

Pulling the other one: 1st- and 2nd-order visual information interact to determine perceived location

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Abstract

We demonstrate that the 1st- and 2nd-order characteristics of a visual stimulus can have a profound influence on each other in terms of perceived position. We use the parameter of spatial separation to selectively manipulate the effect of one characteristic upon the other. 1st-order features have their largest effect upon the perceived position of 2nd-order structure when separation is small, whilst the reciprocal effect is maximal at large separations. Implications for models of 1st- and 2nd-order interaction are discussed. © 2003 Elsevier Ltd. All rights reserved.

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1. Introduction

It has long been known that the human visual system utilises variations in the luminance profile of objects to make decisions concerning their orientation, position, depth and motion within the visual environment. We also possess the ability to make similar judgements about objects which are defined by variations in contrast or texture relative to their surroundings. The ecological advantages of this additional processing stream are clear (Derrington, 2001), and considerable advances have been made in understanding the physiology (Mareschal & Baker, 1998; Shapley, 1994; Spitzer & Hochstein, 1985; von der Heydt & Peterhans, 1989; Zhou & Baker, 1994, 1996) and psychology of this capacity (Arsenault, Wilkinson, & Kingdom, 1999; Badcock & Derrington, 1985; Chubb & Sperling, 1988; Dakin & Mareschal, 2000; Dakin, Williams, & Hess, 1999; Edwards & Badcock, 1995; Ledgeway & Smith, 1994; Lin & Wilson, 1996; McGraw, Levi, & Whitaker, 1999; Wenderoth, Clifford, & Ma Wyatt, 2001; Zeigler & Hess, 1999). What remains unclear is the extent to which luminance-defined (often referred to as 1st-order) and contrast-defined (2nd-

order) visual processing mechanisms interact. For example, does the nature of the 2nd-order percept depend upon the characteristics of its 1st-order input? Similarly, might a 1st-order percept be subsequently influenced by the output of the 2nd-order system into which it feeds?

There is compelling evidence to suggest that the *precision* with which well-separated 2nd-order stimuli can be localised in space is independent of the orientation, spatial frequency or colour of the 1st-order texture which defines it (Burbeck, 1987, 1988; Kooi, De Valois, & Switkes, 1991; Toet & Koenderink, 1988). This would seem to be an attractive property of the visual system—in that objects can be located with the same precision irrespective of the type of visual information which defines them. However, despite these observations of precision, there exist some convincing illusory effects which suggest that the 2nd-order percept is far from independent of its 1st-order input, and vice versa (Dakin et al., 1999; McOwan & Johnston, 1996; Morgan & Baldassi, 1997; Morgan, Mason, & Baldassi, 2000; Skillen, Whitaker, Popple, & McGraw, 2002). The Fraser twisted cord illusion is an example of a 2nd-order object whose orientation is biased by the orientation of the 1st-order structure defining the cord (Fraser, 1908). In the motion domain, the perceived position of an object can be markedly biased in the direction of motion of the texture within the object (De

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Valois & De Valois, 1991). Similarly, judgements of 1st-order characteristics such as orientation have been shown to be biased by the orientation of the 2nd-order window in which they are contained (Dakin et al., 1999; Morgan et al., 2000).

Observations such as these confirm that 1st- and 2nd-order percepts are far from independent of each other, but beg the question of how such interactions occur, and what function, if any, they may serve. One viewpoint is that the interaction effects occur at an early stage of visual processing (Dakin et al., 1999). For example, changes in the relative orientation of 1st- and 2nd-order structure produce predictable changes in the spatial frequency and orientation bandwidth of the 1st-order structure. It has been suggested that linear spatial channel-based filter models (Wilson, 1986) account well for the effects of 2nd-order structure upon 1st-order percepts, although the failure of such models to account for reciprocal effects is a matter for concern (Dakin et al., 1999). A very different view is that interactions between the two processing streams occur at a relatively late stage of visual processing. Both 1st- and 2nd-order signals are available to higher levels of processing, and interaction may take place at this level (Morgan et al., 2000; Skillen et al., 2002). However, the process of extracting a veridical 1st- and 2nd-order signal only to allow them to interact at a later stage has been questioned on the grounds of plausibility (Dakin et al., 1999).

The inter-dependence of the physical 1st- and 2nd-order characteristics of the orientation-defined stimuli used in many previous studies can be avoided using a different type of stimulus (Fig. 1). Three elements (Gabor patches) are presented one above the other, and the observer is required to judge the horizontal location of features of the central element relative to the outer elements. Observers can be asked to make one of two types of judgement—either alignment of the luminance modulation within each patch or alignment of the entire contrast-defined patch (Akutsu & Levi, 1998; Whitaker, Bradley, Barrett, & McGraw, 2002). In the left-hand stimulus, the 2nd-order contrast modulation (the envelope) of the central patch has been offset leftwards whilst the 1st-order grating (the carrier) is in physical alignment. Despite this, most observers perceive an illusory leftwards shift of the carrier grating within the central element. In the right-hand figure, the contrast envelopes (2nd-order structure) of each element are aligned, whilst there is a horizontal offset (rightwards) of the carrier grating (1st-order structure) of the central element. Observers tend to perceive the entire central patch shifted rightwards in the direction of the 1st-order carrier offset. Importantly, this type of modification has no effect upon the spatial frequency or orientation bandwidth of the individual stimulus elements, and simply represents a change in the relative

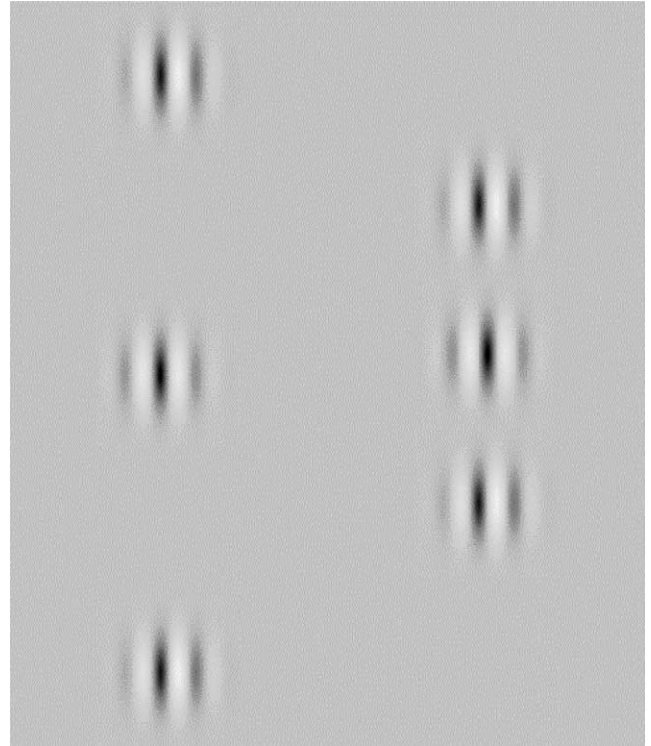


Fig. 1. Two examples of the alignment tasks used in the study. Three elements (Gabor patches) are presented one above the other, and the observer is required to judge the horizontal location of features of the central element relative to the outer elements. In the left-hand stimulus, the 2nd-order contrast modulation (the envelope) of the central patch has been offset leftwards whilst the 1st-order grating (the carrier) is in physical alignment. Despite this, most observers perceive an illusory leftwards shift of the carrier grating within the central element. In the right-hand figure, the contrast envelopes (2nd-order structure) of each element are aligned, whilst there is a horizontal offset (rightwards) of the carrier grating (1st-order structure) of the central element. Observers tend to perceive the entire central patch shifted rightwards in the direction of the 1st-order carrier offset. The two examples represent the largest (left) and smallest (right) inter-element separation used.

phase of the carrier and its contrast envelope. Furthermore, this type of stimulus arrangement allows us to vary the relative salience of the 1st- and 2nd-order cues to spatial offset independently. Changes in the vertical separation of the three elements are known to have differential effects depending upon the spatial scale of analysis. Large separations (such as the left-hand stimulus in Fig. 1) selectively affect offset judgements for high frequency stimuli (Whitaker & MacVeigh, 1991; Whitaker et al., 2002). This will preferentially affect the ability of observers to judge the relatively high frequency, band-pass carrier information in comparison to the lower-frequency, low-pass envelope spectral characteristics. We therefore systematically examine the ability of observers to make 1st-order judgements of carrier alignment in the presence of 2nd-order offsets, and vice versa, across a range of inter-element separations.

2. Methods

2.1. Stimuli

All stimuli consisted of three vertically separated Gabor patches. The outer two elements were always identical in sine carrier phase, and were in perfect vertical alignment. The mathematical representation of each outer element was therefore

$$\text{Luminance} = L + \left(\exp \frac{-(x^2 + y^2)}{2\sigma^2} \times LC \sin(2\pi fx) \right)$$

where x and y are the respective horizontal and vertical distances from the centre of the stimulus ensemble. Mean luminance, L was 30 cd m^{-2} and stimulus contrast, C was 1. Spatial frequency, f , of the carrier grating was 1.5 c deg^{-2} and the standard deviation of the Gaussian envelope (σ) was 0.44° . The separation between the central element and each of the outer elements was varied between 2.65° and 5.3° .

Stimuli were presented for 500 ms on a 20-in. Electron d2 monitor. The non-linear luminance response of the display was linearised by using the inverse function of the luminance response as measured using a Minolta CS-100 photometer. The host computer was a Starmax 4000/200. The contrast resolution of the monitor was increased to 12-bit using a video summation device constructed according to Pelli and Zhang (1991). All stimuli were generated using the macro capabilities of the public domain software NIH image™ 1.61 (developed by the US National Institutes of Health and available from the Internet by anonymous FTP from zippy.nimh.nih.gov).

2.2. Procedures

Subjects were required to make a horizontal positional judgement of the central element relative to the outer elements. No feedback was provided. During any experimental run, subjects were asked to make one of two judgements.

2.2.1. Carrier alignment judgement

Subjects were required to judge the horizontal position of the carrier of the central element relative to the carrier within the outer reference elements. The envelope of this central element could be offset relative to the midpoint (sine phase) of the carrier with one of seven possible offset values, equally spaced around alignment. The central element was defined as

$$\text{Luminance} = L + \left(- \exp \frac{-((x + (k\delta x))^2 s + y^2)}{2\sigma^2} \right) \times LC \sin(2\pi fx)$$

where $k = -3, -2, -1, 0, 1, 2$ or 3 and $\delta x = 1.317'$.

On any given trial, any one of these seven *envelope offsets* could be presented. Alignment thresholds and PSEs for the *carrier judgements* were established using a forced-choice methodology in which the central element could be presented in one of seven possible horizontal positions (x) relative to the outer elements. The central patch was displaced rigidly, with an equal displacement of carrier and envelope. A total of 30 responses were collected for each of these positions. The resulting psychometric functions were analysed using logistic regression.

2.2.2. Envelope alignment judgement

Subjects were required to judge the horizontal position of the envelope of the central element relative to the envelope of the outer reference elements. The carrier of the central element could be offset relative to the carrier of the outer elements with one of 12 possible offset values spanning one complete cycle of the carrier grating. The mathematical description of the central element was defined as:

$$\text{Luminance} = L + \left(- \exp \frac{-(x^2 + y^2)}{2\sigma^2} \times LC \sin(2\pi fx + k\delta\phi) \right)$$

where $k = -6, -5, -4, -3, -2, -1, 0, 1, 2, 3, 4$ or 5 and $\delta\phi = \pi/6$ (30° of phase angle).

On any given trial, any one of these 12 carrier offsets could be presented. Alignment thresholds and PSEs for the envelope judgements were established using a forced-choice methodology in which the central element could be presented in one of seven horizontal positions (x) relative to the outer elements. Again, a rigid displacement of the entire central patch was used. A total of 30 responses were collected for each of these positions. The resulting psychometric functions were analysed using logistic regression.

2.3. Subjects

Three of the authors acted as observers (DW, PVM, DK). All had normal or corrected-to-normal visual acuity. Viewing was binocular, and carried out in a dimly lit room.

3. Results

3.1. Carrier alignment judgement

Psychometric functions were obtained for the judgement of carrier position at each of several envelope offsets relative to the centre of the carrier grating ($3.951'$ leftwards to $3.951'$ rightwards). Subjects were instructed to ignore the envelope information when

making judgements about the position of the carrier. If the offset of the envelope relative to the carrier had no effect, psychometric functions would coincide. This was not the case. The conditions in which the envelopes were offset leftwards produced fewer ‘rightwards’ responses than conditions in which the envelopes were offset rightwards. In other words, the displacement of the envelope relative to the carrier resulted in a perceived offset of the carrier in the direction of the envelope. This effect was quantified by establishing the PSE of each psychometric function—the offset of the central Gabor patch which resulted in a 50% response level. Results are shown in Fig. 2. In order to negate the effect of a rightwards offset of the envelope (positive value on the abscissa), the entire patch has to be displaced leftwards (negative value on the ordinate) in order to maintain perceptual alignment of the central carrier relative to the carrier in the outer reference patches. The Gabor patch offset required to maintain alignment changes approximately linearly as a function of the envelope offset from the centre of the carrier grating. For each observer, the gradient of the relationship (which reflects the magnitude of the illusory effect) is shallowest for the smallest patch separation but increases consistently as separation is increased. Note, however, that although the trend is consistent across observers, the absolute magnitude of the illusory effect varies (note the difference in range of the ordinate across observers).

Despite the considerable biases induced by the envelope offset, the precision of the carrier judgements (i.e. thresholds) showed no dependence upon envelope location. For this reason, we averaged the thresholds of each observer across envelope conditions, and plot the data in Fig. 3. Thresholds are, however, very much dependent upon the separation of the Gabor patches, rising sharply with increasing separation. This is a characteristic of positional judgements using narrow-band stimuli (Whitaker & MacVeigh, 1991; Whitaker et al., 2002).

3.2. Envelope alignment judgement

Psychometric functions for judgement of envelope offset were made for each of the 12 carrier phases, specified in relation to the peak of the envelope. Subjects were instructed to disregard carrier information and made judgements only on the relative position of the envelopes. The resulting data were analysed to reveal the physical offset of the Gabor patch required to maintain perceived alignment of the envelopes. Data are shown in Fig. 4 which plots Gabor patch offset as a function of carrier phase. If the carrier phase had no effect upon the perceived position of the envelope, these functions would be flat. Instead, patch offset shows a systematic variation as a function of carrier phase. Data are fitted

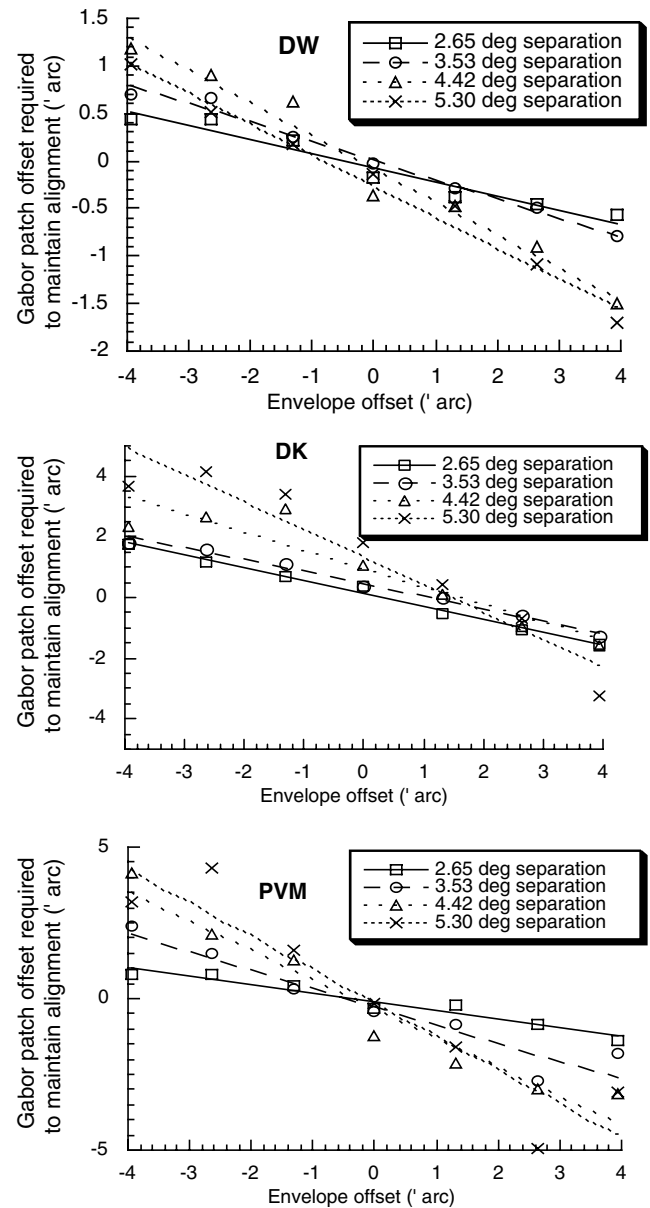


Fig. 2. PSEs for carrier alignment plotted against the envelope offset of the central element. For both abscissa and ordinate, positive values represent rightward offsets and vice versa. Envelope offsets require an offset of the carrier in the opposite direction in order to maintain perceptual alignment. The effect is approximately linear, but becomes more marked at larger inter-element separations. Note, however, the different y-axis scale for each observer.

with a sinusoidal function in which the deviation from baseline offset is given by

$$(A/2) \sin(\phi)$$

where A is the full amplitude of the deviation and ϕ is the phase of the sinusoidal function. Values for each of these parameters is shown in Table 1. For all subjects, the largest effect on perceived patch position is obtained

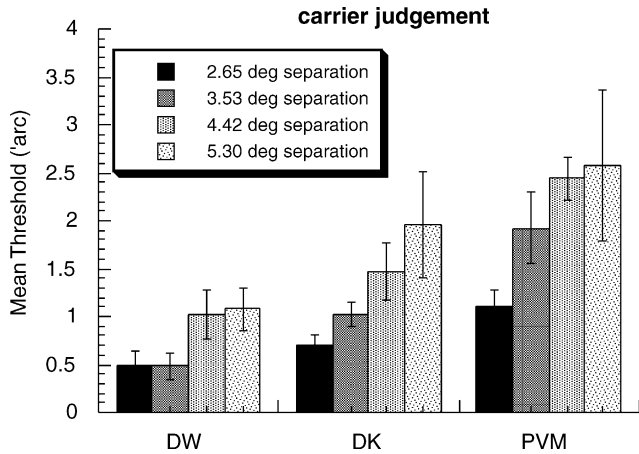


Fig. 3. For each observer, *thresholds* for carrier judgement increase as a function of inter-element separation. Data represent the mean threshold, averaged across the seven envelope offset conditions. Standard deviations are shown.

for the smallest patch separation. In addition, for this separation the points of inflection of the data sets are close to zero phase angle. As the phase of the carrier is shifted leftwards within the envelope (negative phase offsets), a rightwards shift (positive value) of the entire patch is required to maintain perceived alignment, and vice versa. In other words, changes in the position of the carrier pull the perceived location of the envelope in the same direction. The magnitude of this effect varies systematically in approximation to the sine of the carrier phase angle.

At larger separations, the phase of the carrier has a progressively lesser effect upon the perceived envelope position (Table 1). In addition, the phase angle of the point of inflection appears to increase for each observer, although it should be noted that this estimate becomes less reliable as separation increases (and hence the amplitudes of the functions decrease).

Thresholds for envelope judgements demonstrated no dependence on carrier phase offset. Therefore, we again averaged thresholds across this parameter and the data are shown in Fig. 5. Note the absence of an increase in thresholds as a function of separation, consistent with the fact that Gabor envelope and Gaussian blob alignment thresholds remain independent of separation until inter-element separation exceeds approximately 15σ (Hess & Hayes, 1993; Toet, van Eekhout, Simons, & Koenderink, 1987; Whitaker et al., 2002). The largest separation used in the present study was 13.25σ . The independence of envelope alignment thresholds and separation reflects the fact that the Gaussian envelope of the Gabor patch is low-pass, and therefore tolerant to the effects of separation (Whitaker et al., 2002).

In summary, the influence of envelope offset on judgements of carrier alignment is greatest at large ele-

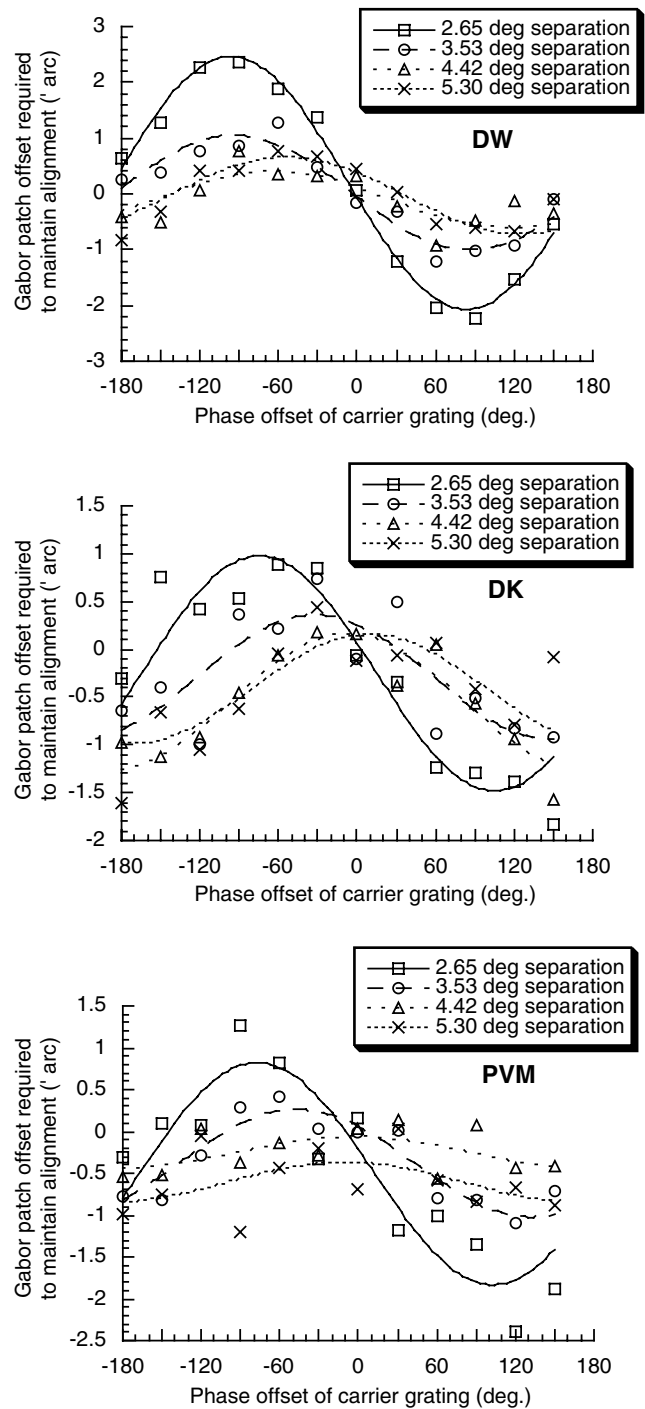


Fig. 4. PSEs for envelope alignment plotted against the phase offset of the carrier grating within the central element. Zero phase offset represents sine phase (identical to the flanking elements), negative offsets are leftwards and vice versa. Clearly, envelope offsets in the opposite direction to the carrier offset are required to maintain perceived envelope alignment. The magnitude of the effect is well described by the sine of the carrier phase, and is greatest at small inter-element separations. Note, however, the different y-axis scale for each observer.

ment separations, whilst carrier offsets exert their greatest influence on envelope judgements when the element separation is small.

Table 1
Parameters from the least squares curve fit to the data of Fig. 5

	Separation (deg)	Amplitude (arc min)	ϕ (deg, phase angle)	R
DW	2.65	4.53	-6.4	0.99
	3.53	2.06	-4.1	0.96
	4.42	1.01	25.6	0.78
	5.30	1.37	36.8	0.90
DK	2.65	2.46	15.2	0.93
	3.53	1.30	58.0	0.79
	4.42	1.42	82.7	0.93
	5.30	1.14	99.8	0.75
PVM	2.65	2.66	12.7	0.90
	3.53	1.29	43.0	0.93
	4.42	0.38	86.1	0.53
	5.30	0.48	80.2	0.46

See text for further details.

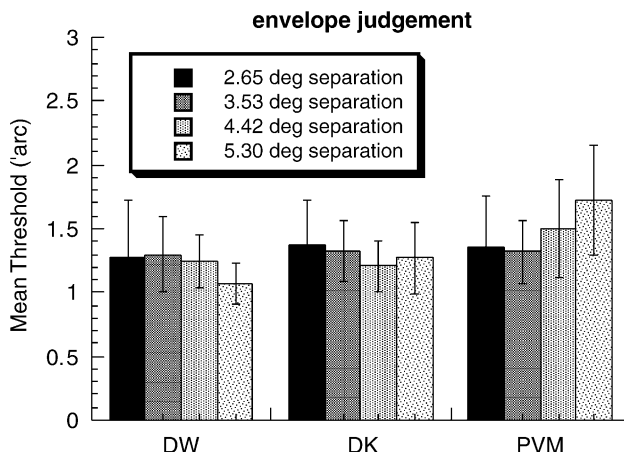


Fig. 5. For each observer, *thresholds* for envelope judgement remain relatively constant as a function of inter-element separation, indicating that factors other than separation represent the limiting factors in envelope positional judgement precision. Data represent mean thresholds, averaged across the 12 carrier phase offset conditions. Standard deviations are shown.

4. Discussion

The present results indicate that the perceived location of the 1st-order structure of a stimulus can be markedly affected by the position of its 2nd-order envelope. Similarly, the perceived position of the 2nd-order envelope is systematically affected by phase variations of its 1st-order content. Such results mirror the findings of Dakin et al. (1999) who found reciprocal interactions between 1st- and 2nd-order structure in the orientation domain. It is important to point out, however, that whereas variations in the orientation of a carrier grating within a 2nd-order envelope result in changes to the spectral bandwidth of the stimuli, the phase changes which we have used produce no change in the spatial frequency or orientation bandwidth of the individual Gabor patches. Thus, the misperceptions we report represent unequivocal evidence that the signals

corresponding to 1st- and 2nd-order spatial structure can influence each other at some stage prior to the decision stage at which spatial position is established.

The stimuli which we have employed provide a useful way to investigate these interactions, since the manipulation of element separation allows the salience of one component (1st-order structure) to be varied relative to the other (2nd-order structure). Our results confirm the importance of the relative salience of 1st- and 2nd-order information in determining the ultimate percept. In our first experiment, carrier judgements were made whilst envelope information was systematically varied. It was at large separations, where carrier salience is relatively compromised, that the largest effect of 2nd-order structure on the perceived location of 1st-order structure was found. Conversely, in the second experiment, the smallest separation produced the greatest effect of carrier phase upon 2nd-order envelope judgements, indicative of the fact that it is in this region where carrier salience is at its highest level. A quantitative demonstration of these statements can be made if we plot the amplitude of the interaction effects shown in Figs. 2 and 4 against thresholds for carrier judgements taken from Fig. 3. As carrier thresholds increase (Fig. 6), the influence of the carrier upon envelope judgements degrades (filled symbols) whilst the effect of the envelope upon the carrier becomes more pronounced (open symbols).

Our findings clearly point to a relatively late-stage interaction between 1st- and 2nd-order information. The results cannot be explained by induced changes in the spectral characteristics of the stimulus elements, nor could an early interaction at the level of the individual stimulus elements explain the strong effects of stimulus separation. The picture which emerges is of a final percept which is a late-stage combination of 1st- and 2nd-order information, weighted according to the relative reliability of each component, which itself depends critically upon stimulus configuration.

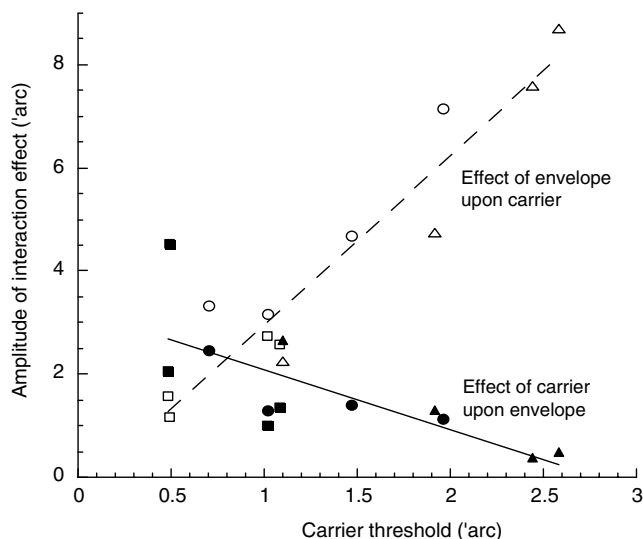


Fig. 6. Amplitude of the interaction effects between carrier and envelope as a function of the carrier threshold. Different symbols represent different observers: subject DW (squares), DK (circles) and PVM (triangles). Open symbols are data from Fig. 2 and represent the effect of envelope misalignment upon carrier judgement. Filled symbols are data from Fig. 4 and represent the effect of carrier offset upon envelope judgement.

Keeble and Hess (1998) also used a stimulus arrangement in which the horizontal location of a central Gabor patch was judged relative to two outer patches. In the stimulus condition most relevant to the present study, they examined a situation in which the carriers of the outer two patches were oblique (both pointing either leftwards or rightwards of the central element). The PSE for alignment of the central patch was biased significantly in the direction of the imaginary contour formed by the outer patches. Keeble and Hess (1998) also examined alignment thresholds in a condition in which all carriers were vertical, but the phase of the central patch was randomised. The prediction based upon the present results (Fig. 4) would be that the perceived position of the central patch would vary from trial to trial due to the randomised phase of the central element, therefore leading to elevated thresholds. However, this was not the case. The reason for this may be the moderately large separation which they used (6λ). As Fig. 4 clearly shows, the effect of carrier phase upon the position of the envelope falls off rapidly with increasing separation. It might be revealing to examine the randomised phase condition of Keeble and Hess (1998) at a smaller separation.

Our findings show that the perceived location of an object can be biased by positional information provided by the internal structure of the object, and vice versa. Moreover, these interaction effects are critically dependent upon separation between the object and its surroundings against which the judgement of relative position is made. The importance of separation is also

evident in the findings of Akutsu, McGraw, and Levi (1999) who measured alignment biases for Gabor patches which had carrier gratings in alignment, yet had envelopes which were made asymmetric, ie skewed leftwards or rightwards. At large separations (where our data suggest that the carrier will have little effect upon positional judgements), alignment biases were consistent with the use of the centroid of the skewed envelope (Whitaker, McGraw, Pacey, & Barrett, 1996), despite a consequent misalignment of the carrier grating. This was not the case at small separations, where biases deviated from that based upon the centroid of the envelope and shifted towards an alignment position based upon the carrier gratings.

For both carrier and envelope judgements, our positional thresholds were independent of the strong biases induced by the stimulus arrangement. Such independence is well established in the literature of geometrical illusions (Morgan, Hole, & Glennerster, 1990). However, recent studies of 1st- and 2nd-order interactions in the orientation domain (Dakin et al., 1999; Skillen et al., 2002) have found elevated orientation thresholds in the region where 1st- and 2nd-order cues conflict (although see the data of Morgan et al. (2000) for a counter-view). Skillen et al. (2002) suggest that these elevated thresholds may reflect trial-to-trial variations in the relative salience of 1st- and 2nd-order signals, leading to elevated thresholds. It is not clear why such discrepancies exist within the orientation domain, nor why they do not occur in the positional judgements of the present experiment, which show no such threshold elevation under conflicting cue conditions. It may be that, where one stimulus parameter represents a clear limiting factor to performance (separation in terms of carrier judgement and envelope size in terms of envelope judgements) these dominant factors mask any variance associated with cue combination.

It is important to highlight that the interaction between 1st- and 2nd-order cues within a stimulus configuration such as the one we have used is unavoidable. We asked observers to make judgements about a specific stimulus characteristic, yet it was evidently impossible to selectively ignore other characteristics. The effects therefore reflect non-volitional, automatic combinatorial processes within the human visual system. Beyond V2 (where the 2nd-order signal is thought to become explicit within the filter \rightarrow rectify \rightarrow filter pathway (Mareschal & Baker, 1998)), both the 1st- and 2nd-order signals are available to contribute to any decision making process. In terms of judgements of position at least, it appears that neither signal can be consciously ignored. The real world consequences are that, when we want to localise a specific part of an object, it seems that we are influenced by the object as a whole. Similarly, when we want to specify the whole object, we are susceptible to variations in the internal content (texture) of

the object. Clearly, neither of these interactions between local and global characteristics represents a particularly attractive property of a sensory system. Nevertheless, the binding process enabled through the assimilation of various sources of information must offer advantages which far outweigh the side-effects to which we commonly assign the term ‘visual illusions’. It may be increasingly profitable to consider the vast array of geometric visual illusions in terms of 1st- and 2nd-order cue combination of the type reported here.

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References

- Akutsu, H., & Levi, D. M. (1998). Selective attention to specific location cues: the peak and center of a patch are equally accessible as location cues. *Perception*, 27, 1015–1023.
- Akutsu, H., McGraw, P. V., & Levi, D. M. (1999). Alignment of separated patches: multiple location tags. *Vision Research*, 39, 789–801.
- Arsenault, A. S., Wilkinson, F., & Kingdom, F. A. A. (1999). Modulation frequency and orientation tuning of second-order texture mechanisms. *Journal of Optical Society of America A*, 16, 427–435.
- Badcock, D. R., & Derrington, A. M. (1985). Detecting the displacement of periodic patterns. *Vision Research*, 25, 1253–1258.
- Burbeck, C. A. (1987). Position and spatial-frequency in large-scale localization judgements. *Vision Research*, 27, 417–427.
- Burbeck, C. A. (1988). Large-scale relative localization across spatial frequency channels. *Vision Research*, 28, 857–859.
- Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli—a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, 5, 1986–2007.
- Dakin, S. C., & Mareschal, I. (2000). Sensitivity to amplitude modulation depends on carrier spatial frequency and orientation. *Vision Research*, 40, 311–329.
- Dakin, S. C., Williams, C. B., & Hess, R. F. (1999). The interaction of first- and second-order cues to orientation. *Vision Research*, 39, 2867–2884.
- Derrington, A. (2001). Second-order visual processing. *Optics & Photonics News* (January), 18–20.
- De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research*, 31, 1627–1631.
- Edwards, M., & Badcock, D. R. (1995). Global motion perception—no interaction between first and second order motion pathways. *Vision Research*, 35, 2589–2602.
- Fraser, J. (1908). A new illusion of visual direction. *British Journal of Psychology*, 2, 307–320.
- Hess, R. F., & Hayes, A. (1993). Neural recruitment explains “Weber’s law” of spatial position. *Vision Research*, 33, 1673–1684.
- Keeble, D. R. T., & Hess, R. F. (1998). Orientation masks 3-Gabor alignment performance. *Vision Research*, 38, 827–840.
- Kooi, F. L., De Valois, R. L., & Switkes, E. (1991). Spatial localization across channels. *Vision Research*, 31, 1627–1631.
- Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion detection mechanisms for first- and second-order motion in human vision. *Vision Research*, 34, 2727–2740.
- Lin, L. M., & Wilson, H. R. (1996). Fourier and non-Fourier pattern discrimination compared. *Vision Research*, 36, 1907–1918.
- Mareschal, I., & Baker, C. L. (1998). A cortical locus for the processing of contrast-defined contours. *Nature Neuroscience*, 1, 150–154.
- McGraw, P. V., Levi, D. M., & Whitaker, D. (1999). Spatial characteristics of the second-order visual pathway revealed by positional adaptation. *Nature Neuroscience*, 2, 479–484.
- McOwan, P. W., & Johnston, A. (1996). A second-order pattern reveals separate strategies for encoding orientation in two-dimensional space and space-time. *Vision Research*, 36, 425–430.
- Morgan, M. J., & Baldassi, S. (1997). How the visual system encodes the orientation of a texture and why it makes mistakes. *Current Biology*, 7, 999–1002.
- Morgan, M. J., Hole, G. J., & Glennerster, A. (1990). Biases and sensitivities in geometrical illusions. *Vision Research*, 30, 1793–1810.
- Morgan, M. J., Mason, A. J. S., & Baldassi, S. (2000). Are there separate first-order and second-order mechanisms for orientation discrimination? *Vision Research*, 40, 1751–1763.
- Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on micro-computer displays. *Vision Research*, 31, 1337–1350.
- Shapley, R. M. (1994). Linearity and non-linearity in cortical receptive fields. *CIBA Foundation symposium, higher-order processing in the visual system* (Vol. 184, pp. 71–81). Chichester: Wiley.
- Skillen, J., Whitaker, D., Popple, A. V., & McGraw, P. V. (2002). The importance of spatial scale in determining illusions of orientation. *Vision Research*, 42, 2447–2455.
- Spitzer, H., & Hochstein, L. I. (1985). Simple-cell and complex-cell response dependencies on stimulation parameters. *Journal of Neurophysiology*, 53, 1244–1265.
- Toet, A., & Koenderink, J. J. (1988). Differential spatial discrimination thresholds for Gabor patches. *Vision Research*, 28, 133–143.
- Toet, A., van Eekhout, M. P., Simons, H. L. J. J., & Koenderink, J. J. (1987). Scale invariant features of differential spatial displacement discrimination. *Vision Research*, 27, 441–451.
- von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. 1. Lines of pattern discontinuity. *Journal of Neuroscience*, 9, 1731–1748.
- Wenderoth, P., Clifford, C. W. G., & Ma Wyatt, A. (2001). Hierarchy of interactions in the processing of contrast-defined contours. *Journal of Optical Society of America A*, 18, 2190–2196.
- Whitaker, D., Bradley, A., Barrett, B. T., & McGraw, P. V. (2002). Isolation of stimulus characteristics contributing to Weber’s law for position. *Vision Research*, 42, 1137–1148.
- Whitaker, D., & MacVeigh, D. (1991). Interaction of spatial frequency and separation in Vernier acuity. *Vision Research*, 31, 1205–1212.
- Whitaker, D., McGraw, P. V., Pacey, I., & Barrett, B. T. (1996). Centroid analysis predicts visual localization of first- and second-order stimuli. *Vision Research*, 36, 2957–2970.
- Wilson, H. R. (1986). Responses of spatial mechanisms can explain Vernier acuity. *Vision Research*, 26, 453–469.
- Zeigler, L. R., & Hess, R. F. (1999). Stereoscopic depth but not shape perception from second order stimuli. *Vision Research*, 39, 1491–1507.
- Zhou, Y. X., & Baker, C. L. (1994). Envelope-responsive neurons in area 17 and area 18 of cat. *Journal of Neurophysiology*, 72, 2134–2150.
- Zhou, Y. X., & Baker, C. L. (1996). Spatial properties of envelope responsive cells in area 17 and 18 neurons of the cat. *Journal of Neurophysiology*, 75, 1038–1050.