field. Surround stimuli often modulate the response to a stimulus in the receptive field.

Originally the receptive field was defined as the region of the retina in which a stimulus produces a response in the cell. It was later realized that this region depends on the properties of the stimulus. The largest fields are found when the stimulus is a disk grating that is increased in radius until the response no longer increases. This region is called the summation receptive field, sRF. This radius depends on the contrast of the stimulus. The receptive field is smaller for high-contrast stimuli (sRFhigh) than for low-contrast stimuli (sRFlow). However, there are not two discrete field sizes as the summation field radius varies continuously with contrast (Angelucci & Shushruth, 2014).

The predominant lateral effect is suppression, but many lateral contexts increase the cell response. Their effects depend on the type and position of the surround and the contrasts of both center and surround. A response increase is often referred to as "facilitation" although this term has a different meaning in psychophysics. I use the term "enhancement" for an effect in which one stimulus increases the response to another stimulus. When the stimuli are low contrast, enhancement of the response to a line stimulus is produced by discrete collinear lateral stimuli within sRFlow but outside sRFhigh (Kapadia, Ito, Gilbert, & Westheimer, 1995; Levitt & Lund, 1997). But there is also enhancement from lateral stimuli further away from the center. Polat, Mizobe, Pettet, Kasamatsu, and Norcia (1998), using Gabor targets and Gabor flankers at 80%

contrast, 3–4 λ away from the target, found four classes of cells in the cat striate cortex: cells whose response was increased when the center stimulus was low contrast and suppressed when it was high contrast (34%), cells whose response was increased at all contrasts (33%), cells suppressed at all contrasts (19%), and cells on which the flankers had no effect (14%). Orthogonal flankers had primarily suppressive effects. Chen, Kasamatsu, Polat, and Norcia (2001) did a similar study with collinear context and got similar results except that they also found cells whose response was decreased at low contrast and increased at high contrast.

In macaque V1 cells, annular grating surrounds matched to the spatial frequency, temporal frequency, and phase to which the RF center is tuned and close to but not in the sRFlow most often produce suppression of the response to a center stimulus (Cavanaugh, Bair, & Movshon, 2002a; Ichida, Schwabe, Bressloff, & Angelucci, 2007). Suppression predominates even when both center and surround contrasts are low. The receptive field surround is not always symmetric; suppression can be along one axis, often from the end zones (Cavanaugh et al., 2002a). It is not clear whether the different result from that in the cat studies is due to a difference in species, context shape, or separation.

Effect of spatial configuration

Some studies have varied the spatial properties of the stimuli. In one paradigm, the response is measured to a single disk grating whose radius is varied. As the radius increases, the response increases until the radius reaches the edge of the summation receptive field. This field is smaller when the contrast is high than when the contrast is low. Beyond the maximum, the response decreases smoothly to a level above the maintained discharge (Cavanaugh et al., 2002a; Ichida et al., 2007). See Figure 2, left. Thus, high and low contrasts have opposite effects in the region between sRFhigh and sRFlow. When a high-contrast stimulus is enlarged into this region, the response starts to decrease, but when the stimulus is low contrast, the response continues to increase. At all contrasts, as the stimulus is made still larger, the response is increasingly suppressed over radii at least twice as large as sRFlow. So suppression is being produced from a region just outside the receptive field. For still larger radii, the response is roughly constant, but there is sometimes a second small response peak at larger radii (Shushruth et al., 2009). These experiments have been done with disk gratings of different contrasts. As the contrast decreases, the response versus radius function moves downward, and the peak shifts to the right, consistent with an increase in receptive field size. As contrast decreases, the factor by which the response decreases beyond the peak is
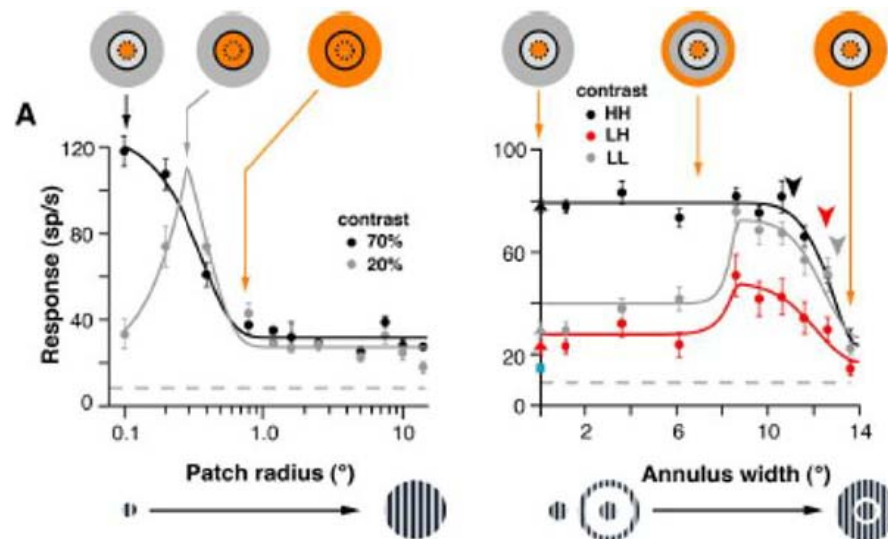
Figure 2. Left: patch size experiment. The leftmost stimulus just fills sRFhigh. Right: encroaching annulus experiment. Here the center grating radius was 0.1°, and the innermost radius of the surround was 0.4°. Far surround enhancement was maximum about 6° away. The contrasts on the right are H: 0.7 and L: 0.4. The first symbol is the test contrast, and the second symbol is the annulus contrast. From Ichida et al. (2007). Reprinted with permission.

smaller (Cavanaugh et al., 2002a). De Angelis, Freeman, and Ohzawa (1994); Sceniak, Hawken, and Shapley (2001); and Sceniak, Ringach, Hawken, and Shapley (1999) have done similar experiments.

In another paradigm, the only stimulus is a high-contrast annulus. The annulus has a large outer radius, and the inner radius is varied (Cavanaugh et al., 2002a). When the inner radius is large, the annulus produces little or no response. When the annulus encroaches on the sRFlow, the response begins to increase, and it continues to increase until the annulus fills in, becoming a disk grating.

In a third paradigm, there is a disk grating in the sRFhigh, and an annulus grows inward from a large outer radius to sRFlow (Ichida et al., 2007). The effect of the annulus depends on the center contrast. When the center contrast is high, the response is high, and there is no effect of the annulus when its inner radius is large. When the annulus gets closer, it increasingly suppresses the response (Figure 2, right). When the center contrast is low, the response is low when the inner radius is large, but at an inner radius much larger than sRFlow, the response starts to increase (gray and red curves). This enhancement is often a factor of two or more. At a smaller inner radius but still well outside sRFlow, the response starts to decrease. The larger the response to the center alone, the greater is the decrease so that, when the annulus abuts the sRFlow, all center stimuli produce low response rates. The enhancement of responses to a low-contrast center is greater when the surround is low contrast (gray) than when it is high contrast. These surround effects are found in all layers of V1 in the macaque, but there is no far surround in the input layer, layer 4C (Angelucci & Shushruth, 2014). It is interesting that, when a disk grows out from the center, the enhancement is rarely apparent. Apparently, the suppression from the near surround overcomes the enhancement that is produced by a far surround in the absence of a near surround. There is a lot of variation in the size and position of these regions from cell to cell, and approximately 40% of cells do not show lateral enhancement.

Effects of center and surround contrasts

In addition to studying the effect of spatial configuration, Cavanaugh et al. (2002a) fixed the spatial configuration and varied the contrasts of the center and the surrounding annulus. The center
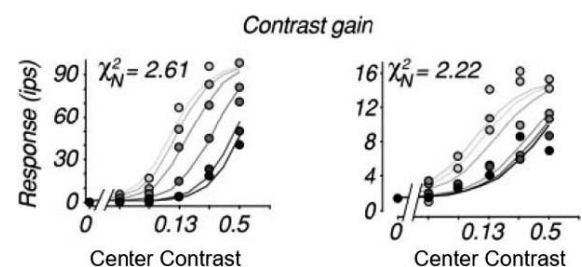

Figure 3. The response of two sample V1 cells to a center contrast in sRFhigh in the presence of a surround abutting sRFlow. The surround contrasts of 0, 0.03, 0.06, 0.12, 0.25, and 0.5 are indicated by data points from light to dark. As surround contrast increases, the response function decreases and changes shape. From Cavanaugh et al. (2002a). Reprinted with permission.

stimulus was the same size or slightly smaller than the sRFhigh. The inner diameter of the annulus was just outside sRFlow. They measured the response as a function of the center contrast at several surround contrasts (see Figure 3). When the surround contrast was zero, the response function was S-shaped. As the surround contrast increased, the surround increasingly suppressed the response, and the steepest region of the function moved to higher contrasts so that, at high surround contrasts, the response is an accelerating function of center contrast over the entire range tested. They fitted three models to their data: a response gain model, a subtraction model, and a contrast gain model. The contrast gain model fitted their data best. In this model, the effect of the surround is not a simple multiplicative reduction of the response. The response is a function of the ratio of the center contrast to the sum of a function of the surround contrast plus a constant. Their model is a simplified version of the Foley (1994) model of contrast masking. Note that these close surrounds only suppress, and more distant surrounds enhance.

Relative orientation

Cavanaugh, Bair, and Movshon (2002b) used annular surrounds abutting sRFlow and found only suppression when center and surround had the same orientation. Suppression is greatest when the surround has the same orientation as the center, and it decreases as the orientation difference increases. When the center contrast is low, suppression is greater. Shushruth et al. (2009) confirmed the relative orientation effect and showed that suppression sometimes transforms into enhancement for orthogonal surrounds. Shushruth et al. (2013) showed that the orientation tuning of surround suppression is broader when the surround is outside sRFlow and that human perception shows a similar difference in tuning to very near and farther surrounds. Their far surrounds were close enough to the center to produce large suppressive effects. Surprisingly, the tuning of the far surround depends on the orientation of the center stimulus, not the orientation of the receptive field. The strongest suppression occurs when the center stimulus and the surround have the same orientation even when the cell is tuned to a different orientation (Shushruth et al., 2012).

Relative position

Cavanaugh et al. (2002b) measured the effects of relative position. When the context has the same orientation as the center, collinear context suppresses most, and context on the sides suppresses least. Orthogonal context suppresses most when it is at the sides of the test pattern, least when it is at ends, but

position effects are not large for either relative orientation. For all relative positions, same orientation context suppresses more than orthogonal context.

Time–distance relationships

Suppression from the far surround is delayed slightly relative to the response to the center stimulus. This delay averages about 9 ms, and it does not depend on the inner radius of the surround, but latency increases as the strength of the lateral signal decreases (Bair, Cavanaugh, & Movshon, 2003). Other studies show somewhat longer delays but not more than 60 ms (Angelucci & Shushruth, 2014). Suppression sometimes arrives faster than the center response. Suppression is predominantly sustained for near context and transient for distant context. Lateral suppression can propagate at ~1 m/s, much faster than expected for horizontal connections (Bair et al., 2003). When the stimulus is a disk grating larger than the receptive field, there are two components to suppression: an orientation-untuned component that has no delay and an orientation-tuned component that is delayed by 17 ms. When both the test and the mask are confined to sRFhigh, only the untuned component is seen. These latencies are less than those found psychophysically by Yu and Levi (1999).

Anatomical circuits for surround modulation

Three types of neural connections are involved in lateral effects: feed-forward connections from the lateral geniculate nucleus (LGN), long-range horizontal connections in V1, and feedback connections from extrastriate cortex. LGN cells have a surround that overlaps and extends beyond their receptive fields as traditionally defined (Angelucci & Shushruth, 2014). These surrounds are smaller than the surrounds of V1 cells. LGN cells project to layer 4C in macaque V1. Neurons in several layers of V1 project to other V1 neurons in the same layer. Both excitatory and inhibitory neurons in layers 2/3 project to other neurons with receptive fields centered at different positions but with similar orientation tuning. Connections in other layers do not have this property. These neurons generate only subthreshold responses in their target cells. Weak electrical stimulation of horizontal circuits elicits only excitatory postsynaptic potentials (EPSPs); strong stimulation elicits EPSPs followed by strong inhibitory postsynaptic potentials. The monosynaptic spread of these signals is commensurate with the size of sRFlow, so they do not account for more remote effects. These neurons have low conduction velocities: ~0.1 m/s. Their connections seem likely to underlie near surround modulation, including spatial summation at low contrast and collinear facilitation.

V1 sends feed-forward connections to V2, V3, and V5/MT, each of which sends excitatory feedback projections to V1. The feedback goes to layers 1, 2/3, 4B, and 6 in V1. It does not drive V1 cells, but it does enhance their responses to a stimulus in their receptive fields. The feedback connections have approximately the spatial extent to provide the basis for far surround modulation. Both feed-forward and feedback connections between V1 and V2 conduct at 2–6 m/s, more than 10 times faster than horizontal connections. This very fast conduction accounts for the fact that there is almost no difference in the latency of far surround effects from different distances.

Schwabe, Obermayer, Angelucci, and Bressloff (2006) proposed a network model to account for lateral effects on macaque V1 cell responses. The model attributes effects of context stimuli in the far surround (beyond sRFlow) to feedback from extrastriate neurons. When the center stimulus is low contrast so that the response is small, a lateral stimulus further excites the center via feedback and increases the cell response. Enhancement occurs even though the feedback also produces inhibition because there is a threshold on inhibitory signals. However, the gain of inhibitory neurons is higher, so when the stimulus is high contrast, inhibition dominates. This model accounts for both far surround enhancement and suppression found by Ichida et al. (2007). Schwabe, Ichida, Shushruth, Mangapathy, and Angelucci (2010) tested the model by showing that responses to low contrasts are suppressed less than responses to high contrasts as predicted by the model. They also show that some of the excitation is produced by feedback. The model combines excitation and inhibition additively unlike other models that assume inhibition acts divisively (Albrecht & Geisler, 1991; Geisler & Albrecht, 1992; Heeger, 1992). It is not clear how wide a range of data the model can describe.

fMRI

Zenger-Landolt and Heeger (2003) measured TvCp functions and fMRI responses for contrast detection and discrimination in three observers. Their target was an annulus that had a grating context both inside and outside the annulus. The entire stimulus was a contrast reversing 4 Hz, 1.1 c/° sinusoidal grating presented for 750 ms. The annular target region extended from 4.5° to 7.8° eccentricity, and the surround region filled the rest of a 16.4° radius circle. The surround was very close to the target, separated only by a thin black line. The target annulus was divided into eight segments. The task was to determine whether or not one of the segments had a lower contrast than the other seven (a yes/no task). On half the trials, all segments had the same contrast. The higher contrast was adjusted using a staircase to determine the contrast at which a difference was detected on 79% of trials. There were eight pedestal contrasts. The surround contrast was zero or one. In the absence of the surround, the TvCp had close to the usual full dipper form. The surround increased thresholds at all but the highest surround contrast. So the TvCp function is similar to other TvCp functions for close surrounds. For the fMRI measurements, there were four target contrasts: 0.1, 0.2, 0.4, and 0.8. The fMRI amplitude increased with target contrast. The surround reduced the amplitude substantially with proportionally more suppression at the lowest contrasts, consistent with the thresholds. There was very good agreement between response amplitude and threshold in V1 but not in V2 and V3. Thus, V1 fMRI responses seem to predict contrast discrimination thresholds in humans.

Experiments

There is a large literature on lateral effects on pattern vision. It is established that lateral context affects perceived contrast, detection, and discrimination and that single units in V1 are affected by lateral stimuli outside their receptive fields. These effects increase and decrease detection and discrimination thresholds and perceived contrast. There is no model that encompasses all of the evidence in even one of these domains. One of the problems is that a large number of stimulus variables influence these effects. No study includes all or even most of these. The review of the literature indicates that the contrasts of both the test stimulus and the context and their separation are critically important variables. The nature of the context, particularly whether it consists of a surrounding annulus or a pair of Gabor patterns is also important. This study focuses on these variables. It consists of seven experiments in which thresholds are measured as a function of context contrast, TvCc, or pedestal and context contrast, Tv(Cp, Cc). The measurements are made over a range of separations and for both annular and Gabor pattern contexts. The experiments were conducted in a manner consistent with the Declaration of Helsinki.

Methods

Apparatus was a display system consisting of a computer, a Cambridge Research Systems graphics board (model VSG 2/5 with 15 bits of intensity resolution), and a Clinton monochrome display model DS2190P with a P45 phosphor, a resolution of 1,184 × 848 pixels, and a frame rate of 100 Hz.
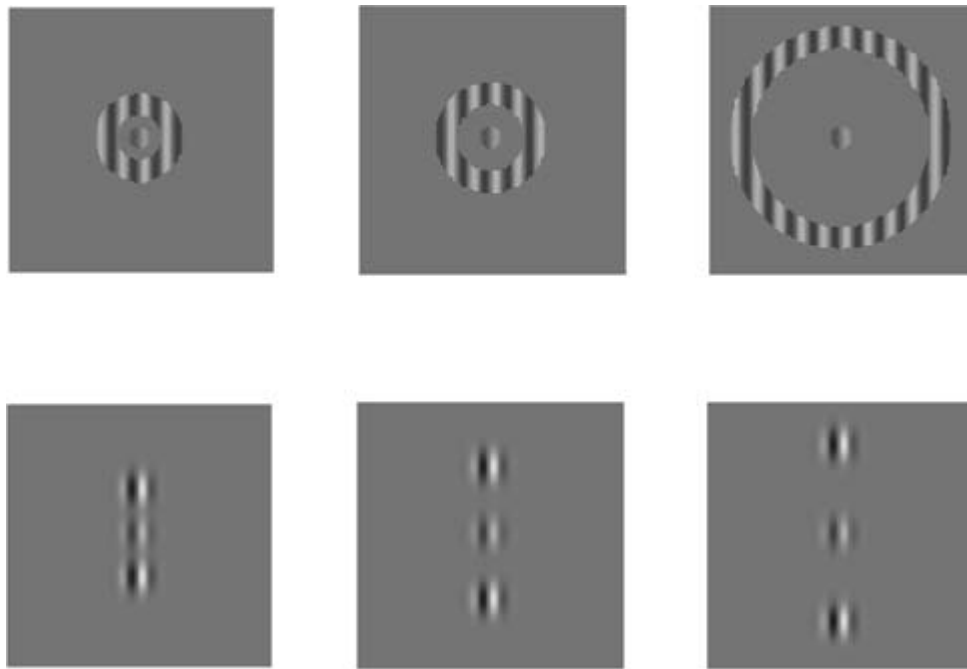
Figure 4. Examples of the stimuli used in the experiments. Top: disk target with annular context. Bottom: Gabor context with Gabor context. The spatial frequency was 4 c/°. The width of the annuli varied over experiments. The standard deviation of the Gabor patterns was 0.15° (0.6 wavelength) except in Experiment 5. In two of the experiments, the separation between target and context varied.

Stimuli

Many features of the method were the same in most of the experiments. I describe the common features here and the exceptions under the descriptions of the individual experiments.

The background luminance varied between experiments; it was in the range of 20 to 50 cd/m^2. The fixation mark was four short lines with a luminance just enough higher than the background so that they could be clearly seen. If extended through the center, these would form a plus sign with the center at the fixation point, but they did not extend through the region where the target was presented. These were on continuously during experiments, and observers were instructed to fixate at the point where the lines would intersect. All the target stimuli were centered on the fixation point.

The target stimuli were small disk gratings or Gabor patterns (see Figure 4). Context patterns were annuli containing gratings, Gabor patterns, or disk gratings superimposed on the target area so that the context and the target were added. All stimulus elements had a spatial frequency of 4 c/° and were in phase spatially and coincident in time. Examples of the stimuli are shown in Figure 1. All were presented simultaneously for 100 ms with a rectangular temporal waveform.

The disk grating targets had a radius of 0.125°, so they contained one cycle of the grating. The grating was in sine phase relative to the center of the target. For the annular surrounds, the width of the surround

and the separation between target and surround varied within and between experiments. The Gabor targets had a standard deviation of 0.15° except in Experiment 5, and were in sine phase relative to their center. The Gabor flankers had the same spatial waveform as the Gabor target, differing only in position and contrast. Small targets were chosen because human pattern mechanisms are tuned to patterns of about this size (Foley, Varadharajan, Koh, & Farias, 2007).

Procedure

The observer sat 114.7 cm from the display, and a chin rest was used to keep the observer's head in this position. Viewing was binocular with natural pupils. Eye level was approximately at the center of the screen where the fixation mark was located. A two-interval, temporal forced-choice paradigm was used. On each trial, the higher contrast test pattern was presented randomly in one of two temporal intervals. The intervals were 100 ms in duration except for Experiment 5, with an interstimulus interval of 500 ms. The observer responded by moving a lever up or down indicating whether the higher contrast was in the first or second interval. A tone was presented during the intervals when the stimuli were present. Each response was followed by another tone that indicated whether the response was correct or incorrect. The instructions

directed the observers to attend for the target and to ignore the context.

The Quest algorithm (Watson & Pelli, 1983) was used to seek the target contrast that produced 81% correct responses. The Quest sequence was preceded by a block of relatively easy trials with decreasing target contrast. If an error was made on these trials, the sequence would restart at a higher contrast. These trials were followed by 40 trials in the Quest sequence. The Quest algorithm requires an estimate of the steepness parameter of the psychometric function. This was made on the basis of psychometric function data from other experiments. As long as there are a lot of trials near the threshold, it can be accurately estimated even if the steepness parameter estimate is not perfectly accurate.

The observers were university students between the ages of 19 and 26. They were selected from a larger group of applicants based on vision tests and the ability to understand and perform the task. All had acuity of 20/20 or better, most without optical correction. They had contrast thresholds for the two small, brief test stimuli of less than 0.03. They were not knowledgeable about the phenomena or the hypotheses being tested. Observers did several practice sessions on each task prior to the experimental sessions. Most of them served in 10 or more experiments, so they became highly practiced.

Contrasts are expressed in decibels (dB), and the number of decibels equals $20 \log_{10}$ (contrast). Because all the contrasts are less than one, contrasts in dB are negative numbers. Separations are measured from the center of the target to the center of the context and are expressed in wavelengths. Because the spatial frequency is 4 c/°, one wavelength equals 0.25°. The smooth curves in the graphs correspond to the best fit of a model that is described in the next section.

Experiment 1: Detection of a disk grating with an annular context grating

Effects of separation and annulus contrast

In this experiment, thresholds were measured for the detection of the disk grating target. The target was presented simultaneously with an annular surround except in the condition in which the annulus contrast was zero. The annulus varied in separation and contrast. All annuli had an area of $2.95^{\circ 2}$, so they became narrower as separation increased. The closest annulus overlapped the target, and the second closest abutted the target. The mean thresholds over four observers are shown in Figure 5. The threshold for each observer is the mean of the thresholds determined by five Quest sequences. In this and the other
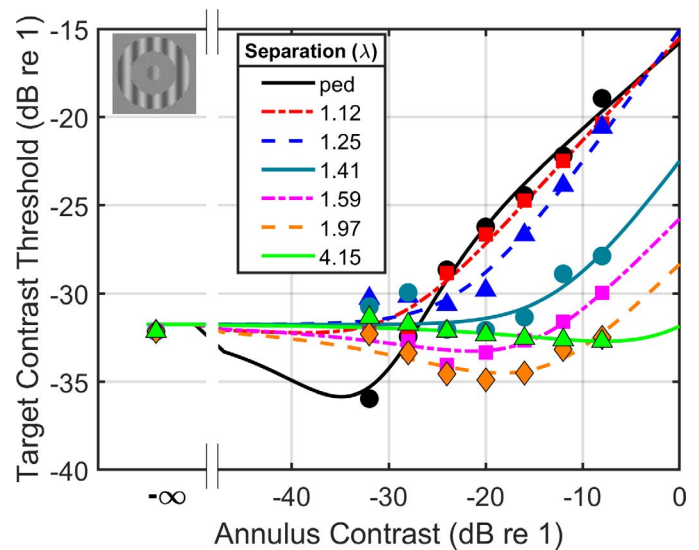

Figure 5. Experiment 1. Mean target contrast threshold over four observers as a function of surround contrast. The TvCp function (black) is shown for comparison. The parameter is the center-to-center separation of the surround from the target in wavelengths. The mean standard error of these group mean thresholds is 0.57 dB.

experiments, the threshold was also measured as a function of the contrast of a spatially matching pedestal and is shown in the graphs for comparison. In the conditions in which an annulus was presented, there was no pedestal.

When the annulus partially overlaps or abuts the target, its only effect is to raise thresholds, but it does not raise them quite as much as the pedestal alone. An annulus that abuts the target masks somewhat less than the overlapping annulus. At larger separations, the TvCc function has a shallow dipper shape, rising above the detection threshold at mid-separations. The minimum occurs at higher annulus contrasts as the separation increases.

Yu et al. (2003) found that a collinear annulus at 2.1 λ produced a shallow dipper-shaped TvCc function. There are no studies using disk-annuli stimuli that examined the effects of separation on detection with annular context patterns. TvCc functions for the detection of Gabor patterns in the presence of Gabor flankers have a similar form (Polat & Sagi, 1993).

Experiment 2: Detection of Gabor target with Gabor flankers

Effects of separation and flanker contrast

Experiment 2 was similar except that the target and context were Gabor patterns. All three Gabor patterns had a mid-frequency of 4 c/° and a standard deviation
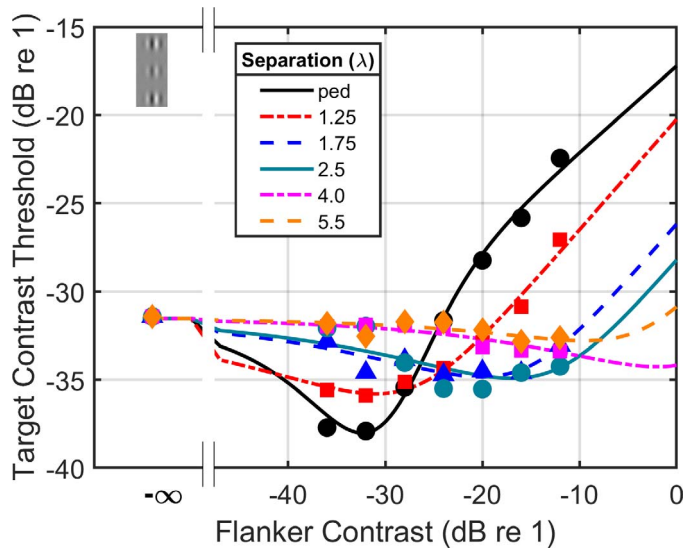
Figure 6. Experiment 2. Mean target contrast threshold over four observers as a function of flanker contrast. The parameter is the center-to-center separation of the flankers from the target in wavelengths. The observers were the same as in Experiment 1. The TvCp function (black) is shown for comparison. The threshold for each observer was measured in four to six QUEST sequences. The mean standard error of these group mean thresholds is 0.47 dB.
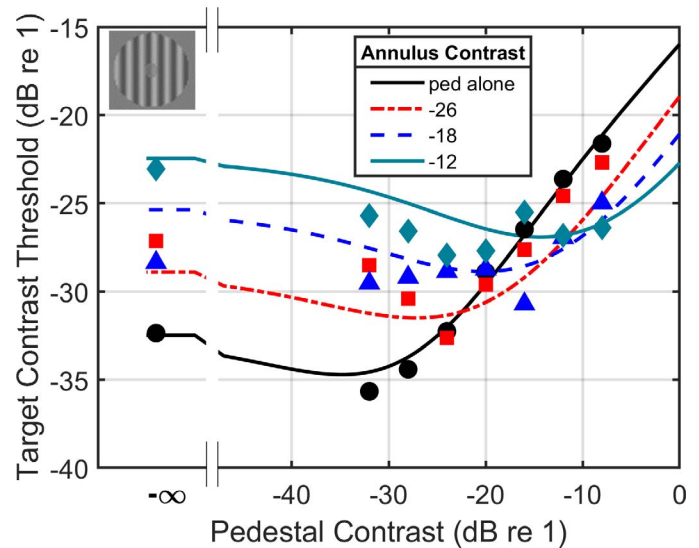

Figure 7. Experiment 3. Mean target threshold over five observers as a function of pedestal contrast. The parameter is annulus contrast. Data points correspond to the mean threshold over five observers, all different from the observers in the first two experiments. The threshold for each observer was measured in seven Quest sequences. The standard error of these group mean thresholds is 1.1 dB.

of 0.15°. The separations covered a wider range than in Experiment 1. Each pattern was presented in a square window that was 0.625° (2.5 λ) on a side. None of the patterns overlapped. Otherwise, the experiment was like Experiment 1 except for the separations used. The results are shown in Figure 6.

The TvCc functions are similar in form to those of Experiment 1 except that no monotonic masking function was found at these separations. At a separation of 1.25 λ, the Gabor flankers produce a full dipper-shaped TvCc function. At the corresponding mid-radius of 1.25 λ in Experiment 1, there is no facilitation. So the specific form of the TvCc function at this separation is different for annular and Gabor contexts. This experiment is comparable to a study by Zenger and Sagi (1996). They measured TvCc functions at different separations. They found dipper-shaped TvCc functions at separations of 2, 3, and 4 λ that did not rise above the detection threshold. Using a similar configuration with a Gabor target and Gabor flankers at 2.93 λ, Solomon and Morgan (2000) also found facilitation dipper-shaped functions. However, when they used a ring of eight Gabor patterns around the target at the same separation, these produced very shallow, full dipper-shaped TvCs functions, not the facilitation dipper functions found here.

Experiment 3: Discrimination of disk contrast with a wide abutting annulus

Effects of pedestal and annulus contrasts

In this experiment, the context is an annulus that abuts the target. In most conditions, the target is presented on a pedestal with the same spatial waveform as the target. Here a wide annulus (4.5 cycles wide, area 4.83°²) abuts the target. Both the pedestal contrast and the annulus contrast are independent variables. The task is to indicate which of the two contrasts presented on a trial is higher (contrast discrimination). The thresholds are shown in Figure 7.

When the only context is the pedestal, the TvCp function has the familiar full dipper form. When there is no pedestal (leftmost points) the annular context increases the threshold. As the pedestal contrast increases, the threshold decreases, going below the threshold for the pedestal alone, and then increases. The pedestal contrast at the minimum moves to the right as annulus contrast increases, so the functions for different values of Cc cross.

These data resemble those produced by an orthogonal superimposed mask (Foley, 1994; Ross & Speed, 1991). The form of the TvCp functions is different from all five forms described in the literature review.

Yu and Levi (2000) did a more limited version of this experiment in which they had a single value of Cp (0.4) and a range of values of Cc. They plotted the threshold against the values of Cc. When there was no surround,

Figure 8. Experiment 4. Mean target threshold over four observers as a function of pedestal contrast. The observers were the same four that were in Experiments 1 and 2. The parameter is annulus contrast. Data points correspond to the mean threshold over the four observers. The threshold for each observer was measured in five to seven Quest sequences. The mean standard error of these group mean thresholds is 0.40 dB.
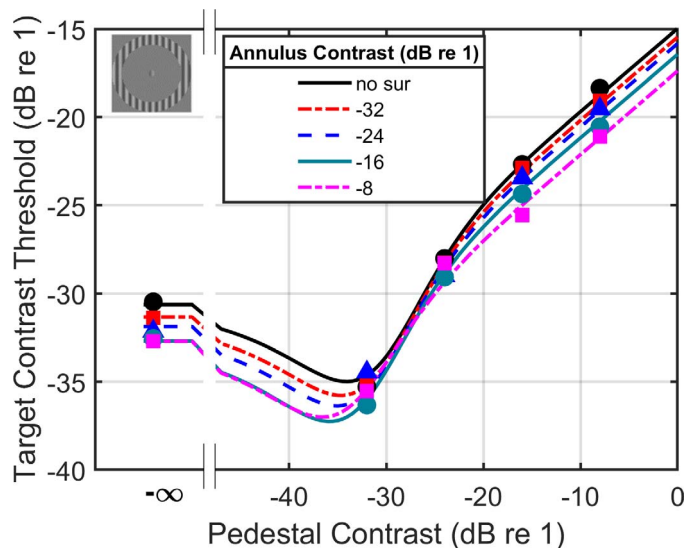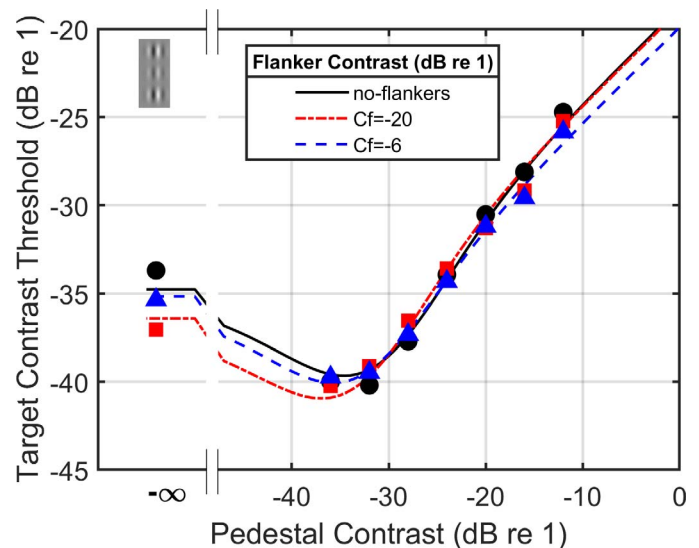

Figure 9. Experiment 5. Mean target threshold over four observers as a function of pedestal contrast. The observers were the same four that were in Experiments 1 and 2. The parameter is flanker contrast. Data points correspond to the mean threshold over the four observers. The threshold for each observer was measured in five to seven Quest sequences. The mean standard error of these data points is 0.57 dB.

the pedestal increased the threshold. As the surround contrast increased, the threshold decreased to a minimum at the point at which Cc = Cp and then increased. They call this phenomenon "unmasking." In Figure 7, the minima are near the points at which Cp = Cc.

Experiment 4: Detection of Disk Target With A Wide Remote Annulus

Effects of pedestal and annulus contrasts

This experiment was like Experiment 3 except there was a gap between the target and the inner radius of the annulus (0.56°, 2.25 λ) and the outer radius of the annulus was 1.365°, 5.46 λ, so that the mid-radius was 3.86 λ. It had the same area as the annulus in Experiment 3 (4.83°²). There were eight pedestal contrasts and four annulus contrasts plus a pedestal-alone condition.

The results are shown in Figure 8. At this separation, the annulus has a very different effect than when it abuts the target and pedestal. It reduces detection thresholds instead of raising them. It also reduces the contrast-discrimination threshold with the largest decreases at the highest pedestal and annulus contrasts. The TvCp functions are quite different from those found by Chen and Tyler (2008) using Gabor flankers at 4.2 λ; they found increased thresholds for all pedestal contrasts that were above detection threshold. How-

ever, they are similar to the TvCp functions found by Yu et al. (2003). Their close surrounds had little effect on the threshold when Cp = 0, but they reduced thresholds at high pedestal contrasts. As in Figure 8, the reduction increased as Cp increased, so the minimum is not at the point at which Cp = Cs. Their small effects at Cp = 0 may be due to their smaller separation. There must be a separation at which the effect of lateral context on detection changes from masking to facilitation.

Experiment 5: Detection of Gabor target with Gabor flankers

Effects of flanker and pedestal contrasts

This experiment was a replication of a condition reported by Chen and Tyler (2008). The target and flankers were identical Gabor patterns in cosine phase relative to the fixation point. Their center frequency was 4 c/°, and they had a standard deviation of 0.177°, 0.708 λ. The flankers were collinear with the target and located above and below at a center-to-center separation of 2.8 λ. Target and flankers were presented simultaneously for 90 ms. The flanker contrasts were 0, −20 dB, and −6 dB.

The results are shown in Figure 9. As for the disk and annulus, the Gabor flankers decrease thresholds for the Gabor targets at both low and high pedestal contrasts. When the pedestal contrast is 0, the −20 dB
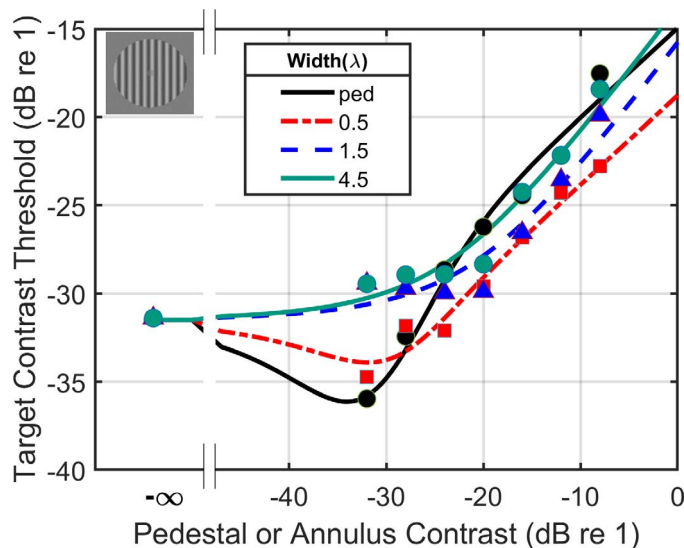
Figure 10. Experiment 6. Mean target threshold over three observers as a function of annulus contrast. The parameter is annulus width in cycles of the grating frequency. The corresponding mid-radii are 0.75, 1.25, and 2.75 wavelengths. Data points correspond to the mean threshold over three of the four observers in Experiment 1. The threshold for each observer was measured in four to six Quest sequences. The pedestal alone TvCp function is shown for comparison. The standard error of these group mean thresholds is 0.85 dB. The pedestal data are from Experiment 1.

flankers decrease the threshold more than the −6 dB flankers as would be expected from the relation between target threshold and flanker contrast found in Experiment 2. Chen and Tyler (2002, 2008) found that, for above-threshold pedestal contrasts, the flankers increase the contrast threshold by approximately a constant factor of about 1–3 dB. They confirmed a result that they obtained in two earlier studies (Chen & Tyler, 2001, 2002). More recently, Chen has found that there are large individual differences in performance with a substantial proportion of observers producing decreased contrast-discrimination thresholds in the presence of flankers (C-C. Chen, personal communication).

Experiment 6: Detection of disk target with abutting annulus

Effect of annulus width

Here the annulus always abutted the target, and there were three annulus widths: 0.5, 1.5, and 4.5 cycles. Target thresholds were measured as a function of the annulus contrast. The results are shown in Figure 10. The TvCp function for the pedestal alone is shown for comparison.

The narrowest annulus produces a full dipper TvCc function, but thresholds are increased at low Cc and

decreased at high Cc relative to the effect of the pedestal alone. This is similar to the effect of close flankers in Figure 3. When the annulus is wider, there is no threshold decrease and a larger threshold increase. This is consistent with Experiment 1 in which a wide abutting annulus does not reduce thresholds and masks slightly less than the pedestal alone.

Apparently there is a small region adjacent to the target (roughly 0.5 to 1.0 wavelengths separation) over which annulus excitation is large relative to annulus inhibition. Some of this excitation may come from the outer region of sRFlow, which is in the effective receptive field when contrast is low. If the context is wider (Experiment 1, mid-radius 1.25 and the two wider conditions in Experiment 6), the facilitation disappears. It may be overwhelmed by the inhibition produced by these wider annuli.

Experiment 7: Detection of a disk target with superimposed disk mask

Effect of mask radius

Here, the target was the same disk grating used in Experiments 1, 3, 4, and 6. The context was a disk grating of the same spatial frequency, orientation, and phase with a radius that was equal to or greater than that of the target. This is equivalent to a pedestal and an abutting annulus both of the same contrast, but it differs from the other experiments with a pedestal and annulus in that, in them, the contrast of pedestal and annulus varied independently. Here they are the same. Yu and Levi (1997) showed that, if a pedestal for a grating target is extended beyond the target, the threshold increases and then decreases as the mask length increases, going below the threshold for the pedestal alone. They refer to this as end-stopping. Here the entire TvCc function is measured for three mask sizes. The results are shown in Figure 11. A mask slightly larger than the target raises thresholds at all mask contrasts relative to the threshold on the pedestal alone. A mask much larger than the target raises thresholds at low mask contrasts and lowers them at high mask contrasts.

In the next section, a model is described that accounts for the data of all seven experiments.

Models

Background

Nachmias and Sansbury (1974) showed that, when a target is superimposed on a pedestal, the target threshold decreases and then increases as the pedestal
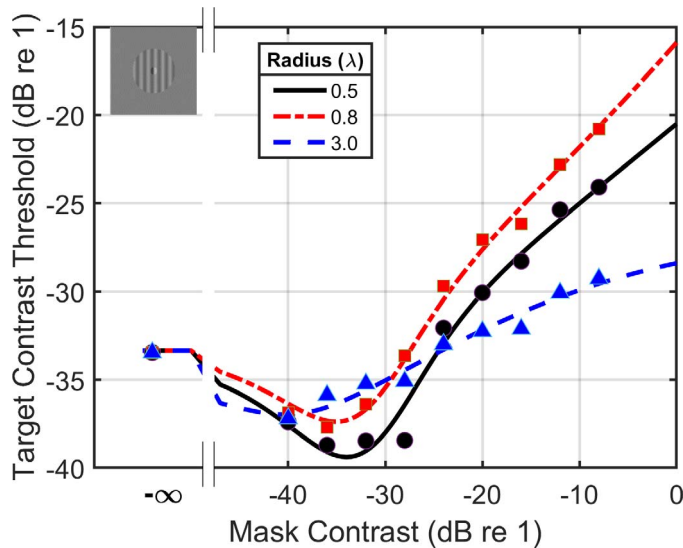
Figure 11. Experiment 7. Mean target contrast threshold as a function of disk mask contrast for three sizes of disk mask. The smallest disk mask is the same size as the target. There were six observers, all different from the observers in the other experiments. For each observer, each threshold was measured in four to six Quest sequences. The mean standard error was 0.57 dB.

contrast increases. To explain this, they hypothesized that the response to the pedestal increases as an S-shaped function of the pedestal contrast so that the response function becomes steep at low Cp, producing low discrimination thresholds, and shallow at high Cp, producing high thresholds. Stromeyer and Klein (1974) proposed a mathematical form for this function. Foley and Legge (1981) studied the relation between mask contrast and threshold more thoroughly and showed that a single S-shaped function can account for the psychometric functions for detection and near thresh-old contrast discrimination. Legge and Foley (1980) extended this analysis to higher contrasts and showed that a single response function can account for both contrast discrimination and masking by superimposed gratings of different spatial frequencies but the same orientation. Ross and Speed (1991) showed that, when mask orientation was varied, a single response function cannot account for the effects. Foley (1994) measured TvCp functions in the presence of superimposed masks in different orientations and proposed a model in which all mask orientations divisively inhibit the mechanism that detects the target and a narrower range of orientations excite in addition to inhibiting. Watson and Solomon (1997) proposed a version of this model that specifies the spatial frequency channels that determine the excitation and inhibition produced by any stimulus.

Chen and Tyler (2001, 2002, 2008) measured TvCp functions in the presence of high-contrast Gabor flankers. The Foley (1994) model does not fit their data.

They proposed that lateral contrast multiplicatively changes both the excitatory and inhibitory sensitivities of the detecting mechanism rather than adding excitation and/or inhibition. In the succeeding years, several models have been proposed that incorporate both multiplicative and additive effects. Meese (2004) and Meese et al. (2007) examined several variations of the general raise then added a model with the goal of describing the effects of superimposed and lateral context that is either parallel or orthogonal. The Meese (2004) model does not include multiplicative changes in sensitivity; the Meese et al. (2007) model does include these. The models have only two exponents: one for excitation and one for inhibition. The multiplicatory inhibitory terms increase linearly with context contrast. Context models have also been extended to dichoptic and monoptic masking (Maehara & Goryo, 2005; Meese, Georgeson, & Baker, 2006). They require more terms because the effects of a dichoptic mask are more complex than those of a monoptic or binocular mask. Dichoptic masking is not considered in this article.

Models fitted to the experimental data

To model the results of the present study, I started with two general models that incorporate both multiplicative and additive effects and allowed these effects to vary nonlinearly with context contrast. The two models differ in how the signals from the center and the surround are combined. In the "add then raise to a power model" (AR), these terms are added first and then raised to a power. In the "raise to a power and then add model" (RA), each term is raised to a power before they are added. The two powers may be different.

One or the other model fitted each of the seven data sets well. I then simplified the model by eliminating parameters that did not produce a statistically significant reduction in root-mean-squared-error (RSME) when included in the model.

In describing the models, I use the symbol m to refer to all context patterns other than pedestals. In this study, most of these are positioned laterally to the target.

Stimulus parameters

C_p Contrast of the pedestal
C_{tp} Contrast of the target and pedestal
C_m Contrast of the context

Model parameters

S_{tpe} Excitatory sensitivity to the target and pedestal
S_{tpi} Inhibitory sensitivity to the target and pedestal
p Exponent of excitation by the target and pedestal and context in AR

q Exponent of inhibition by the target and pedestal and context in AR

Z Maintained inhibition

S_{me} Additive excitatory sensitivity to the context

S_{mi} Additive inhibitory sensitivity to the context

$p2$ Exponent of excitation added by the context in RA

$q2$ Exponent of inhibition added by the context in RA

K_{me} Multiplicative excitatory sensitivity to the context

K_{mi} Multiplicative inhibitory sensitivity to the context

$p3$ Exponent of multiplicative excitation

$q3$ Exponent of multiplicative inhibition

The responses in the general AR model are

$$R_{pm} = \frac{\left[\left(1 + K_{me}C_m^{p3}\right)S_{tpe}C_p + S_{me}C_m\right]^p}{\left[\left(1 + K_{mi}C_m^{q3}\right)S_{tpi}C_p + (S_{mi}C_m)\right]^q + Z} \quad (1)$$

$$R_{tpm} = \frac{\left[\left(1 + K_{me}C_m^{p3}\right)S_{tpe}C_{tp} + S_{me}C_m\right]^p}{\left[\left(1 + K_{mi}C_m^{q3}\right)S_{tpi}C_{tp} + (S_{mi}C_m)\right]^q + Z} \quad (2)$$

The only difference between the two equations is that C_p in the first is replaced by C_{tp} in the second. The Foley (1994) AR model is obtained by eliminating the terms containing K_{me} or K_{mi}. The responses in the RA model are

$$R_{pm} = \frac{\left[\left(1 + K_{me}C_m^{p3}\right)\left(S_{tpe}C_p\right)^p\right] + \left[sign(S_{me})abs(S_{me}C_m)^{p2}\right]}{\left[\left(1 + K_{mi}C_m^{q3}\right)\left(S_{tpi}C_p\right)^q\right] + \left[sign(S_{mi})abs(S_{mi}C_m)^{q2}\right] + Z} \quad (3)$$

$$R_{tpm} = \frac{\left[\left(1 + K_{me}C_m^{p3}\right)\left(S_{tpe}C_{tp}\right)^p\right] + \left[sign(S_{me})abs(S_{me}C_m)^{p2}\right]}{\left[\left(1 + K_{mi}C_m^{q3}\right)\left(S_{tpi}C_{tp}\right)^q\right] + \left[sign(S_{mi})abs(S_{mi}C_m)^{q2}\right] + Z} \quad (4)$$

In fitting the RA model, the parameter S_{mi} sometimes was negative. It is for this reason that the absolute value of the additive sensitivity term is taken before raising the term to a power, and after raising, the sign is prefixed to this inhibitory term. The Foley (1994) RA model is obtained by eliminating the terms containing K_{me} or K_{mi}.

These general models allow the sensitivities to the pedestal/target to be modulated by a term that depends on the contrast of the context, C_m. Each of these modulation terms has two parameters: the sensitivity to the multiplicative effect and the power to which the context contrast is raised. This elaboration of the Foley model adds four context-dependent parameters for a maximum of 12 free parameters for a context that varies only in contrast. Six of the parameters are context dependent although, as will be seen, all six are never required. In practice, three to five free context parameters provided a fit that was not improved to a statistically significant extent ($p < 0.05$) by adding more free parameters. In the AR version, $p2$ and $q2$ do not appear, so this model has a maximum of 10 free parameters. Effects also depend on the form, position, and orientation of the context, and at least some of the parameters vary with these.

Both models assume that performance on a two-alternative, forced-choice trial depends on the re-sponses of the detecting mechanism to the pedestal and context alone and to the target plus the pedestal and the context. These responses are perturbed by internal random Gaussian noise with a constant standard deviation. The constant standard deviation assumption is probably wrong, but as Klein and Levi (2009) have shown, a model of forced-choice data in which the standard deviation varies with the signal is indistinguishable from another model with constant standard deviation. The target is assumed to be at threshold when

$$R_{tpm} - R_{pm} = 1. \quad (5)$$

Five parameters are required to fit TvCp functions for a target on a spatially matched pedestal: S_{tpe}, S_{tpi}, p, q, and Z. S_{tpe} is arbitrarily set to 100 to set the scale of the responses and has no effect on the fit, so four of these parameters are free. The RA model allows for two additive context sensitivity parameters, S_{me} and S_{mi}, and two multiplicative context sensitivity parameters, K_{me} and K_{mi}, each with its exponent, $p2$, $q2$, $p3$, and $q3$. Context effects depend on the form, position, and orientation of the context, so one or more of the context parameters must change with these factors.

Model fits

Process

Often models are fitted to data of individual observers because there are nonrandom differences between visual systems. Here, most of the observers were very similar in sensitivity, and the measured functions were similar except for some irregularity that appeared to be random. The mean function across observers is smoother and appears to be a good representation of individual performance. For that reason, thresholds were averaged over the three to six observers that participated in each experiment, and each of the two models was fitted independently to the mean threshold data of each experiment averaged over observers.

Because observers and stimuli varied across experiments and many of the parameters are stimulus dependent, it did not make sense to fit all the data as a single data set. Data for individual observers are provided in Supplementary File S1.

For each data set, both AR and RA models were fitted. To perform each fit, a set of parameter values was selected, which were estimated to be near to the best values. Starting from these values, a least-squares minimization algorithm (fminsearch in MATLAB; MathWorks, Natick, MA) was used to find the parameter values that produced the best fit, which was taken to be the fit with the lowest RMSE. After a fit was completed, a second fit was made, starting from the parameters of the best fit and varying them over a narrower range around these values. This fitting procedure was repeated many times with different starting values. Many fits are necessary because there are many local minima in the RMSE space. Overall, at least 20 sets of starting values were used for each data set.

Early in the process, it became apparent that, in every case, some of the parameters could be eliminated without a statistically significant ($p < 0.05$) increase in the RMSE. Sensitivity parameters could be eliminated by setting them to zero. Exponents could be eliminated as free parameters by setting them equal to other exponents or to one. Only if including a parameter produced a statistically significant improvement in fit was that parameter included in the best model. Different sets of free parameters were tested to determine which submodel best described the data set. Adding additional free parameters usually reduces the RMSE, so statistical tests were performed to determine whether the reduction in RMSE was statistically significant. When the model with fewer parameters is not a special case of the model with more parameters, this test is not applicable, and the model that produced the lowest RSME was taken as the best unless this model required two or more free parameters than the second best model. The method only determines which model fits the data best. It does not exclude other

models. The model fitting shows that the models found to be best fit the data better than the more restricted versions of these models. The RMSE of the best models was approximately 0.5 dB (6%) except for Experiment 3, in which it was 1.1 dB (14%).

It is clear from previous research that, to account for the threshold versus pedestal contrast (TvCp) functions, five parameters are required: S_{tpe}, S_{tpi}, p, q, and Z. One of these parameters can be arbitrarily set without affecting the fit. S_{tpe} was set equal to 100. There are eight other parameters that might be used to account for context effects: S_{me}, $p2$, S_{mi}, $q2$, K_{me}, $p3$, K_{mi}, and $q3$. When context patterns were present, they always had effects, so it was clear that at least one context sensitivity parameter was needed. The fitting results showed that, for every context in every experiment, at least two sensitivity parameters were needed: an excitatory sensitivity parameter and an inhibitory sensitivity parameter.

Description of the fits

Table 1 contains the experimental and model parameters of the seven fits. Foley (1994) found that the AR model fitted superimposed masking data better than the RA model. He hypothesized that the RA model might apply when the context is displaced from the target. That hypothesis was confirmed in the present study. In all four experiments in which there was a gap between the target and the context (Experiments 1, 2, 4, and 5), an RA model fitted the data best. In the three experiments in which the context abutted or was superimposed on the target (Experiments 3, 6, and 7), an AR model fitted the data best.

Table 1 is a summary of the fits to the seven data sets, including stimulus parameters and parameters of the best fitting model. The table includes the mid-radius and the width of the context patterns in wavelengths for each experiment. It gives the model type, AR or RA; the number of free parameters; and the RMSE for each best fit.

Considering that different groups of observers were involved, the common parameters, S_{me}, p, S_{mi}, q, and Z are in reasonably good agreement across the seven experiments and with previous experiments although the parameters in Experiment 3, which involved a different group of observers, are somewhat different than the others.

For six of the seven data sets, a best fit was found with sensitivity parameters, K_{me} and S_{mi}, free. The exponent of K_{me}, $p3$, was also free and was much smaller than p and q, averaging 0.61. A single value of $p3$ was sufficient over different context separations.

The sensitivity parameters, K_{me} and S_{mi}, varied with the shape, position, and size of the context. In Experiment 6 with a very narrow abutting annulus, K_{me}

Experiment	1						2				
Context	Annulus						Pair of Gabor patterns				
Mid-radius (wl)	1.12	1.25	1.41	1.59	1.97	4.14	1.25	1.75	2.5	4	5.5
Width or SD (wl)	1.676	1.5	1.326	1.18	0.95	3.3	SD = 0.6 wl				
Model	RA						RA				
Free parameters	17						15				
S_{tpe}	100	100	100	100	100	100	100	100	100	100	100
p	2.70	2.70	2.70	2.70	2.70	2.70	3.16	3.16	3.16	3.16	3.16
S_{tpi}	88.49	88.49	88.49	88.49	88.49	88.49	84.15	84.15	84.15	84.15	84.15
q	2.21	2.21	2.21	2.21	2.21	2.21	2.67	2.67	2.67	2.67	2.67
Z	6.82	6.82	6.82	6.82	6.82	6.82	13.28	13.28	13.28	13.28	13.28
K_{me}	4.80	0.10	0.95	3.73	6.32	0.65	39.04	10.28	8.35	1.76	1.12
$p3$	0.78	0.78	0.78	0.78	0.78	0.78	0.07	0.07	0.07	0.07	0.07
S_{mi}	68.80	32.30	10.58	14.45	12.32	2.55	58.68	16.12	11.29	1.94	3.80
$q2$	$=q$	$=q$	$=q$	$=q$	$=q$	$=q$	$=q$	$=q$	$=q$	$=q$	$=q$
S_{me}	0	0	0	0	0	0	0	0	0	0	0
$p2$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$
RMSE (dB)	0.567						0.469				

Table 1. Parameters of the stimuli and the best fitting version of the model for each of the seven data sets. [1]The mid-radius is radius of the portion of the disk outside the target. [2]Width is the width outside the target.

| Experiment	3	4	5	6			7			
Context	Annulus	Annulus	Gabors	Annulus			Disk mask			
Mid-radius (wl)	2.75	3.92	2.80	0.75	1.25	2.75	0.00[1]	0.65[1]	1.75[1]	
Width or SD (wl)	4.5	3.34	SD = 0.71 wl	0.5	1.5	4.5	0.00[2]	0.65[2]	1.75[2]	
Model	AR	RA	RA	AR			AR			
Free parameters	9	9	8	8			9			Mean
S_{tpe}	100	100	100	100	100	100	100	100	100	100
p	1.69	2.99	2.28	2.81	2.81	2.81	2.95	2.95	2.95	2.65
S_{tpi}	50.52	95.39	61.25	86.84	86.84	86.84	80.62	80.62	80.62	78.18
q	1.28	2.48	1.83	2.34	2.34	2.34	2.41	2.41	2.41	2.17
Z	3.07	11.24	2.72	8.61	8.61	8.61	5.79	5.79	5.79	7.36
K_{me}	1.05	0.58	0.13	0	0	0		−0.18	0.79	
$p3$	0.86	0.66	1.21	1	1	1		0.27	0.27	0.61
S_{mi}	52.08	−32.36	−1.02	65.22	14.46	19.95		3.42	113.83	
$q2$	$=q$	0.76	0.0001	$=q$	$=q$	$=q$		$=q$	$=q$	
S_{me}	0	3.49	2.59	55.65	0	0		0	0	
$p2$	$=p$	$=p$	$=p$	$=p$	$=p$	$=p$		$=p$	$=p$	
RMSE (dB)	1.102	0.402	0.571	0.853			0.585			0.650

Table 1. Extended
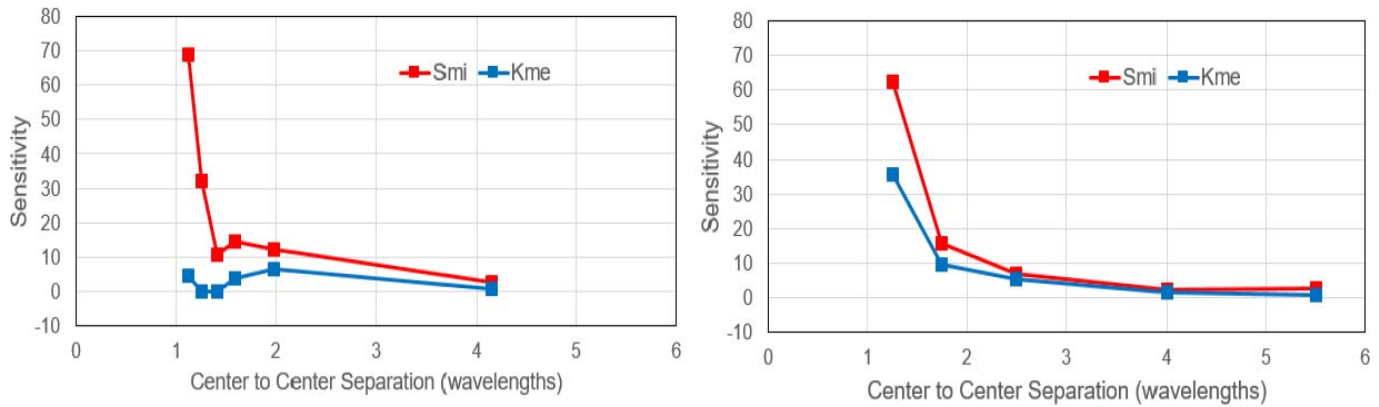
Figure 12. Sensitivity parameters S_{mi} and K_{me} as a function of separation. Left: Experiment 1, disk and annulus. Right: Experiment 2, Gabor pattern with Gabor flankers.

$= 0$ and the parameters were S_{me} and S_{mi}, although $S_{me} = 0$ for the two larger annuli. The model with S_{me} and S_{mi} free is the model that fits superimposed masking data (Foley, 1994). So a very narrow abutting annulus seems to act like a superimposed mask. This may be a consequence of its primarily stimulating the receptive field rather than the surround.

In the two experiments in which the separation was 2.8 wavelengths or more (Experiments 4 and 5), two other parameters were required to produce a best fit, S_{me} and $q2$. S_{me} had a small positive value, implying that context adds excitation in these experiments. Also, in these two experiments S_{mi} had a negative value, indicating that these remote contexts decreased the additive inhibition. The exponent of additive inhibition, $q2$, was much smaller than in the other experiments, indicating that additive inhibition decreases slowly as context contrast increases. The $q2 = 0.0001$ value in Experiment 5 means that S_{mi} is essentially indeterminate because any positive number raised to the zero power equals one, and therefore, the additive inhibition from the context was approximately -1. In these experiments, both C_m and C_p were independent variables, so the experiments covered a larger region of the stimulus space than those in which there was no pedestal.

Although the models shown are the best in the sense that I have defined this, often differences in RMSE were close to the border between significant and insignificant differences. For Experiment 4, there is another un-nested model that fits the data essentially equally well. In this model K_{me}, K_{mi}, and S_{me} vary.

The context sensitivities K_{me} and S_{mi} vary both within and between experiments. This is expected because the context configurations vary in shape, size, and position. However, it is of interest to compare the sensitivity parameters across context configurations. Consider the two experiments in which separation varied, Experiments 1 and 2. As shown in Table 1, the data of these

experiments were best fitted by a RA model with two context sensitivity parameters K_{me} and S_{mi}. Figure 12 shows how these parameters vary with the separation between target and context. These sensitivities are sensitivities to the specific context stimuli that were presented, but because, in each experiment, the area of all the context patterns was the same, these sensitivities reflect how the underlying sensitivity to these context patterns varies with distance.

Both sensitivities K_{me} and S_{mi} decrease with separation although, for the annular contexts, there is a local minimum for both sensitivities between 1 and 2 λ with excitatory sensitivity going essentially to zero. Beyond 1.5 λ, the ratio of excitatory to inhibitory sensitivity increases, and the context produces facilitation dipper-shaped TvCc functions. At the largest separations, both sensitivities decrease to near zero. The local minimum is not apparent in the Gabor flanker data, but that may be because the data points were more widely spaced. It could also be that the narrow region that is almost exclusively inhibitory does not extend through the end zones above and below the target. The principal difference between the two context types is in sensitivity to multiplicative excitation, K_{me}. The K_{me} values are much greater for the Gabor flankers than for the annuli at small separations, but the S_{mi} values are similar. This has the effect that Gabor flankers at 1.25 wavelengths facilitate substantially, but annuli at the same mid-radius only mask. The finding that close collinear Gabor flankers reduce thresholds more than full annuli that have much larger area is consistent with results in the literature (Solomon & Morgan, 2000; Yu et al., 2002).

In Experiment 6, the narrowest annulus (0.5 λ) produces a full dipper TvCc function, indicating that it excites as well as inhibits. Wider abutting annuli in Experiments 6 and 1 only mask. This may seem surprising because in Experiments 1, 3, 4, and 7, separated or wide annuli decrease thresholds. The difference is that Experiment 6 is a detection experiment, so it depends only
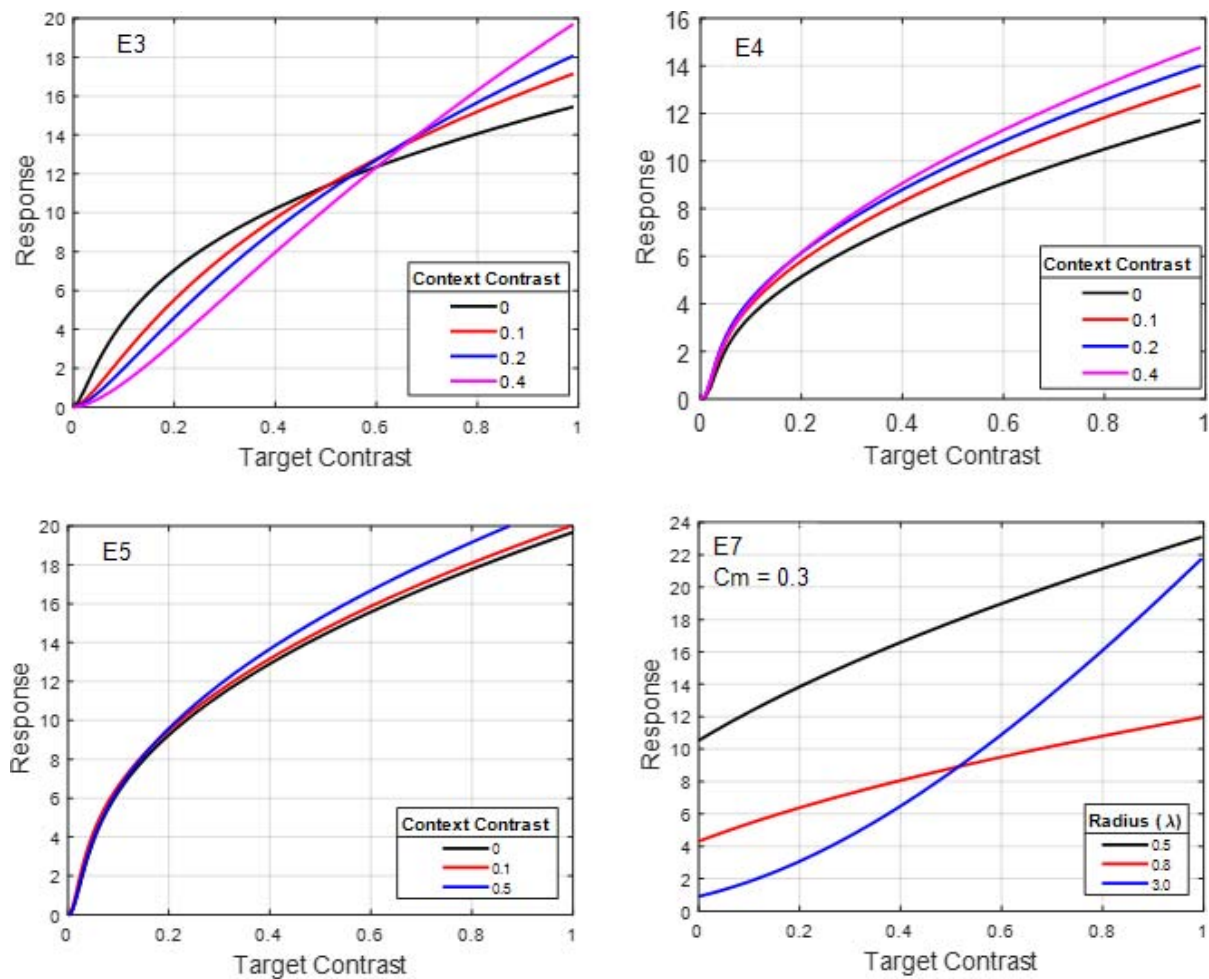
Figure 13. Response functions in the four experiments in which both pedestal contrast and context contrast vary. The response function changes form as the context moves away from the target. Abutting context is suppressive except at high pedestal contrasts. Remote context is enhancing. In Experiment 7, the disk mask consists of a pedestal and an abutting annulus of the same contrast. Here $C_m = C_p$ and the response to the target varies with this contrast. The Experiment 7 graph shows the response to a target superimposed on a mask of contrast 0.3.

on the low end of the response functions, which is steepest for the narrowest annulus. The finding that both K_{me} and S_{mi} decrease as width increases is surprising. It suggests that different regions of the context may have opposite effects on these sensitivities.

The superimposed disk mask in Experiment 7 may be thought of as a pedestal and an abutting annulus, but unlike in the other experiments, their contrasts are equal and vary together. The required parameters are again K_{me} and S_{mi}, but for the middle-sized mask, K_{me} is −0.18. This means that the narrow abutting annulus increasingly reduces excitation as its contrast increases. For the very large disk mask $K_{me} = 0.79$, so the wide abutting annulus increases excitation.

A decrease in inhibition or an increase in excitation are alternative ways to increase responses. Yu and Levi (1997, 1998a, 1998b) suggested that lateral context might subtract from inhibition. Meese et al. (2005) also found evidence for subtractive inhibition. In fits to Experiments 4 and 5, subtractive inhibition does contribute to the fit, but multiplicative excitation has a greater effect. In all the other fits, the context adds inhibition, and responses are increased by multiplicative excitation. So the decrease in thresholds produced by lateral context here appears to be due to an increase in excitation rather than a decrease in inhibition. Sato, Haider, Hausser, and Carandini (2016) have shown that, in the mouse cortex, lateral context acts on excitation rather than inhibition. Changes in K_{me} and S_{mi} have complex effects on the response to the pedestal/target. These effects are clarified by an examination of the mechanism response functions.

Mechanism responses

Although the focus of this study has been on thresholds, the core of the model is an equation that

describes how the response of the detecting mechanism depends on the contrast of the pedestal/test and the context. Figure 13 shows these functions for the three experiments in which C_p and C_c varied independently: Experiment 3, abutting annulus; Experiment 4, annulus centered 3.92 λ away; Experiment 5, pair of Gabor flankers at 2.8 λ; and the one experiment in which there was a disk mask, Experiment 7. The graphs show that the response to the center stimulus (pedestal/test) varies greatly depending on the lateral context.

When the context is of medium width and abutting (Experiment 3, Figure 13), the context decreases the response at low C_{tp} and increases the response at high C_{tp} so that the response functions for context present crossover the function for the pedestal alone. The changing form of the response function causes the steepest region of the function to move to higher contrast as the context contrast increases. This causes the threshold to go down and then up as pedestal contrast passes through this steep region. This explains the unmasking of a target produced by a surround, a phenomenon discovered by Yu and Levi (1997). They fixed the pedestal contrast and varied the surround contrast to produce a minimum threshold when $C_m = C_p$. Experiment 3 illustrates the same phenomenon, and the response functions in Figure 13 show how this phenomenon is produced.

When the context is separated from the target by 2.8 λ or more (Experiments 4 and 5), the response functions are quite different. The context increases the response and also the steepness of the response function over most of the pedestal/target contrast range. This steeper response function reduces discrimination thresholds at both low and high pedestal contrast, an effect quite different from that of an abutting annulus. The steeper response functions are a consequence of differences in the model parameters that depend on the context. S_{mi} is low relative to K_{me} for these separated contexts. As context contrast increases, the steepening of the response function generally increases. However, in Experiment 5, the effect is non-monotonic with context contrast at low pedestal contrasts although this non-monotonicity is difficult to see in this graph. It produces the non-monotonic relation between context contrast and detection threshold seen in Experiment 2.

In Experiment 7, the context is a disk mask that corresponds to a pedestal and an abutting annulus of the same contrast, so the two contrasts covary. When the mask is slightly larger than the target, it increases thresholds more than the pedestal alone over the high mask contrast range; when the mask is much larger than the target, it increases thresholds less than the pedestal alone over this range. This cannot be explained by a single response function for each mask size. Because the form of the response function depends on the context

contrast (here the region of the disk mask that extends beyond the pedestal) and the context contrast covaries with the pedestal contrast, there is a different response function for every mask contrast. The best we can do is to pick a mask contrast and compute the response to a target superimposed on that mask. The figure labeled "E7" shows the response to a target superimposed on a mask contrast of 0.3 for each of the three conditions. Both of the larger masks reduce the response to the target, which is what we would expect from physiological end-stopping. However, the function that relates the response to the target contrast is very different in the three conditions. For the mask slightly larger than the target, the steepness of the response function is less than for the pedestal alone, and steepness decreases as target contrast increases. For the largest mask, the steepness rises in an accelerating manner. Thus, although the abutting surround is always suppressive, the response to a target superimposed on it can increase rapidly or slowly, depending on the surround sensitivity parameters. This answers the question of how a large disk mask can suppress responses and, at the same time, reduce thresholds.

I do not show response functions for the experiments in which there was no pedestal (Experiments 1, 2, and 6). The model was fitted to these data and the parameters estimated, so response functions can be computed. However, because there was no pedestal and most of the target thresholds were relatively low, the parameter estimates are based on a relatively small region of the stimulus space and the inferred response functions are not reliable at high pedestal contrasts.

The results of Experiment 6 may seem inconsistent with the Experiment 7 results. In Experiment 6, the contexts were annuli of varying width. As annulus width increases, masking increases, and the corresponding response functions are increasingly suppressed. Yet Experiment 7 shows that a narrow mask raises discrimination thresholds more than a wider one. Experiment 6 is a detection experiment, so the critical region of the response functions is near the origin. In this region, the response is increasingly suppressed as the annulus width increases (see Figure 11). This produces the increase in thresholds with annulus width in Experiment 6 and at the lower mask contrasts in Experiment 7. However, at higher contrasts, the response function for the large mask is steeper than that for the small mask or the pedestal.

Perceived contrast

How is the model of contrast detection and discrimination presented here related to perceived contrast? As described in the review, the effects of lateral context on perceived contrast as measured in
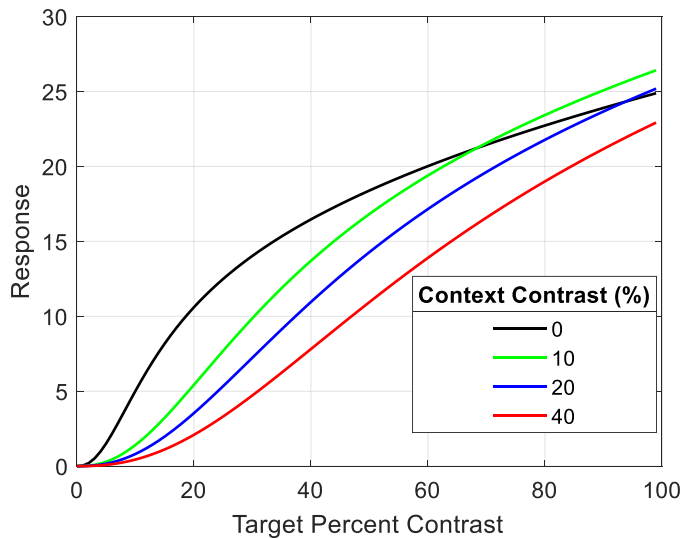
Figure 14. Response functions for the Xing and Heeger model. The parameters are $a = 0.01$, $p = 2.4$, $q = 2.0$, $W_e = 0.1$, $pe = 0.1$, $W_i = 0.6$, and $qi = 1$. Here contrast is expressed as percentage contrast. The parameter k sets the response scale. Here, it is arbitrarily set to 0.4.

contrast-matching studies are not completely consistent. Some studies show that surrounds increase the perceived contrast of higher contrast centers. Both Ejima and Takahashi (1985) and Xing and Heeger (2000, 2001) got this result. Most studies do not use high-contrast test patterns and do not show this contrast enhancement.

Xing and Heeger (2001) studied the effect of lateral context on contrast matching and proposed a model of their data based on the following response function:

$$R_t = \frac{k\left((1 + W_e C_t^{pe})C_t^{p} + W_{e2} C_s^{pe2}\right)}{\left(1 + a C_t^{q} + W_i C_s^{qi}\right)}, \quad (6)$$

where C_t is the contrast of the target; C_s is the contrast of the surround; and k, a, W_e, W_{e2}, and W_i are sensitivities. This model is formally equivalent to the special case of the RA model that was fitted to the data of Experiments 1, 2, 4, and 5 in this article. Xing and Heeger (2001) found that they did not need the second term in the numerator (additive excitation). This term was not needed in the present study except when the context was separated from the target by 2.8 or more wavelengths. The one difference from the present analysis is that the Xing–Heeger (2001) model is an RA model. In the present study, an AR model fitted data best when the context abutted the target, the condition closest to the Xing–Heeger (2001) experiment.

Figure 14 shows a set of contrast response functions computed using the Xing and Heeger (2001) model with parameters from their fits to their contrast-matching data. Here contrast is expressed as percentage

contrast, and the response scale depends on the arbitrary value of k, which has no effect on the fit. Their parameters, when transformed into the parameters of the present study, have similar values to those found in this study. This correspondence suggests that the responses on which detection and discrimination are based may be the same as those that determine perceived contrast. Perhaps we are close to a model that unifies detection, discrimination, and perceived contrast in the presence of lateral context. However, there are inconsistencies with respect to the effects of separated context on perceived contrast, with which the predominant effect is suppression although enhancement is found in some studies. For example, Ejima and Takahashi (1983) showed that, as the width of a low-contrast grating increases, its perceived contrast increases up to a width of at least 10 cycles. Cannon and Fullenkamp (1991) showed that, when a narrow annulus is increasingly separated from the target, perceived contrast is minimum for an abutting annulus and then increases up to a separation of 9.6 cycles. The increase, however, never takes the perceived contrast above the value with no surround. In the discrimination experiments, Experiments 4 and 5, in which the context was away from the target, the predominant effect is to increase the response to the target.

Relation to V1 cell responses

Although the physiology is done mostly on macaque V1 cells away from the central fovea and the psychophysics is done on human subjects in the central fovea, there are some important points of correspondence. In the single-unit studies, the receptive field is often mapped, and care is taken to ensure that the center stimulus is in sRFhigh and the surround is outside sRFlow. With such a stimulus configuration, near surrounds suppress responses at all center contrasts that have been tested. Cavanaugh et al. (2002a) measured the response of V1 cells as a function of center and near annulus contrast (Figure 3 in this article). As surround contrast increases, the response functions are suppressed, and the steepest region moves to higher contrast. The response functions in Experiment 3 have this same form and are fitted by an AR model that also fits the single-unit data. The parameters are somewhat different, allowing the Experiment 3 response functions to rise above the function for the pedestal alone at high pedestal contrasts. Nevertheless, there is good correspondence between the V1 data and the Experiment 3 discrimination thresholds for near surrounds. For far surrounds, in both cells (Angelucci & Shushruth, 2014) and in the psychophysical model, there is enhancement by same-orientation surrounds although parametric studies of cells have not been

reported for separated contexts. In the cells, enhancement has not been found at high center contrast. In the model, it occurs at all the center contrasts at which psychophysical measurements have been made, but there are few measurements at high contrast.

The analysis of Experiment 7 allows us to understand what context just beyond the sRF does. Single-unit studies show that, if a stimulus is extended beyond the size of the receptive field, the cell response decreases and stays low as the size continues to increase (end-stopping). Psychophysical studies show that, if a stimulus is detected on a mask that increases in size, the threshold increases with mask size up to a point and then decreases. Westheimer (1967) showed this for spots, and Yu and Levi (1997) showed it for gratings. How could a decrease in response produce a decrease in thresholds? Westheimer proposed that, as the mask size increases, it increasingly inhibits the response to the target, requiring the target contrast to increase to reach threshold, but at some size, the mask begins to reduce the inhibition, thus increasing the response to the target and decreasing the threshold. Yu and Levi (2000) propose essentially the same explanation and make it more explicit by proposing that the large mask subtracts inhibition from the denominator of a divisive inhibition model. Both explanations require that that the response to the target decreases as mask size increases up to a point and then begins to increase, but this is opposite to what the single-unit studies show. If the response does not increase for large masks, what produces the threshold reduction? The analysis of Experiment 7 shows how this may happen. Large masks continue to suppress the response, but the response to the target rises more steeply, producing a reduction in the discrimination thresholds over most of the mask contrast range. What happens with remote context is quite different. It increases responses, making the entire response function steeper, thereby decreasing thresholds.

Toward a more general model

It is possible to make some generalizations about how the sensitivities vary over space. When a narrow context abuts the target, it produces both excitation and inhibition that produce a full dipper TvCc function (Experiment 6), much like the effect of a pedestal alone. It excites less than the pedestal at low contrast and more at high contrasts so that the TvCc function crosses over that for the pedestal alone. The response function for the narrow context rises faster than the function for the pedestal alone at low annulus contrasts, but it then crosses the pedestal response function to rise more slowly. For somewhat wider abutting contexts, inhibition dominates, and the response is suppressed (Experiments 1 and 6), but it is sometimes enhanced at the highest pedestal contrasts (Experiment 3). For still wider contexts (Experiment 7) or separated contexts (Experiments 1, 2, 4, and 5) excitation is strong relative to inhibition, thus increasing responses and decreasing thresholds. Both excitation and inhibition are produced by contexts that extend at least 4.5 wavelengths from the target center. Both effects decrease as the context moves away from the target, and the balance between them changes with separation and width to produce a wide range of context effects.

The models presented here are not complete. They fit data and, thus, provide a description of results, but they do not predict the effects of other context configurations. For example, sensitivities to annular and Gabor contexts are quite different. We would like to have a model that predicts the sensitivity to any context pattern in any position. If there are underlying excitatory and inhibitory functions of space such that the sensitivity to any context pattern is the integral of that pattern's spatial waveform and the underlying spatial sensitivity function, then such a general model is possible. Because sensitivities sometimes decrease as the area of a context pattern increases and some context pattern sensitivities are negative, the product of the waveform and the sensitivity function would have to be negative in some regions. Context sensitivity also depends on spatial and temporal frequency and phase, so it must be distributed over many differently tuned lateral mechanisms. The models fitted here describe and, to a limited extent, predict performance for one domain of context effects. There are other models, some of which differ in substantial ways.

Other models

Lu and Dosher (2008) developed the pattern template model (PTM) of masking by noise and showed that it accounts for a wide range of noise-masking results. They also showed that these results exclude other models. Although more complex, the PTM is formally similar to Foley's (1994) model of superimposed context effects. In the PTM, the excitation of a receptive field–like perceptual template is divided by a contrast gain signal that is more broadly tuned and depends primarily on the noise, but the target also contributes to the contrast gain. As in the models fitted in this paper, the template is specified only by its excitatory and inhibitory sensitivities. The model does not provide for an effect of context on the sensitivity of the template, but it could be elaborated to do so.

To account for novel spatial summation effects that they discovered, Meese and Summers (2007) propose a model in which, after correction for retinal contrast-sensitivity inhomogeneity, the entire stimulus is filtered through spatial-frequency and orientation

filters. The outputs at every point are rectified and raised to the 2.4 power. They are then summed over the entire image to provide the numerator of the response function. The outputs are raised to the 2.0 power, summed over the image, and then added to a constant to provide the denominator of the response function. Thus, the response is computed over the entire image rather than a smaller V1 cell–like receptive field with excitatory and inhibitory sensitivities that vary differently over space. Because sensitivity is uniform over the image except for the correction for sensitivity loss with eccentricity, the model does not account for excitatory and inhibitory lateral context effects although it probably could be elaborated to do so. Meese (2010) extends the research on spatial summation to a novel class of stimuli consisting of arrays of micropatterns, again showing that substantial spatial summation extends over large areas. Here, he proposes a three-stage model in which the stages are (a) spatial filtering, (b) summation over coherent textures, and (c) pooling over orthogonal textures. Meese and Baker (2013) show that an RA model in which a context pattern produces both additive excitation and inhibition accounts for TvC functions across four domains: eyes, space, time, and pattern. Often the additive excitation is mandatory and has the effect of increasing thresholds (dilution masking) because it pushes the response up to less steep ranges of the response function. However, when the target is confined to a central area, sometimes excitation from the surround does not occur. Attention seems to exercise some control.

When the task is to segregate two regions of a scene that are similar in their elements but differ in texture, there is a large literature that indicates that two levels of filtering are required with a nonlinear transform between them. The second-level filters usually have larger receptive fields. Graham and Sutter (1998) review early research on this phenomenon. The nonlinear transform between the stages has been shown to have an expansive excitatory nonlinearity and a divisive gain control signal that compresses the responses at high contrast (Graham & Sutter, 2000).

Difficulty in accounting for phase effects led to two-stage models for context effects in detection. Zenger and Sagi (1996) used a paradigm in which two separated Gabor flankers had opposite phases to each other. They found that this produced less facilitation than flankers with the same phase. At the first stage of their model, there are filters tuned to phase, spatial frequency, and orientation. Their output is full-wave rectified and input to large and broadly tuned excitatory and inhibitory filters at a second stage. The output of the excitatory filter undergoes an accelerating transform and is divided by the output of the inhibitory

filter. They assign parameters to the model and show that the simulation produces TvCc functions that resemble their data.

Solomon and Morgan (2000) proposed a two-stage model to account for the complex interactions they found between context position, number, and relative phase. Their model is an extension of a one-stage model proposed by Solomon et al. (1999) to account for facilitation by flanks that were opposite in sign to the target. The effects are described in the section of this article on relative size effects in detection. In their model, there are two stages of filtering. At the first stage, the filters at each point are matched to the spatial frequency, orientation, and phase of the Gabor stimulus patterns. The response at each position undergoes a nonlinear transform that depends only on the contrast at that position. The resulting spatial activity pattern goes to the stage 2 filter array. The stage 2 filters are four times larger and are tuned to one fourth the spatial frequency. They receive input from both the in-phase and the opposite phase filters at the first stage. Random noise is added to the second-level responses, which determine the observer's decision. Because the second-level filters are tuned to a lower spatial frequency, some of the context patterns in the stimulus produce inhibition. This explains why some of the context Gabor patterns in their circular array raise thresholds rather than lower them. The phase insensitivity of the second-stage filters explains how out-of-phase context can mask.

An experiment by Henning and Wichmann (2007) motivated a reconsideration of models of detection, masking, and discrimination that rely on the response of a single mechanism or template tuned to the target stimulus. They showed that the threshold decrease that occurs when a target is presented on a low-contrast pedestal is reduced when broadband noise is presented but completely disappears when noise with a notch around the target frequency is presented. This suggested that performance in this task depends on signals from units tuned to a range of spatial frequencies.

Goris, Wichmann, and Henning (2009) show that this effect is inconsistent with Foley's (1994) model. They propose a model in which near-threshold detection performance depends on the responses of an array of units differently tuned to spatial frequency and orientation. The detection decision depends on the distribution of responses over these units. They propose that it depends on a weighted average of these responses with weights based on the magnitude of the responses, and they demonstrate using simulation that this model can account for Henning and Wichmann's (2007) results.

Goris, Putzeys, Wagemans, and Wichmann (2013) propose a more elaborate version of this model in which the observer's decision is determined by a

maximum likelihood estimate of which interval contained the target based on the responses of a population of cells in the primary visual cortex. They show that, with a few parameters, this model can fit data on detection, adaptation, and discrimination data. The model does not account for lateral context effects, but it probably could be elaborated to do so.

Conclusion

The study of lateral context effects in pattern vision has yielded some inconsistent results as well as some consistent ones. Variation both between and within observers is one factor behind the inconsistencies. There is general agreement that patterns at least several wavelengths away from the target pattern change detection and discrimination thresholds and perceived contrast. These changes include both increases and decreases. They depend in complex ways on context type, contrast, and separation although they generally decrease as separation increases.

The models fitted to the data in this study are generalized versions of models in the literature. They fit the data of the seven experiments described in this paper well, and it is clear that they fit most of the data on lateral effects. As would be expected, parameter values vary with the form and position of the context. They are usually consistent for similar configurations, but there are exceptions to this. There are phenomena that are inconsistent with these models, which show that more complex models are needed. So the study of lateral effects on pattern detection and discrimination is not done. We need more and better measurements and more complete models.

Keywords: contrast, detection, discrimination, context, masking, perception, model

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References

Adini, Y., & Sagi, D. (2001). Recurrent networks in human visual cortex: Psychophysical evidence. *Journal of the Optical Society of America A-Optics Image Science and Vision*, *18*(9), 2228–2236, https://doi.org/10.1364/Josaa.18.002228.

Adini, Y., Sagi, D., & Tsodyks, M. (1997). Excitatory-inhibitory network in the visual cortex: Psychophysical evidence. *Proceedings of the National Academy of Science, USA*, *94*(19), 10426–10431, https://doi.org/10.1073/pnas.94.19.10426.

Albrecht, D. G., & Geisler, W. S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual-cortex. *Visual Neuroscience*, *7*(6), 531–546, https://doi.org/10.1017/S0952523800010336.

Angelucci, A., & Shushruth, S. (2014). Beyond the classical receptive field: Surround modulation in primary visual cortex. *New Visual Neurosciences* (pp. 425–444). Cambridge, MA: MIT Press.

Bair, W., Cavanaugh, J. R., & Movshon, J. A. (2003). Time course and time-distance relationships for surround suppression in macaque V1 neurons. *Journal of Neuroscience*, *23*(20), 7690–7701.

Blakeslee, B., Cope, D., & McCourt, M. E. (2016). The Oriented Difference of Gaussians (ODOG) model of brightness perception: Overview and executable Mathematica notebooks. *Behavior Research Methods*, *48*(1), 306–312, https://doi.org/10.3758/s13428-015-0573-4.

Blakeslee, B., & McCourt, M. E. (1999). A multiscale spatial filtering account of the White effect, simultaneous brightness contrast and grating induction. *Vision Research*, *39*(26), 4361–4377, https://doi.org/10.10-16/S0042-6989(99)00119-4.

Blakeslee, B., Reetz, D., & McCourt, M. E. (2008). Coming to terms with lightness and brightness: Effects of stimulus configuration and instructions on brightness and lightness judgments. *Journal of Vision*, *8*(11):3, 1–14, https://doi.org/10.1167/8.11.3. [PubMed] [Article]

Cannon, M. W., & Fullenkamp, S. C. (1991). Spatial interactions in apparent contrast – Inhibitory effects among grating patterns of different spatial-frequencies, spatial positions and orientations. *Vision Research*, *31*(11), 1985–1998, https://doi.org/10.1016/0042-6989(91)90193-9.

Cannon, M. W., & Fullenkamp, S. C. (1993). Spatial interactions in apparent contrast – Individual-differences in enhancement and suppression effects. *Vision Research*, *33*(12), 1685–1695, https://doi.org/10.1016/0042-6989(93)90034-T.

Cannon, M. W., & Fullenkamp, S. C. (1996). A model for inhibitory lateral interaction effects in perceived contrast. *Vision Research*, 36(8), 1115–1125, https://doi.org/10.1016/0042-6989(95)00180-8.

Cavanaugh, J. R., Bair, W., & Movshon, J. A. (2002a). Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *Journal of Neurophysiology*, 88(5), 2530–2546.

Cavanaugh, J. R., Bair, W., & Movshon, J. A. (2002b). Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons. *Journal of Neurophysiology*, 88(5), 2547–2556.

Chen, C. C., Kasamatsu, T., Polat, U., & Norcia, A. M. (2001). Contrast response characteristics of long-range lateral interactions in cat striate cortex. *Neuroreport*, 12(4), 655–661, https://doi.org/10.1097/00001756-200103260-00008.

Chen, C. C., & Tyler, C. W. (2000). Spatial long-range modulation of contrast discrimination. *SPIE Proceedings*, 4080, 87–93.

Chen, C. C., & Tyler, C. W. (2001). Lateral sensitivity modulation explains the flanker effect in contrast discrimination. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268(1466), 509–516.

Chen, C. C., & Tyler, C. W. (2002). Lateral modulation of contrast discrimination: Flanker orientation effects. *Journal of Vision*, 2(6):8, 520–530, https://doi.org/10.1167/2.6.8. [PubMed] [Article]

Chen, C. C., & Tyler, C. W. (2008). Excitatory and inhibitory interaction fields of flankers revealed by contrast-masking functions. *Journal of Vision*, 8(4):10, 1–14, https://doi.org/10.1167/8.4.10. [PubMed] [Article]

De Angelis, G. C., Freeman, R. D., & Ohzawa, I. (1994). Length and width tuning of neurons in the cats primary visual-cortex. *Journal of Neurophysiology*, 71(1), 347–374.

Dresp, B. (1993). Bright lines and edges facilitate the detection of small light targets. *Spatial Vision*, 7(3), 213–225, https://doi.org/10.1163/156856893x00379.

Ejima, Y., & Miura, K. Y. (1984). Change in detection threshold caused by peripheral gratings – Dependence on contrast and separation. *Vision Research*, 24(4), 367–372.

Ejima, Y., & Takahashi, S. (1983). Effects of high-contrast peripheral patterns on the detection threshold of sinusoidal targets. *Journal of the Optical Society of America*, 73(12), 1695–1700.

Ejima, Y., & Takahashi, S. (1985). Apparent contrast of a sinusoidal grating in the simultaneous presence of peripheral gratings. *Vision Research*, 25(9), 1223–1232.

Foley, J. M. (1994). Human luminance pattern-vision mechanisms – Masking experiments require a new model. *Journal of the Optical Society of America A-Optics Image Science and Vision*, 11(6), 1710–1719.

Foley, J. M., & Legge, G. E. (1981). Contrast detection and near-threshold discrimination in human-vision. *Vision Research*, 21(7), 1041–1053.

Foley, J. M., & McCourt, M. E. (1985). Visual grating induction. *Journal of the Optical Society of America A-Optics Image Science and Vision*, 2(7), 1220–1230.

Foley, J. M., Varadharajan, S., Koh, C. C., & Farias, M. C. Q. (2007). Detection of Gabor patterns of different sizes, shapes, phases and eccentricities. *Vision Research*, 47(1), 85–107, doi:10.1016/j.visres.2006.09.005.

Geisler, W. S., & Albrecht, D. G. (1992). Cortical neurons: Isolation of contrast gain control. *Vision Research*, 32(8), 1409–1410.

Goris, R. L. T., Putzeys, T., Wagemans, J., & Wichmann, F. A. (2013). A neural population model for visual pattern detection. *Psychological Review*, 120(3), 472–496, https://doi.org/10.1037/a0033136.

Goris, R. L. T., Wichmann, F. A., & Henning, G. B. (2009). A neurophysiologically plausible population code model for human contrast discrimination. *Journal of Vision*, 9(7):15, 1–22, https://doi.org/10.1167/9.7.15. [PubMed] [Article]

Graham, N., & Sutter, A. (1998). Spatial summation in simple (Fourier) and complex (non-Fourier) texture channels. *Vision Research*, 38(2), 231–257, https://doi.org/10.1016/s0042-6989(97)00154-5.

Graham, N., & Sutter, A. (2000). Normalization: Contrast-gain control in simple (Fourier) and complex (non-Fourier) pathways of pattern vision. *Vision Research*, 40(20), 2737–2761, https://doi.org/10.1016/s0042-6989(00)00123-1.

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, 9(2), 181–197.

Heinemann, E. G. (1955). Simultaneous brightness induction as a function of inducing- field and test field luminances. *Journal of Experimental Psychology*, 50(2), 89–96, https://doi.org/10.1037/h0040919.

Henning, G. B., & Wichmann, F. A. (2007). Some observations on the pedestal effect. *Journal of Vision*, 7(1):3, 1–15, https://doi.org/10.1167/7.1.3. [PubMed] [Article]

Ichida, J. M., Schwabe, L., Bressloff, P. C., &

Angelucci, A. (2007). Response facilitation from the "suppressive" receptive field surround of macaque V1 neurons. *Journal of Neurophysiology, 98*(4), 2168–2181, https://doi.org/10.1152/jn.00298.2007.

Ishikawa, A., Shimegi, S., & Sato, H. (2006). Meta-contrast masking suggests interaction between visual pathways with different spatial and temporal properties. *Vision Research, 46*(13), 2130–2138, https://doi.org/10.1016/j.visres.2005.12.013.

Kapadia, M. K., Ito, M., Gilbert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context – Parallel studies in human observers and in V1 of alert monkeys. *Neuron, 15*(4), 843–856, https://doi.org/10.1016/0896-6273(95)90175-2.

Klein, S. A., & Levi, D. M. (2009). Stochastic model for detection of signals in noise. *Journal of the Optical Society of America A-Optics Image Science and Vision, 26*(11), B110–B126.

Legge, G. E., & Foley, J. M. (1980). Contrast masking in human-vision. *Journal of the Optical Society of America, 70*(12), 1458–1471.

Levitt, J. B., & Lund, J. S. (1997, May 1). Contrast dependence of contextual effects in primate visual cortex. *Nature, 387*(6628), 73–76, https://doi.org/10.1038/387073a0.

Lu, Z. L., & Dosher, B. A. (2008). Characterizing observers using external noise and observer models: Assessing internal representations with external noise. *Psychological Review, 115*(1), 44–82, https://doi.org/10.1037/0033-295x.115.1.44.

Maehara, G., & Goryo, K. (2005). Binocular, monocular and dichoptic pattern masking. *Optical Review, 12*(2), 76–82.

McCourt, M. E. (1982). A spatial frequency dependent grating-induction effect. *Vision Research, 22*(1), 119–134, https://doi.org/10.1016/0042-6989(82)90173-0.

McCourt, M. E., & Kingdom, F. A. A. (1996). Facilitation of luminance grating detection by induced gratings. *Vision Research, 36*(16), 2563–2573, https://doi.org/10.1016/0042-6989(95)00244-8.

Meese, T. S. (2004). Area summation and masking. *Journal of Vision, 4*(10):8, 930–943, https://doi.org/10.1167/4.10.8. [PubMed] [Article]

Meese, T. S. (2010). Spatially extensive summation of contrast energy is revealed by contrast detection of micro-pattern textures. *Journal of Vision, 10*(8):14, 1–21, https://doi.org/10.1167/10.8.14. [PubMed] [Article]

Meese, T. S., & Baker, D. H. (2013). A common rule for integration and suppression of luminance contrast across eyes, space, time, and pattern. *I-Perception, 4*(1), 1–16, https://doi.org/10.1068/i0556.

Meese, T. S., Georgeson, M. A., & Baker, D. H. (2006). Binocular contrast vision at and above threshold. *Journal of Vision, 6*(11):7, 1224–1243, https://doi.org/10.1167/6.11.7. [PubMed] [Article]

Meese, T. S., & Hess, R. F. (2004). Low spatial frequencies are suppressively masked across spatial scale, orientation, field position, and eye of origin. *Journal of Vision, 4*(10):2, 843–859, https://doi.org/10.1167/4.10.2. [PubMed] [Article]

Meese, T. S., Hess, R. F., & Williams, C. B. (2005). Size matters, but not for everyone: Individual differences for contrast discrimination. *Journal of Vision, 5*(11):2, 928–947, https://doi.org/10.1167/5.11.2. [PubMed] [Article]

Meese, T. S., & Holmes, D. J. (2007). Spatial and temporal dependencies of cross-orientation suppression in human vision. *Proceedings of the Royal Society B-Biological Sciences, 274*(1606), 127–136, https://doi.org/10.1098/rspb.2006.3697.

Meese, T. S., & Summers, R. J. (2007). Area summation in human vision at and above detection threshold. *Proceedings of the Royal Society B-Biological Sciences, 274*(1627), 2891–2900, https://doi.org/10.1098/rspb.2007.0957.

Meese, T. S., Summers, R. J., Holmes, D. J., & Wallis, S. A. (2007). Contextual modulation involves suppression and facilitation from the center and the surround. *Journal of Vision, 7*(4):7, 1–21, https://doi.org/10.1167/7.4.7. [PubMed] [Article]

Nachmias, J., & Sansbury, R. V. (1974). Grating contrast – Discrimination may be better than detection. *Vision Research, 14*(10), 1039–1042.

Nurminen, L., Peromaa, T., & Laurinen, P. (2010). Surround suppression and facilitation in the fovea: Very long-range spatial interactions in contrast perception. *Journal of Vision, 10*(13):9, 1–13, https://doi.org/10.1167/10.13.9. [PubMed] [Article]

Olzak, L. A., & Laurinen, P. I. (1999). Multiple gain control processes in contrast-contrast phenomena. *Vision Research, 39*(24), 3983–3987.

Petrov, Y., Carandini, M., & McKee, S. (2005). Two distinct mechanisms of suppression in human vision. *Journal of Neuroscience, 25*(38), 8704–8707.

Petrov, Y., & McKee, S. P. (2009). The time course of contrast masking reveals two distinct mechanisms of human surround suppression. *Journal of Vision, 9*(1):21, 1–11, https://doi.org/10.1167/9.1.21. [PubMed] [Article]

Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., &

Norcia, A. M. (1998, February 5). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature*, *391*(6667), 580–584.

Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research*, *33*(7), 993–999.

Polat, U., & Sagi, D. (1994). The architecture of perceptual spatial interactions. *Vision Research*, *34*(1), 73–78.

Ross, J., & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *246*(1315), 61–69.

Sato, T. K., Haider, B., Hausser, M., & Carandini, M. (2016). An excitatory basis for divisive normalization in visual cortex. *Nature Neuroscience*, *19*(4), 568–570, https://doi.org/10.1038/nn.4249.

Sceniak, M. P., Hawken, M. J., & Shapley, R. (2001). Visual spatial characterization of macaque V1 neurons. *Journal of Neurophysiology*, *85*(5), 1873–1887.

Sceniak, M. P., Ringach, D. L., Hawken, M. J., & Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nature Neuroscience*, *2*(8), 733–739, https://doi.org/10.1038/11197.

Schwabe, L., Ichida, J. M., Shushruth, S., Mangapathy, P., & Angelucci, A. (2010). Contrast-dependence of surround suppression in macaque V1: Experimental testing of a recurrent network model. *Neuroimage*, *52*(3), 777–792, https://doi.org/10.1016/j.neuroimage.2010.01.032.

Schwabe, L., Obermayer, K., Angelucci, A., & Bressloff, P. C. (2006). The role of feedback in shaping the extra-classical receptive field of cortical neurons: A recurrent network model. *Journal of Neuroscience*, *26*(36), 9117–9129, https://doi.org/10.1523/Jneurosci.1253-06.2006.

Shushruth, S., Ichida, J. M., Levitt, J. B., & Angelucci, A. (2009). Comparison of spatial summation properties of neurons in macaque V1 and V2. *Journal of Neurophysiology*, *102*(4), 2069–2083, https://doi.org/10.1152/jn.00512.2009.

Shushruth, S., Mangapathy, P., Ichida, J. M., Bressloff, P. C., Schwabe, L., & Angelucci, A. (2012). Strong recurrent networks compute the orientation tuning of surround modulation in the primate primary visual cortex. *Journal of Neuroscience*, *32*(1), 308–321, https://doi.org/10.1523/jneurosci.3789-11.2012.

Shushruth, S., Nurminen, L., Bijanzadeh, M., Ichida, J. M., Vanni, S., & Angelucci, A. (2013). Different orientation tuning of near- and far-surround suppression in macaque primary visual cortex mirrors their tuning in human perception. *Journal of Neuroscience*, *33*(1), 106–119, https://doi.org/10.1523/Jneurosci.2518-12.2013.

Solomon, J. A., & Morgan, M. J. (2000). Facilitation from collinear flanks is cancelled by non-collinear flanks. *Vision Research*, *40*(3), 279–286, https://doi.org/10.1016/S0275-5408(99)00059-9.

Solomon, J. A., & Morgan, M. J. (2006). Stochastic recalibration: Contextual effects on perceived tilt. *Proceedings of the Royal Society B-Biological Sciences*, *273*(1601), 2681–2686, https://doi.org/10.1098/rspb.2006.3634.

Solomon, J. A., Sperling, G., & Chubb, C. (1993). The lateral inhibition of perceived contrast is indifferent to on-center off-center segregation, but specific to orientation. *Vision Research*, *33*(18), 2671–2683, https://doi.org/10.1016/0042-6989(93)90227-N.

Solomon, J. A., Watson, A. B., & Morgan, M. J. (1999). Transducer model produces facilitation from opposite-sign flanks. *Vision Research*, *39*(5), 987–992.

Stromeyer, C. F., & Klein, S. (1974). Spatial frequency channels in human vision as asymmetric (edge) mechanisms. *Vision Research*, *14*(12), 1409–1420.

Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120.

Watson, A. B., & Solomon, J. A. (1997). Model of visual contrast gain control and pattern masking. *Journal of the Optical Society of America A-Optics Image Science and Vision*, *14*(9), 2379–2391.

Westheimer, G. (1967). Spatial interaction in human cone vision. *Journal of Physiology–London*, *190*, 139–154.

Williams, C. B., & Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America A-Optics Image Science and Vision*, *15*(8), 2046–2051, https://doi.org/10.1364/Josaa.15.002046.

Woods, R. L., Nugent, A. K., & Peli, E. (2002). Lateral interactions: Size does matter. *Vision Research*, *42*(6), 733–745.

Xing, J., & Heeger, D. J. (2000). Center-surround interactions in foveal and peripheral vision. *Vision Research*, *40*(22), 3065–3072.

Xing, J., & Heeger, D. J. (2001). Measurement and modeling of center-surround suppression and enhancement. *Vision Research*, *41*(5), 571–583.

Yu, C., Klein, S. A., & Levi, D. M. (2001). Surround modulation of perceived contrast and the role of

brightness induction. *Journal of Vision*, *1*(1):3, 18–31, https://doi.org/10.1167/1.1.3. [PubMed] [Article]

Yu, C., Klein, S. A., & Levi, D. M. (2002). Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms. *Journal of Vision*, *2*(3):4, 243–255, https://doi.org/10.1167/2.3.4. [PubMed] [Article]

Yu, C., Klein, S. A., & Levi, D. M. (2003). Cross- and iso-oriented surrounds modulate the contrast response function: The effect of surround contrast. *Journal of Vision*, *3*(8):1, 527–540, https://doi.org/10.1167/3.8.1. [PubMed] [Article]

Yu, C., & Levi, D. M. (1997). End stopping and length tuning in psychophysical spatial filters. *Journal of the Optical Society of America A-Optics Image Science and Vision*, *14*(9), 2346–2354.

Yu, C., & Levi, D. M. (1998a). Rectification nonlinearity in cortical end-stopped perceptive fields. *Vision Research*, *38*(22), 3517–3530.

Yu, C., & Levi, D. M. (1998b). Spatial-frequency and orientation tuning in psychophysical end- stopping. *Visual Neuroscience*, *15*(4), 585–595.

Yu, C., & Levi, D. M. (1999). The time course of psychophysical end-stopping. *Vision Research*, *39*(12), 2063–2073.

Yu, C., & Levi, D. M. (2000). Surround modulation in human vision unmasked by masking experiments. *Nature Neuroscience*, *3*(7), 724–728.

Zenger-Landolt, B., & Heeger, D. J. (2003). Response suppression in V1 agrees with psychophysics of surround masking. *Journal of Neuroscience*, *23*(17), 6884–6893.

Zenger-Landolt, B., & Koch, C. (2001). Flanker effects in peripheral contrast discrimination – Psychophysics and modeling. *Vision Research*, *41*(27), 3663–3675.

Zenger, B., & Sagi, D. (1996). Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection. *Vision Research*, *36*(16), 2497–2513.