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Investigating local network interactions underlying first- and second-order processing

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Abstract

We compared the spatial lateral interactions for first-order cues to those for second-order cues, and investigated spatial interactions between these two types of cues. We measured the apparent modulation depth of a target Gabor at fixation, in the presence and the absence of horizontally flanking Gabors. The Gabors' gratings were either added to (first-order) or multiplied with (second-order) binary 2-D noise. Apparent "contrast" or modulation depth (i.e., the perceived difference between the high and low luminance regions for the first-order stimulus, or between the high and low contrast regions for the second-order stimulus) was measured with a modulation depth-matching paradigm. For each observer, the first- and second-order Gabors were equated for apparent modulation depth without the flankers. Our results indicate that at the smallest inter-element spacing, the perceived reduction in modulation depth is significantly smaller for the second-order than for the first-order stimuli. Further, lateral interactions operate over shorter distances and the spatial frequency and orientation tuning of the suppression effect are broader for second- than first-order stimuli. Finally, first- and second-order information interact in an asymmetrical fashion; second-order flankers do not reduce the apparent modulation depth of the first-order target, whilst first-order flankers reduce the apparent modulation depth of the second-order target.

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1. Introduction

Contextual interactions are prevalent in visual perception. The literature from research in psychophysics provides several examples in which the perception of aspects of an image is influenced to some extent by the features of other neighboring local elements or by characteristics of the ensemble itself. For example, the local properties of micropatterns are perceptually linked into salient contours according to a specific set of rules (Field, Hayes, & Hess, 1993). Texture boundaries are segregated, in part, by the coding of local element features, and by detecting the difference between adjacent texture regions (Julesz, 1971; Malik & Perona, 1990; Nothdurft, 1985). The detectability of local elements is affected by the local characteristics and by the global configuration of the neighboring stimuli (Polat & Sagi, 1993). The appearance and discriminability of texture

components can be altered by the presence of neighboring elements and their characteristics (Ellemberg, Wilkinson, Wilson, & Arsenault, 1998; Wilkinson, Wilson, & Ellemberg, 1997). Although the exact nature of these lateral interactions remains unfathomed, evidence suggests that there is a general gain control mechanism that underlies the management of contextual interactions (Albrecht & Geisler, 1991; Cannon & Fullenkamp, 1996; Ellemberg et al., 1998; Heeger, 1992).

Several psychophysical paradigms were developed to investigate the influence of lateral interactions on human visual performance. The most common paradigms measure perceived contrast and spatial frequency (Cannon & Fullenkamp, 1991; Ellemberg et al., 1998), discrimination of contrast and orientation (Wilkinson et al., 1997), and detection (Polat & Sagi, 1993) of a central target Gabor as a function of the distance between the target and flanking Gabors and as a function of their local characteristics (e.g., spatial frequency, orientation, contrast). Using a matching task, Ellemberg et al. (1998) measured a reduction of about 20% in the

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perceived contrast and an increase of about 20% in the perceived spatial frequency of a target Gabor when it is flanked by a group of Gabor elements that have the same spatial frequency and orientation. This induction effect extends up to inter-element spacings of about four carrier cycles, providing a clear example that the perception of contrast in a localized region of the visual field can be influenced by the contrast of features located in the adjacent regions.

The investigation of spatial interactions has mainly used stimuli that are defined by spatial and temporal parameters that vary in the luminance domain (first-order cues). However, it is well documented that the human visual system is able to detect objects defined by image attributes other than luminance, such as texture, in which there is no change in mean luminance (second-order cues) and that this is the case for both for spatial vision (Hess, Ledgeway, & Dakin, 2000; McGraw, Levi, & Whitaker, 1999; Prins & Kingdom, 2003), and for the perception of motion (Badcock & Derrington, 1985; Baker & Hess, 1998; Cavanagh & Mather, 1989; Chubb & Sperling, 1988).

Several lines of evidence suggest that first- and second-order stimuli are analysed by different signal processing mechanisms. Neurons in the cat's striate cortex have different spatial and temporal frequency tuning for first-order stimuli than they do for second-order stimuli (Mareschal & Baker, 1998, 1999; Zhou & Baker, 1993). In humans, visual evoked potential latencies are longer and psychophysical reaction times are slower for second-order than for first-order motion-onset (Elleberg et al., 2003a). In young children, sensitivity to second-order motion develops more slowly than sensitivity to first-order motion (Elleberg et al., 2003b), and is more profoundly degraded by strabismus (Simmers, Ledgeway, Hess, & McGraw, 2003). Further, neuropsychological studies report a 'double dissociation' in which lesions in some central areas cause deficits in the perception of second-order motion while relatively sparing first-order motion (Plant & Nakayama, 1993; Vaina & Cowey, 1996), and lesions in other central areas cause deficits in the perception of first-order motion with little effect on second-order motion (Vaina, Makris, Kennedy, & Cowey, 1998; Vaina, Soloviev, Bienfang, & Cowey, 2000). Finally, a functional magnetic resonance imaging study indicates that, although some visual areas (including V3_A, and _HMT+) respond equally to both first- and second-order motion, area V1 responds more strongly to first-order, while the lateral occipital area responds more strongly to second-order motion (Dumoulin, Baker, Hess, & Evans, 2003; also see Smith, Greenlee, Singh, Kraemer, & Hennig, 1998).

Computational modeling suggests that the detection of second-order images requires not only a first stage of linear filtering but also additional processing steps (Chubb & Sperling, 1988, 1989; Wilson, Ferrara, & Yo,

1992). Baker and colleagues found evidence from single-cell recording studies in cats that is consistent with this additional processing (Mareschal & Baker, 1998, 1999; Zhou & Baker, 1993; for a review see Baker, 1999). They recorded responses from neurons to luminance gratings (first-order) and to contrast envelope gratings (second-order) which were created by multiplying a static high spatial frequency sinusoidal grating (carrier) with a drifting low spatial frequency sinusoidal grating (envelope). They found that neurons are tuned to a narrow range of spatial frequencies that is much higher for the second-order carrier than for the first-order luminance grating. Further, in these same neurons, the preferred range of spatial frequency is lower for the second-order contrast envelope than for the first-order luminance grating. These data support a 'filter-rectify-filter' model, in which an early linear filtering occurs when neurons that are sensitive to high spatial frequencies respond to the carrier grating (but see Baloch, Grossberg, Mingolla, & Nogueira, 1999; Johnston & Clifford, 1995). This is followed by a non-linear processing stage (e.g., full-wave, half-wave rectification, or squaring) that introduces first-order characteristics into the neural representation of the second-order image, and a second stage filtering by neurons that are sensitive to lower spatial frequencies. This processing scheme by itself cannot account for responses to luminance gratings because the spatial frequency tuning of the early and late filters do not overlap. Recently, Prins and Kingdom (2003) provided evidence that in the human observer the perception of texture discontinuities is mediated by such a 'filter-rectify-filter' mechanism. Sensitivity to the second-order component of a texture (i.e., its orientation and frequency modulation) composed of densely packed Gabor elements is decreased by the previous adaptation to a first-order grating that matched the characteristics of the first-order signal in the stimulus. This is consistent with other reports suggesting that distinct first- and second order mechanisms underlie spatial vision in humans (Graham & Sutter, 1996, 1998; Lin & Wilson, 1996; Schofield & Georgeson, 1999).

Very little is known about the nature of the cortical interactions mediating the perception of second-order images. However, there is some evidence that the neural substrate underlying first- versus second-order perceptual interactions operates differently. Contour integration and motion trajectory detection, two aspects of visual perception believed to implicate long range intracortical connections, are easily demonstrated for first-order stimuli but are absent for second-order stimuli (Hess et al., 2000). The goal of the present series of experiments was to study the nature of second-order lateral interactions. We ask whether localized second-order images are subjected to the same kind of lateral interactions as those previously found for first-order images. If so, is the origin of these interactions at the

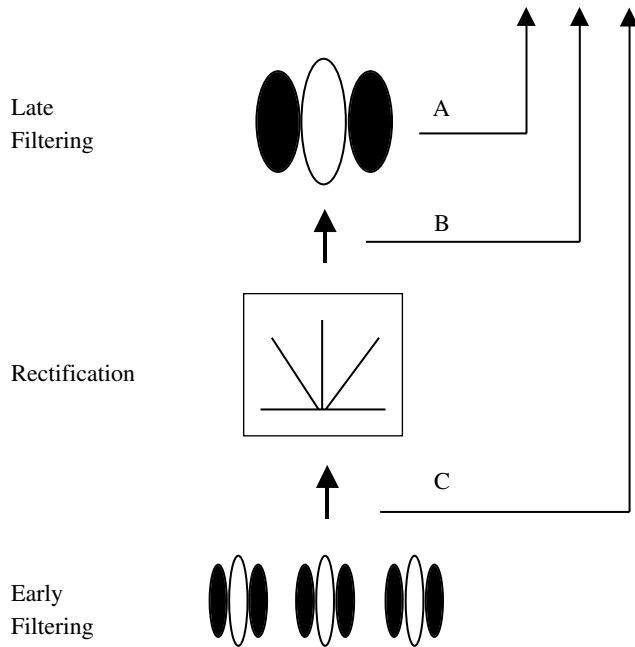


Fig. 1. Schematic representation of the origin of the lateral inhibitory signal in the filter–rectify–filter scheme hypothesized to process second-order information: (A) lateral inhibitory signal that operates after the envelope filtering stage; (B) lateral inhibitory signal that operates after rectification of the carrier signal and (C) lateral inhibitory signal that originates after the initial carrier filtering stage.

level of early first-order filtering (indicated by C in Fig. 1), after rectification of the output of the early filters (indicated by B in Fig. 1), or at the level of the second-stage of filtering in the filter–rectify–filter scheme (indicated by A in Fig. 1). To answer these questions we compared the apparent “contrast” of first- versus second-order Gabor stimuli as a function of the spatial extent of flanking elements and as a function of the local properties of the surrounding elements.

2. Methods

2.1. Observers

Two of the authors and two experienced observers, who were unaware of the issues examined, participated in this study. Each participated to all conditions, except for HAA who was not available to contribute to the spatial frequency and orientation tuning data. Two had normal acuity and the others had corrected to normal acuity.

2.2. Stimuli and apparatus

The stimuli consisted of a horizontal array of spatially localized 2-D Gabors. A Gabor is a sinusoidal modulation of luminance multiplied by a Gaussian

envelope in the horizontal and orthogonal dimensions. The first-order stimuli were created by adding the sinusoidal component of a Gabor to 2-D noise that was binary. This stimulus is represented by the following equation:

$$G(x, y) = L_{\text{mean}} + L_{\text{mean}}(G \cos(2\pi fx) + RC) \times \exp(-x^2/\sigma_x^2) \times \exp(-y^2/\sigma_y^2) \quad (1)$$

where L_{mean} is the mean luminance of the pattern, f is the spatial frequency of the sinusoidal modulation, G is the contrast of the grating, R is the random carrier (having contrast C), and (σ_x) and (σ_y) are vertical and horizontal space constants, respectively.

Unless mentioned otherwise, the orientation of the Gabor’s grating component was vertical and its peak spatial frequency was 3 cpd (therefore, $\lambda = \sigma = 20$ arcmin). The displayed horizontal and vertical spread of each Gabor was 0.58° . The noise carrier had a contrast of 50% and each noise element was 1.9×1.9 arcmin.

The second-order stimuli were created by multiplying the sinusoidal component of a Gabor by 2-D noise that was binary. This produced Gabors with an internal sinusoidal structure that varied in contrast and had a mean luminance that was constant across different regions of the pattern. The geometry of the second-order stimulus is represented in the following equation:

$$G(x, y) = L_{\text{mean}}(1 + (R(M \cos(2\pi fx) + 1) \times \exp(-x^2/\sigma_x^2) \times \exp(-y^2/\sigma_y^2)C/2)) \quad (2)$$

where M is the modulation depth of the sinusoidal component and all other parameters are the same as indicated above. We created our second-order stimuli so that any change in modulation depth varied both the high and low contrast parts of the pattern. Fig. 2 provides an example of the first- and second-order stimulus arrays.

The stimuli and presentation routine were programmed with the Matlab™ Psychophysics Toolbox routine (Brainard, 1997; Pelli, 1997). The experiments were run on a Macintosh G4 computer and the images were displayed on a monitor that had a frame rate of 75 Hz and a resolution of 1152×870 pixels. The display had a mean luminance of 34 cd m^{-2} . The relationship between voltage and screen luminance was measured with a photometer. The Gabors were produced with a subset of achromatic luminance values that were ordered linearly, thus correcting for the monitor’s gamma non-linearity.

2.3. Procedure

Using both eyes, observers viewed the display from a distance of 57 cm. At the beginning of each trial, observers were instructed to fixate a cross at the centre of a uniformly illuminated screen. The apparent

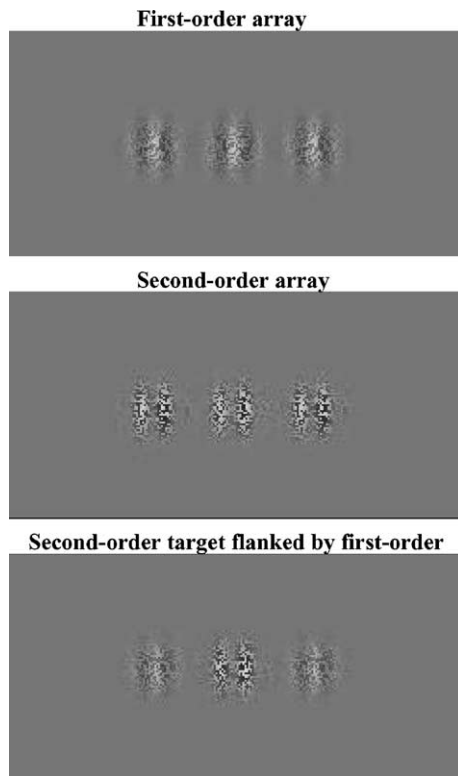


Fig. 2. Schematic representation of the stimuli. The top array presents the first-order Gabors, the middle presents the second-order Gabors and the bottom array provides an example of a second-order Gabor flanked by first-order Gabors.

“contrast” or modulation depth (i.e., the perceived difference between the high and low luminance regions of the first-order stimulus, or between the high and low contrast regions of the second-order stimulus) of a foveated first- or second-order Gabor was measured using a temporal two-alternative forced-choice (2-AFC) procedure and the method of constant stimuli. The position of the target Gabor embedded in the array was indicated by a thin, low contrast marker positioned 0.30° above it that was presented only between trials and not when the stimulus was displayed. On each trial, the modulation depth of the central Gabor in the array was compared to that of a single Gabor appearing in the same spatial location but in the other temporal interval. For each experimental run, five stimulus values (modulation depth of the single “comparison” Gabor) were pre-selected to span the observer’s psychometric function. Twenty-five trials were run for each test value and each observer completed three runs of 125 trials for each condition. Each stimulus was presented for 200 ms, separated by a 500 ms interval during which the screen returned to mean luminance. Each interval was indicated by a tone. For each trial, observers were asked to indicate which interval contained the central Gabor with the highest “contrast”. For comparison, and to obtain a baseline we also measured the apparent “contrast” of an

isolated Gabor pattern. For each condition, the point of subjective equality was determined from the 50% probability level estimated from data that were fitted with a cumulative normal function.

2.3.1. Equating the visibility of the first- and second-order Gabors

For each observer, the visibility of first- and second-order Gabor targets, without flankers, was equated using the matching paradigm described above. One interval, chosen at random, contained a second-order Gabor with a modulation depth of 60% and the other interval contained a first-order Gabor at one of five pre-selected modulation depths, to span the observer’s psychometric function. Each observer was instructed to identify which interval contained the stimulus with the highest “contrast”, or in other words, which had the most visible spatial structure. On the remaining experimental conditions each observer was tested at the modulation depth of 60% for the second-order Gabors and at the modulation depth that corresponded to the match in perceived visibility for first-order Gabors. Therefore, for first-order Gabors, observers DE, HAA, HD, and SG were tested at modulation depths of 32%, 29%, 38%, and 28%, respectively.

2.3.2. Experimental conditions

The apparent “contrast” of the central first-order and second-order targets was measured on separate runs as a function of the following experimental parameters.

(a) Apparent “contrast” of a target as a function of inter-element distance was measured in separate runs for a first-order Gabor surround by first-order flanks and for a second-order Gabor surrounded by second-order flanks. The stimulus array consisted of a foveated Gabor that was flanked laterally by a single Gabor on each side. Inter-element spacing ranged from 1.5 to 6 cycles from the centre of the target to the centre of either of the flankers. In this case a cycle is calculated from the peak spatial frequency of the Gabor’s grating (i.e., 20 arcmin per cycle for a peak spatial frequency of 3 cpd). Therefore, at the smallest inter-element spacing of 1.5 cycles the flankers abutted the target. Because the Gaussian spread of each Gabor was truncated at 2σ , there was no overlap between the Gabors at the smallest inter-element spacing.

(b) The apparent “contrast” of a central Gabor was measured as a function of the orientation and the spatial frequency of the flankers. For both conditions this was tested at the smallest inter-element spacing (1.5 cycles).

(c) The apparent “contrast” of a first-order target was measured when flanked by second-order Gabors, and that apparent “contrast” of a second-order target was measured when flanked by first-order Gabors. This was also tested at the smallest inter-element spacing (1.5 cycles).

3. Results

Fig. 3 presents the effect of lateral flanking Gabors on the apparent “contrast” of a central Gabor for the first-order (filled circles) and second-order (circles) conditions as a function of inter-element spacing, for each observer. To compare the findings for the first- and second-order conditions the data were normalized and are presented in this and the following figures as the percentage reduction from baseline (i.e., apparent “contrast” of the isolated target (baseline) minus the apparent “contrast” of the target in the array, divided by the baseline). The first point indicated by the data is that the reduction in apparent “contrast” extends over a further distance for the first-order condition than for the second-order condition. For the second-order condition, the induction effect breaks down at a spacing of approximately 2.5 cycles for three of the four observers, whilst for the first-order condition it breaks down between twice (DE and HAA) or three times (SG) that distance. For observer HD the induction effect breaks down at a distance of 3.5 cycles for second-order, less than half of the distance found for first-order (5.5 cycles). The second point

indicated by the data is that at the smallest inter-element distance, for three of the four observers (DE, SG, and HAA) the reduction in “contrast” is greater for the first-order stimuli than for the second-order stimuli.

Fig. 4A plots the apparent “contrast” of the target Gabor as a function of the spatial frequency of the flankers for the first-order (filled circles) and second-order conditions (circles). The spatial frequency of the target was always 3 cpd. The spatial frequency of the surround varied in half octave steps from one octave above to one octave below the target’s spatial frequency. The pattern of results is similar across the three observers. For both the first- and second-order conditions, apparent “contrast” is most reduced when the surround and target have the same spatial frequency, and least reduced when the spatial frequency of the surround is one octave away from that of the target. When the surround spatial frequency is one octave away from that of the target, the induction effect is stronger for the second-order condition than for the first-order condition. Fig. 4B presents the shift in apparent “contrast” for the first- and second-order target Gabors on the same scale by plotting the ratio of the percent

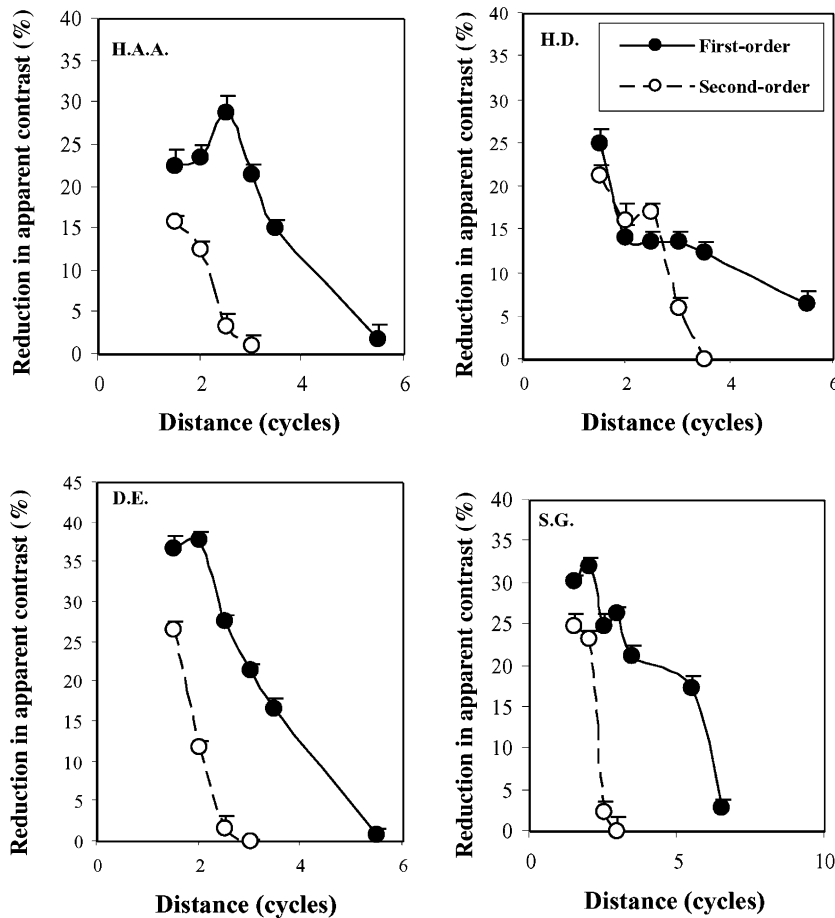


Fig. 3. The percent reduction in apparent “contrast” of the central target for the first-order stimuli (filled circles) and second-order stimuli (circles) as a function of the distance between the target and the flankers. Each graph presents the data of a different participant. Error bars indicate ±1 S.E.

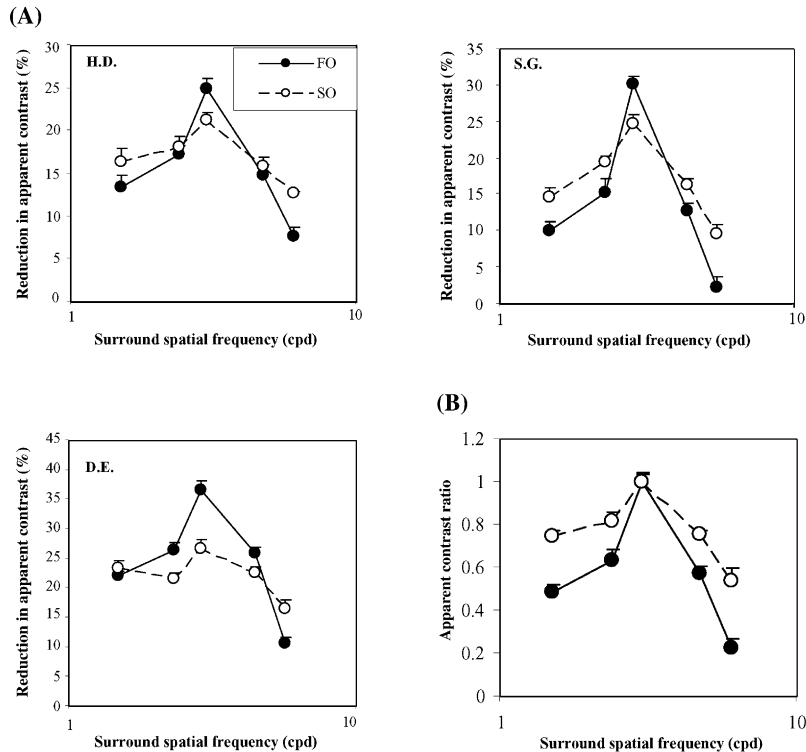


Fig. 4. The percent reduction in apparent “contrast” of the central target for the first-order stimuli (filled circles) and second-order stimuli (circles) as a function of the spatial frequency of the flankers. Graphs A present that data for three different participants and Graph B presents the mean results of the participants on the same scale for the first- and second-order stimuli. Error bars indicate ± 1 S.E.

reduction in apparent “contrast” for each combination of centre/surround spatial frequency to the condition in which the spatial frequency of the centre and surround were matched. Each point on the figure represents the mean for the three observers. These data indicate that the “contrast” induction effect decreases less rapidly for the second-order than for the first-order condition as the difference between centre and surround spatial frequency increases.

Fig. 5 shows the apparent “contrast” of the target for the first- (filled circles) and second-order (circles) conditions as a function of the orientation of the sine-wave component of the flanking Gabors. For both conditions, the “contrast” induction effect decreases as the orientation of the surround shifts away from that of the target. This reduction in the induction effect is much greater for the first-order than for the second-order stimuli. Fig. 5B presents the shift in apparent “contrast” for the first- and second-order target Gabors on the same scale by plotting the ratio of the percent reduction in apparent “contrast” for each combination of centre/surround orientation to the condition in which the orientation of the centre and surround were matched. Each point on the figure represents the mean for the three observers. These results suggest that for the first-order condition, the change in apparent “contrast” depends more on the orientation of the surround than it does for the second-order condition.

Finally, Fig. 6 shows the reduction in apparent “contrast” of a second-order target surrounded by first-order flankers (dark bars) and the apparent “contrast” of a first-order target surrounded by second-order flankers (white bars), for each of the four observers. The results show that, for all but one observer (HAA), the apparent “contrast” of a second-order target is reduced when flankers are first-order Gabors. However, in each case in which there is a reduction, it is never as big as when the flankers are also second-order Gabors. In contrast, for each observer there is little if any change in the apparent “contrast” of a first-order target when it is flanked by second-order Gabors.

4. Discussion

The present study provides evidence for spatial interactions among the mechanisms that process second-order information. At the smallest inter-element spacing tested and when the second-order target and flankers were matched in spatial frequency and orientation we measured a reduction in apparent “contrast” that ranged from 16% to 27%. These findings suggest that the response of second-order mechanisms can be modulated by the neural activity coming from second-order mechanisms in adjacent regions of cortical space. Our findings provide evidence for a network of intra-cortical

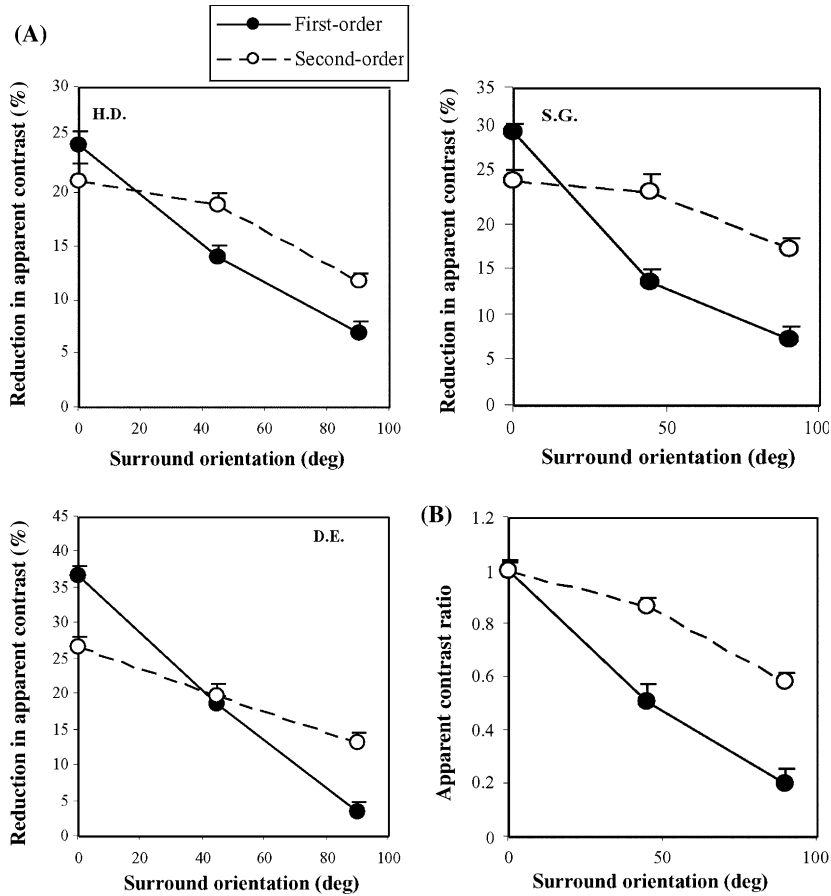


Fig. 5. The percent reduction in apparent “contrast” of the central target for the first-order stimuli (filled circles) and second-order stimuli (circles) as a function of the orientation of the flankers. Graphs A present that data for three different participants and Graph B presents the mean results of the participants on the same scale for the first- and second-order stimuli. Error bars indicate ± 1 S.E.

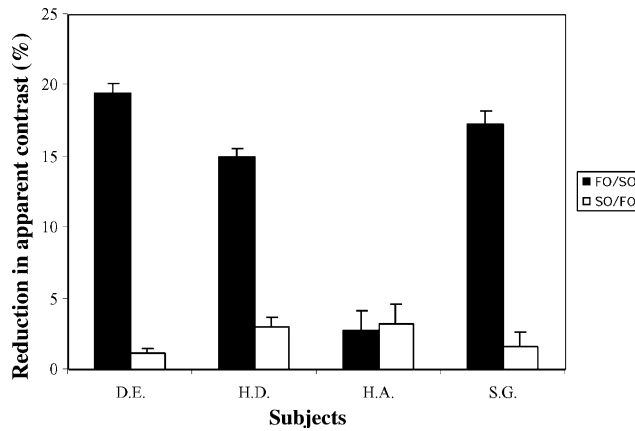


Fig. 6. The percent reduction in apparent “contrast” of a first-order target flanked by second-order Gabors (white bars) and of a second-order target flanked by first-order Gabors (dark bars). Error bars indicate ± 1 S.E.

connections among second-order filters similar to that hypothesized to underlie the perceptual segregation of texture boundaries when there are no first-order cues

(Li, 1999; Malik & Perona, 1990; Stemmler, Usher, & Niebur, 1995).

Despite evidence for spatial lateral interactions among second-order mechanisms, our results also suggest several differences between first- versus second-order lateral interactions. First, the perceived reduction in “contrast” is smaller for the second-order than for the first-order stimuli. The mean reduction in apparent “contrast” at the smallest inter-element spacing for the four observers is 22% for the second-order stimuli and 29% for the first-order stimuli. A two-tailed *t*-test analysis of these data indicates that the reduction in apparent “contrast” is significantly lower for the second-order than for the first-order condition ($t = 3.182, p < 0.05$). It could be argued that despite our careful effort to equate the stimuli for visibility or “contrast”, the difference in the percentage reduction in apparent “contrast” could be the result of a small residual difference in visibility between the first- versus the second-order stimuli. To assess this possibility the apparent “contrast” of a first-order target flanked by first-order Gabors was measured for two participants (DE and HD) at about half of the contrast used previously (16% rather

than 32% for DE and 14% rather than 29% for HD). These findings indicate that reducing the contrast of the first-order stimuli by half does not reduce the amplitude of the “contrast” induction effect, in fact it slightly raises it. Therefore, it is unlikely that the smaller reduction in apparent “contrast” found for the second-order condition can be explained by a difference in visibility or inaccurate “contrast” match between the two types of stimuli. Together our findings suggest that the lateral inhibition among second-order mechanisms is not as strong as it is among first-order mechanisms.

A second important difference is that the “contrast” induction effect extends over much shorter distances for the second-order stimuli than for the first-order stimuli. In fact, the distance over which the “contrast” induction effect occurs for the second-order condition is shorter by a factor of 1.5–3, compared to the distance over which it takes place for the first-order condition. Several single cell investigations in monkeys and cats report that a cell’s response can be modulated by stimuli presented outside its receptive field (DeAngelis, Freeman, & Ohzawa, 1994; Gilbert & Wiesel, 1990; Kapadia, Westheimer, & Gilbert, 1999). Intrinsic connections that extend over about 1.5–2 mm in the monkeys primary visual cortex are likely to be responsible for these interactions (Amir, Harel, & Malach, 1993; Rockland & Lund, 1983; Sincich & Blasdel, 2001). However, these studies did not use stimuli consisting of only second-order cues and did not target groups of neurons of the type identified by Baker and colleagues (Baker, 1999; Mareschal & Baker, 1998; Zhou & Baker, 1993) that respond to second-order images. Therefore, our findings suggest that the network of intra-cortical connections linking neurons responding to second-order local information operates over much shorter distances than that responding to first-order local information.

Our data also show that the induction effect decreases less rapidly for the second-order than for the first-order stimuli as the difference in spatial frequency and orientation between the centre and surround increases. For example, when the centre and surround have the same spatial frequency and orientation the reduction in apparent “contrast” is stronger for the first-order condition, but when the centre and surround differ greatly in spatial frequency or in orientation (1 octave difference) the reduction in apparent “contrast” is stronger for the second-order condition. However, despite the slightly broader tuning for the second-order condition, the induction effect is bandpass for the two conditions. Selective adaptation experiments in humans show elevations in threshold for the identification of the direction of second-order test gratings that are selective to the spatial frequency and direction of motion of the second-order adaptation gratings (Nishida, Ledgeway, & Edwards, 1997). Under those testing conditions, the spatial frequency bandwidths of these motion sensitive mecha-

nisms were comparable for first and second-order information. However, it is important to note that there is no reason to believe that the bandwidths that we are measuring for spatial interactions between static stimuli are the same those measured for moving stimuli using an adaptation paradigm.

The data also suggest that first- and second-order mechanisms interact in an asymmetrical manner. For three of the four participants, the apparent “contrast” of a second-order target is reduced when flankers are first-order Gabors; however, there is no shift in the apparent “contrast” of a first-order target when it is flanked by second-order Gabors. No such asymmetry was found for HAA, who did not experience an induction effect when a second-order Gabor was flanked by first-order Gabors. One possible explanation for the difference in performance between HAA and the three other participants is that for the latter group the “contrast” or signal strength of the first- and second-order stimuli may not have been equated adequately. We assessed this possibility with two participants (DE and HAA) by scaling the visibility of the first- and second-order stimuli by setting them to equal steps of JND (Just Noticeable Difference or discrimination threshold) above their respective detection thresholds (Gurnsey, Sally, & Ball, 2002). We first measured detection thresholds and then discrimination thresholds by means of a temporal 2-AFC procedure and the method of constant stimuli. For detection, the participants were asked to indicate which of two intervals contained the stimulus (a single Gabor, with the same spatial parameters as previously indicated), and for discrimination the participants were asked to indicate in which interval the Gabor had the highest “contrast”. For each experimental run, five stimulus values (modulation depth of the single “comparison” Gabor) were pre-selected to span the observer’s psychometric function. Twenty-five trials were run for each test value and each observer completed three runs of 125 trials for each condition. Each stimulus was presented for 200 ms, separated by a 500 ms interval during which the screen returned to mean luminance. Five consecutive JNDs were measured, each taking as its starting point the result of the previous measurement.

For DE this method yielded scaled “contrasts” of 19% and 51% for the first- and second-order stimuli, respectively (compared to 34% and 60% yielded by the “contrast” matching method used initially). Even when tested with these new “contrasts” the asymmetry remains. For HAA this method yielded scaled “contrasts” of 19% and 52% for the first- and second-order stimuli, respectively (compared to 29% and 60% yielded by the “contrast” matching method used initially). When re-tested with these new contrasts, the results for HAA also remained the same. No “contrast” induction effect was found for either condition. Cannon and Fullenkamp

(1993) report several individual differences in the “contrast” induction effect with luminance modulated patterns. In their large group of participants ($n = 10$) less than one third experienced a reduction in apparent “contrast”, about one third experienced some enhancement and the remainder did not experience the “contrast” induction effect. Therefore, it is possible that individual differences explain the discrepancy between the results of HAA and those of the other three participants.

There are other examples of this type of asymmetry in the literature (e.g., Schofield & Georgeson, 1999). Humans experience nearly no elevations in threshold for the identification of the direction of first-order gratings after adapting to a second-order grating of the same spatial frequency, orientation, and direction of motion (Nishida et al., 1997). In contrast, albeit weak, adaptation to first-order motion raises thresholds for detecting second-order motion. This cross-over-adaptation is not selective to the direction of motion or the spatial frequency of the adaptation stimulus. Further, there is a strong shift in the apparent orientation of a second-order grating surrounded by a first-order grating, but no such induction is found when a first-order grating is surrounded by a second-order grating (Smith, Clifford, & Wenderoth, 2001). These findings are relevant to ours given that such orientation induction effects are typically explained by inhibitory lateral interactions among orientation selective neurons (Blackmore, Carpenter, & Georgeson, 1970; Smith et al., 2001).

In summary, these findings support the hypothesis that the visual system processes first- and second-order information separately. The findings from several studies support the view that there are parallel processing streams: one for first-order and the other for second-order (Baker, 1999; Chubb & Sperling, 1988, 1989; Wilson et al., 1992). In the second-order stream, a non-linear processing stage (e.g., full-wave, half-wave rectification, or squaring) is sandwiched between two stages of linear filtering, the second one at a lower scale than the first. Our data, which are consistent with this general two-stream model also suggest that there are important differences in the network of lateral interactions underlying first- and second-order mechanisms. It is important to note that it could be argued that the second-order information contained in the 2-D Gaussian could influence our pattern of results. However, this is unlikely because there is no induction effect when a first-order target is flanked by second-order Gabors. Under this condition, the Gaussian component is the same for both types of stimuli, yet there is no shift in the apparent contrast of the target. Moreover, because the spatial variation in contrast caused by the envelope is the same for the first- and second-order stimuli, if the envelope played a role in the induction, the results would not

show the first-order versus second-order asymmetry. Finally, any other contrast variations that are not confined to the spatial scale or the orientation of the sinusoidal modulation are also unlikely to influence the overall pattern of results given that we find spatial and orientation tuning, and that, for both the first- and second-order conditions.

It could also be argued that the “contrast” induction effect that we find with the second-order stimuli has a first-order explanation. One such explanation could be that these lateral interactions are elicited only by the first-order component (i.e., the 2-D noise) in the flankers and that the origin of the lateral inhibitory signal is before the non-linearity (represented by C in Fig. 1). However, this explanation is unlikely because the induction effect decreases by more than half when the 1-D contrast modulation in the second-order flankers is orientated perpendicularly to that of the target. Further, there is no induction effect when only the unmodulated carrier flanks the second-order target (data not displayed). Together, our manipulations of envelope spatial frequency and orientation suggest that the inhibitory interactions underlying second-order mechanisms must take place at or after the second-stage of filtering in the filter–rectify–filter scheme (represented by A in Fig. 1).

Contextual interactions like the ones measured in the present study are typically modeled by a divisive gain control represented by the weighted contribution from surround inhibitory signals (Albrecht & Geisler, 1991; Cannon & Fullenkamp, 1996; Ellemberg et al., 1998; Foley, 1994; Heeger, 1992; Snowden & Hammett, 1998). Using a direction discrimination paradigm, the findings of Lu and Sperling (1996) suggest that the gain control mechanisms for first-order and second-order motion processing operate according to different sets of rules (but see Graham & Sutter, 2000). Our results also suggest that the divisive gain control is weighted differently for second-order and first-order information. For second-order information the pooled responses operate over smaller lateral distances and a larger range of spatial frequencies and orientations.

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