
Spatial coherence does not affect contrast discrimination for multiple Gabor stimuli

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Abstract. Gestalt grouping rules imply a process or mechanism for grouping together local features of an object into a perceptual whole. Several psychophysical experiments have been interpreted as evidence for constrained interactions between nearby spatial filter elements and this has led to the hypothesis that element linking might be mediated by these interactions. A common tacit assumption is that these interactions result in response modulation which disturbs a local contrast code. We addressed this possibility by performing contrast discrimination experiments using two-dimensional arrays of multiple Gabor patches arranged either (i) vertically, (ii) in circles (coherent conditions), or (iii) randomly (incoherent condition), as well as for a single Gabor patch. In each condition, contrast increments were applied to either the entire test stimulus (experiment 1) or a single patch whose position was cued (experiment 2). In experiment 3, the texture stimuli were reduced to a single contour by displaying only the central vertical strip. Performance was better for the multiple-patch conditions than for the single-patch condition, but whether the multiple-patch stimulus was coherent or not had no systematic effect on the results in any of the experiments. We conclude that constrained local interactions do not interfere with a local contrast code for our suprathreshold stimuli, suggesting that, in general, this is not the way in which element linking is achieved. The possibility that interactions are involved in enhancing the detectability of contour elements at threshold remains unchallenged by our experiments.

1 Introduction

One well-established feature of early vision is that it contains a set of spatially tuned filter elements that sample the four dimensions of the spatial and Fourier domains (eg Campbell and Robson 1968; Watson 1983, 2000; Wilson et al 1983; Meese and Williams 2000). With this arrangement, each filter element responds only to local regions within the four-dimensional space—a specific band of spatial frequencies and orientations in a specific region within the visual field. Visual stimuli, on the other hand, tend to be continuous in one or more dimensions. For example, image contours tend to be both broad-band and spatially extended, producing continuous activity across groups of filter elements with different preferred spatial frequencies and different receptive field locations. The Gestalt grouping rules of similarity, proximity, good continuation, smoothness, common fate, and closure imply the need for processes or mechanisms for linking spatial filter elements that respond to common spatial structure (Field et al 1993; Kovács and Julesz 1993; Meese 1999; Polat 1999; Geisler et al 2001; also see Westheimer 1999), and contemporary studies have attempted to reveal some of their details. For example, Verghese and Stone (1996, 1997) found that speed discrimination thresholds depended on stimulus manipulations that were thought to promote linking of stimulus regions into a single object or segment them into multiple objects. In the spatial domain, Field et al (1993) created snake-like paths of oriented target elements (Gabor patches) placed in a background of randomly oriented distractors, and found that they could be detected only when elements were approximately

co-aligned and co-oriented, suggesting spatial constraints on the linking process, at least for contours.

In this paper, we examined both one-dimensional contours and two-dimensional textures that were manipulated in ways thought to promote or hinder linking, and we use the general term 'element linking' to refer to this (see section 2 and figure 1). The method by which element linking might be achieved remains unclear, though one possibility is that interactions between appropriate filter elements could be an important part of the process. This idea has received some attention, usually with the assumption that the interactions occur between the same filter elements that are responsible for coding stimulus contrast (Kovács and Julesz 1993; Stemmler et al 1995; Polat 1999). If this is so, then the properties of contrast interactions might be revealed by measuring contrast detection and contrast increment thresholds of appropriately arranged stimulus elements. Bonnef and Sagi (1998) reported results of summation to threshold experiments where oriented stimulus elements (Gabor patches) were assumed to maximally stimulate spatially non-overlapping filter elements. Modest summation was found for these stimuli and was strongest when the Gabor patches were spatially nearby and arranged to form curvilinear contours. The authors suggested that this improvement in performance might be due to the facilitatory interactions alluded to above. Saarinen and Levi (2001) performed an experiment in which observers had to detect the orientation of a C-like pattern of Gabor patches and found that performance was best when local orientations were tangent to the global contour. In other experiments, detection thresholds for a centrally placed Gabor patch have been measured in the presence of suprathreshold flanks (eg Polat and Sagi 1993, 1994; Williams and Hess 1998; Solomon et al 1999; Chen and Tyler 2001). Polat and Sagi (1993) found that, when the flanking Gabor patches were co-oriented with and close to the test, masking occurred, but that when they were sufficiently distant (about 3 wavelengths), detection of the test was enhanced. One possibility is that the enhancement is due to facilitatory interactions from the suprathreshold flanks (Polat and Sagi 1993, 1994). In rather different experiments, Kovács and Julesz (1993) reported a complex set of results for the detectability of contrast increments for Gabor-like patches placed either within, outside, or upon a closed contour which was itself positioned within an otherwise random two-dimensional array of distractor elements. They reported that the presence of the contour impeded contrast increment detection for elements placed upon the contour, but improved contrast increment detection for elements placed just either side of it or well within it. These results were taken to reflect the properties of sensory interactions of filter elements at an early stage of visual processing. In a rather different interpretation of the linking process, Verghese and Stone (1996, 1997) suggested that linking might be achieved by correlating neural activity, and that this might have been responsible for modulating performance in their speed discrimination tasks.

1.1 *Hypotheses and aims*

To clarify our aims, we describe, in general terms, four different hypotheses concerning the methods by which element linking might be achieved. First, local interactions between filter elements could cause suppression or enhancement of local representations of contrast (H_1). Second, local interactions could cause correlation of noise amongst filter elements that are involved in contrast coding (H_2). Third, local interactions might be involved in element linking but be apparent only for certain spatial configurations, spatial frequencies, contrasts, and experimental paradigms. Reasonable but not exclusive interpretations of this situation would be that measurable contrast effects occur only as a side-effect of element linking, or that they are only a threshold phenomenon (H_3). Fourth, contrast disturbing interactions might have nothing to do with element linking (H_0). Collectively, we refer to the first two hypotheses as those

which suppose that linking is generally achieved by contrast-disturbing interactions and the second two as those which do not.

The aim of the present paper is to address these possibilities for both general-purpose element linking and more specific contour-linking. Although it is not possible to devise an experiment to determine between H_3 and H_0 , we were able to address H_1 and H_2 . In H_1 , we assumed that the disturbance of contrast representation is equivalent to the effects of changing pedestal contrast (Legge and Foley 1980). In H_2 , we reasoned that correlated noise would result in the absence of probability summation (Legge and Foley 1980; Verghese and Stone 1996, 1997). We supposed that, if vision worked in either of these ways, it should be possible to tap the linking process differentially by performing contrast discrimination for two-dimensional arrays of coherently and incoherently arranged stimulus elements (Gabor patches). In coherent stimuli, elements were co-aligned and co-oriented (eg figure 1a) or, more generally, carried meaningful global structure (figures 1a and 1b). In incoherent stimuli, elements were randomly oriented (figure 1c). We assumed that only the coherent stimuli would be involved in the linking process. Whether psychophysical performance (contrast discrimination threshold) is expected to be better or worse for the coherent stimuli depends upon model details and is considered further in section 3. For now, the important point is that all models in which the perceptual coherence of visual stimuli is achieved through local contrast-disturbing interactions (ie H_1 and H_2) make the same prediction: that there should be a difference in the results for the coherent and incoherent stimuli.⁽¹⁾ We find, however, that, for the stimuli we used, coherence had no impact on contrast discrimination thresholds. This null-result is inconsistent with H_1 and H_2 . H_3 and H_0 both remain possibilities.

2 General methods

2.1 Equipment

Stimuli were stored in the framestore of a VSG2/3 or VSG2/4 operating in pseudo-12 or pseudo-15 bit modes, respectively; and their presentation was controlled by a Pentium PC. Stimuli were displayed on a linearised monitor with mean luminance of approximately 69 cd m^{-2} and frame rate of 120 Hz. Contrast increments were applied to stimulus elements by a frame-interleaving technique which reduced the picture rate to 60 Hz. Michelson contrast is given by $c/\% = 100[(L_{\max} - L_{\min})/(L_{\max} + L_{\min})]$, where L_{\max} and L_{\min} are the maximum and minimum luminance values of the sine-wave components of the multiple Gabor stimuli.

2.2 Stimuli

In experiments 1 and 2, stimuli consisted of either a single vertical Gabor patch placed in the centre of the display, or arrays of 177 Gabor patches that were placed 0.48 deg apart on the intersections of an imaginary square grid within a circular window with a nominal diameter of 7.2 deg (see figure 1). In two 'coherent' stimulus conditions, each Gabor patch was either vertical (vertical condition, figure 1a) or had an orientation tangent to an imaginary circle centred on the origin of the display monitor (circle condition, figure 1b). In an 'incoherent' stimulus condition, the orientation of each Gabor patch was chosen randomly (random condition, figure 1c). For each experimental session, these random orientations were calculated only once, but were different for each session performed by each observer. A replication of experiment 1 (see below), in which

⁽¹⁾We accept that it might be possible to find parameter sets for current models in which interactions are the same for all three of our global stimuli. However, we would take this as evidence for the failure of those models to achieve general-purpose linking. This would not rule out the possibility that such models might be involved in linking in a more restricted sense such as that outlined in H_3 .

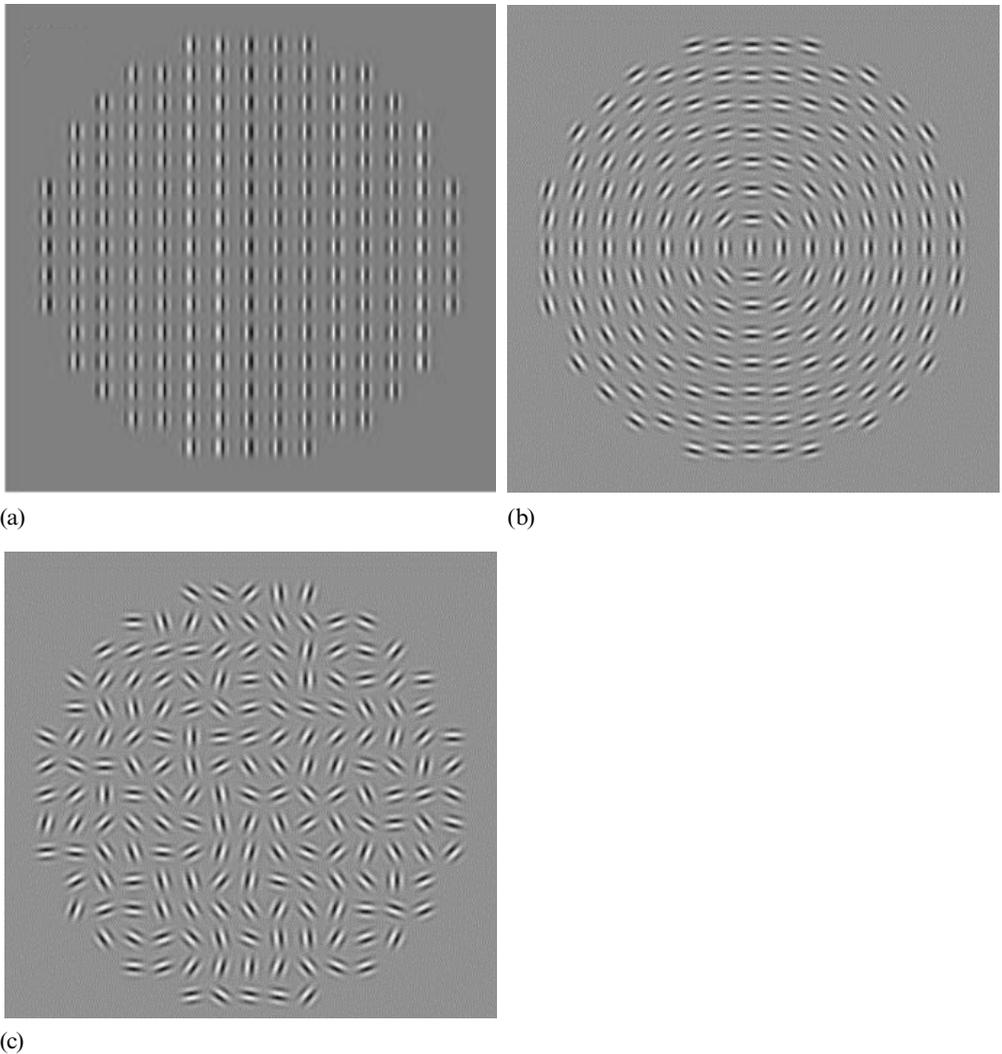


Figure 1. High-contrast examples of the three multiple-patch conditions used in experiments 1 and 2: (a) the vertical condition; (b) the circle condition; (c) the random condition. Together, conditions (a) and (b) are referred to as the coherent conditions. Note that in all conditions, the patches are positioned on a square grid and that the distribution of orientations is similar in (b) and (c). In experiment 1, observers detected a contrast increment applied to every patch in the stimulus. In experiment 2, the contrast increment was applied to just a single patch selected at random. Experiment 1 also used a single-patch condition, where the central patch in (a) was presented in isolation. In experiment 3, the stimulus consisted of just the central vertical strip of 15 elements in (a) and (c).

the randomisation of orientation took place on each trial for the incoherent condition, showed that this detail was unimportant for our results. In both the random condition and the circle condition, the orientations were quantised to steps of 5° . In experiment 3, the stimulus was a vertical one-dimensional array of stimulus elements consisting of the central strip of 15 elements from figure 1a and figure 1c. In this experiment, randomisation of orientation took place on every trial in the random condition. For all three experiments, stimulus duration was 200 ms.

The Gabor patches were the product of a sine-wave (with contrast c) and a unit amplitude two-dimensional Gaussian placed within a $0.48 \text{ deg} \times 0.48 \text{ deg}$ (20×20 pixels) square. For each Gabor, the sine-wave had a spatial frequency of $6.23 \text{ cycles deg}^{-1}$ and the Gaussian had a standard deviation of 0.096 deg (0.6 cycle) in orthogonal orientations (see figure 1). This produced Gabor stimuli with a full-width at half-height of 1.42 cycles . This is the same as those used by Meese and Williams (2000) and similar to a figure of 1.39 cycles used by Bonneh and Sagi (1998) and Polat and Sagi (1993, 1994). In this paper, the Gabor patches were curtailed at the boundaries of a 20×20 pixel square region, though this was not visually apparent, and the stimulus patches appeared circular (see figure 1). In the multiple-patch conditions, the vertical and horizontal spacing between the centre-points of each Gabor was 3 cycles .

In experiments 1 and 3, contrast increments were applied to all of the Gabor patches (global increments). In experiment 2, a contrast increment was applied to just one of the Gabor patches selected at random. Before each trial, a fixation point appeared for 300 ms to precue the location of the Gabor patch that was to contain the contrast increment. The fixation point was removed 500 ms before the onset of the first stimulus interval to avoid forward masking. In all four experiments, the background contrast against which the contrast increments were detected was 30% .

2.3 Control conditions

In addition to the control experiment mentioned above, experiment 1 was repeated by the first author, TSM, with the following modifications: (i) stimulus duration was decreased to 100 ms , (ii) the display window was square, increasing the number of patches in the multiple-patch conditions to 225 , and (iii) the background contrast was increased to 40% . The experiment was also repeated with only the first two modifications. In both cases, the pattern of results was very similar to those reported here indicating that stimulus duration, window shape, and pedestal contrast were not critical variables for our results.

2.4 Procedure and observers

A temporal 2IFC technique was used (the duration between stimulus intervals was 500 ms) and observers detected the presence of contrast increments for different conditions of stimulus coherence in interleaved trials. Responses were made by pressing one of two mouse buttons and auditory feedback was used to indicate the correctness of response. The contrast increment was controlled by a 'three-down, one-up' randomly interleaved staircase procedure (Cornsweet 1962; Wetherill and Levitt 1965; Meese 1995) and contrast increment thresholds were estimated by probit analysis (Finney 1971), typically based on about 100 trials (McKee et al 1985). Mean thresholds and standard errors were calculated from four or more such estimates. Viewing distance was either 100 cm or 114 cm .

The observers were the three authors (TSM, RFH, and CBW) and a naïve but psychophysically well-practised observer (DJH). All observers had normal or optically corrected-to-normal vision.

3 Results and discussion

In dealing with the various models that have been proposed for element linking and summation, it is important to bear in mind the distinction between two different types of local interactions that can be posited. In one case, interactions occur between all filter elements that are neighbours in the spatial dimensions. Consequently, these interactions are not specific for orientation (our experiments do not address the issue of spatial frequency), and we refer to these as 'unconstrained local interactions'. In the second case, interactions occur only between filter elements that are (approximately)

co-oriented and co-aligned (eg Field et al 1993; Polat and Sagi 1993) and we refer to these as 'constrained local interactions'.

3.1 Experiment 1: Global contrast increments for textures

Contrast increment thresholds are shown in figure 2 for each of the four stimulus conditions (different shading) for each of three observers and the average across observers. There are two main observations. First, contrast increment thresholds were lower for the multiple-patch conditions than they were for the single-patch condition. This result contrasts with that of Legge and Foley (1980), who found that contrast discrimination thresholds were not affected by stimulus area in suprathreshold conditions. However, the present data are consistent with later findings, where discrimination thresholds were found to improve with an increase in the number of spatially localised stimulus patches (Bonneh and Sagi 1999; Levi and Klein 2000). Why increasing stimulus area in this way should be of benefit in contrast discrimination is not clear, though there are at least two possibilities. First, it could be that, in the multiple-patch conditions, sensitivity is improved by probability summation between multiple detectors whose noise is less than 100% correlated (Robson and Graham 1981; Meese and Williams 2000). Second, the representation of contrast increments might be facilitated by unconstrained local interactions. In this case, it is not necessary to suppose independent noise for each detector, so the limiting source of noise could be either 100% correlated amongst the detectors, or come after a stage at which facilitatory local interactions occur (Usher et al 1999). Importantly, however, the similarity in the results for the three multiple-patch conditions suggests that, if this account of our data is correct, the interactions must be unconstrained.

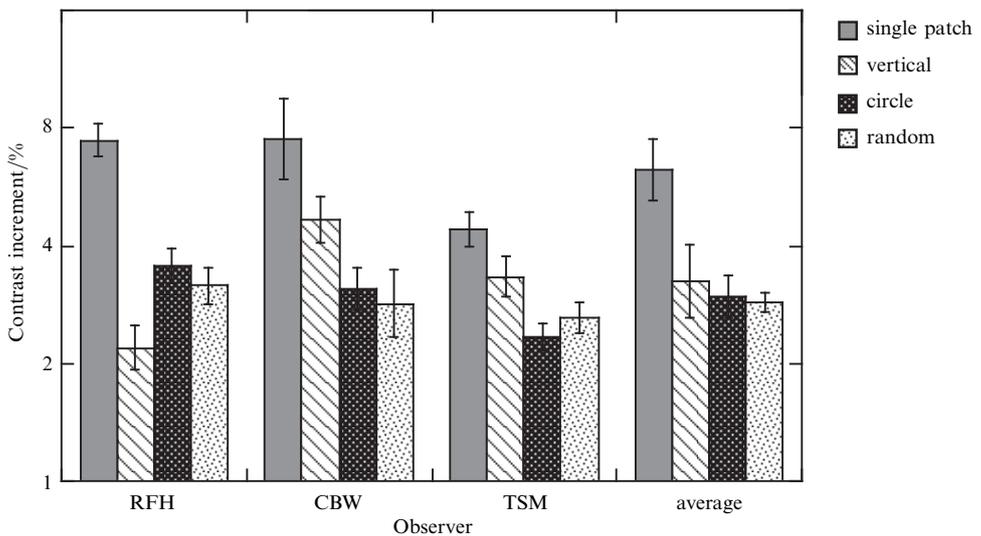


Figure 2. Results for experiment 1 where the contrast increment was applied to all patches in the test interval. Different shading is for different stimuli. Error bars here and in figures 3 and 4 show 1 SE from the mean and represent variation across observers for the average data. Thresholds are similar for the three multiple-patch conditions and lower than in the single-patch condition.

The second observation is that there was no systematic effect for the multiple-patch conditions. Thresholds were very similar for the circle and random conditions, though a little different from the vertical condition. However, these differences were not systematic (see average data), leading us to conclude that the spatial configuration of our stimuli was not tapping a fundamental property of vision in our task. Certainly, the data are inconsistent with the idea that the results for coherent and incoherent stimuli

would be different, as predicted by several proposals for element linking. In one version, constrained local interactions result in mutual inhibition. It has been argued (Kovács and Julesz 1993) that such inhibition would cause filter elements to respond in a more sensitive region of their contrast response functions (Legge and Foley 1980), and so discrimination thresholds should be best for the coherent stimuli. Alternatively, if the inhibitory interactions impacted on a stage after response nonlinearity and the limiting source of noise (eg after a gain control stage; Foley 1994), then discrimination thresholds should be worst for the coherent stimuli. In schemes in which the limiting source of noise is late (Bowne 1990), constrained inhibitory interactions would worsen the signal-to-noise ratio (Verghese and Stone 1997), predicting that performance would be worst for the coherent stimuli. Of course, if constrained interactions were facilitatory (Polat and Sagi 1993), then in all of the above cases, the predictions are the other way around. Nevertheless, none of these predictions is consistent with our results. In a very different hypothesis, filter-element noise is correlated for coherent stimuli (Verghese and Stone 1997), possibly through constrained local interactions. If it is assumed that this leads to a loss of area summation because of a loss of probability summation (Legge and Foley 1980), thresholds should be equally high for the single-patch condition and the two coherent conditions and lowest for the random condition where probability summation would occur. This prediction is also inconsistent with our results.

3.2 *Experiment 2: Local contrast increments for textures*

In experiment 1, the contrast increment was applied to every stimulus patch within the test interval. We have argued above that this challenges several ideas about the way in which element linking might be achieved. As a further test of these ideas we chose to repeat the experiment but to apply the contrast increment to just a single patch, similar to Kovács and Julesz (1993, 1994). In this case, constrained interactions should affect the detectability of the odd-item out (ie the item with the contrast increment) in only the coherent stimulus conditions for the same reasons as outlined above. The results for an experiment performed this way are shown in figure 3.⁽²⁾ There are two main observations, both of which are consistent with the earlier findings and conclusions. First, for each observer, the thresholds for all three coherent stimulus conditions were similar. Second, the thresholds were similar to those found for the single-patch condition in experiment 1. These results further indicate that spatial configuration is unimportant for contrast increment detection in our stimuli.

3.3 *Experiment 3: Global contrast increments for contours*

In experiments 1 and 2 we addressed the general question of element linking using coherent and incoherent textured patterns. Although we found no effect of spatial coherence for these stimuli, this does not rule out the possibility that facilitation occurs between co-oriented and co-aligned filter elements. It could be that enhancement along a contour is counteracted by an inhibitory influence from flanking elements on either side. There is some evidence to support this idea. Polat (1999) found that the enhanced detectability of a centrally placed patch by co-aligned and co-oriented stimulus elements (Polat and Sagi 1993, 1994) was considerably diminished when laterally placed flanks were also introduced. This led Polat (1999) to suggest that lateral interactions might be effective only when the stimulus is a contour. To further examine this, we repeated

⁽²⁾An initial version of this experiment was performed by the same three observers without using a fixation point as a precue (see section 2). In that case, detection thresholds were similar (around 32%) for each of the multiple-patch conditions and all higher than a single-patch condition (between 4% and 8%). The high detection thresholds were probably due to stimulus uncertainty; a view supported by the finding that psychometric functions had steep slopes (average values of Weibull slope parameter $\beta = 5.7$) compared to those in the present experiment (average $\beta = 1.6$).

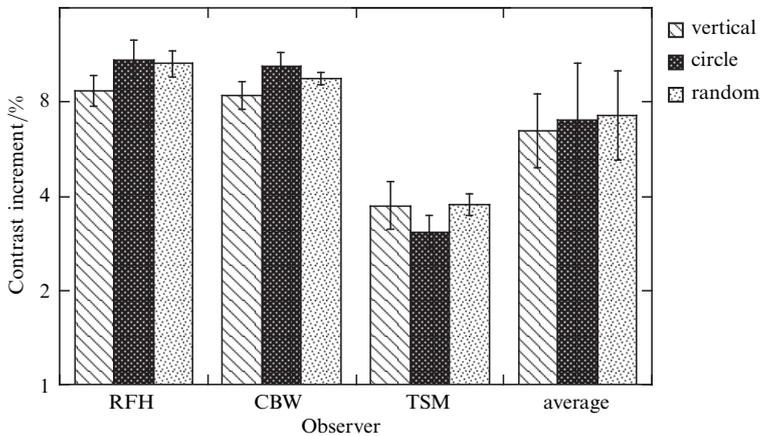


Figure 3. Results for experiment 2 where the observer was precued as to which single stimulus element would contain the contrast increment in the test interval. Thresholds are similar for the three multiple-patch conditions and similar to those found for the single-patch condition in experiment 1 (see figure 2).

experiment 1 using only the central vertical strip of the stimulus elements in figures 1a and 1b. Results for two observers (figure 4) show that there was no advantage for the co-oriented vertical contour over the randomly oriented vertical contour. This is consistent with Levi and Klein's (2000) recent finding that contrast increment thresholds were the same for a circular contour of stimulus elements, regardless of the local orientations of the elements.

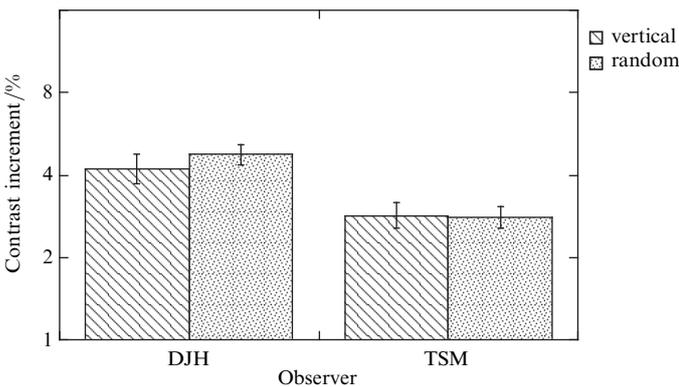


Figure 4. Results for experiment 3 where the stimulus was a vertical one-dimensional array of 15 stimulus elements. For both observers, thresholds are similar for the vertical and random conditions.

4 General discussion

In this paper, stimuli were constructed to test the hypotheses that element linking is achieved through local interactions that disturb either correlation of noise within contrast encoding detectors or contrast coding itself. One of our main assumptions was that our coherent stimuli (figures 1a and 1b) would tap the element-linking process and that our incoherent stimuli (figure 1c) would not. In a vertical condition (figure 1a), all stimulus elements were vertical and were spaced at distances that have been found to produce facilitation at contrast detection threshold (Polat and Sagi 1993, 1994; Solomon et al 1999). In a circle condition (figure 1b), the arrangement of local orientations produced a coherent stimulus that gave an impression of a set of closed concentric circles. This stimulus was inspired by that used by Kovács and Julesz (1993), the main

difference being that our stimulus contained multiple closed contours whereas theirs contained a single closed contour in a figure-ground configuration. In all three of our multiple-patch conditions, the stimulus elements were placed on the intersections of a square grid, ensuring identical element positions for the three conditions. One consequence of this was that in the circle condition (but not the vertical condition), the stimulus did not contain elements that were spatially aligned in the sense of Polat and Sagi (1993). Nevertheless, the circle condition stimulus is valuable because: (a) experiments on contour linking have shown that vision is fairly tolerant of small local misalignments (Field et al 1993), and (b) the stimulus is a compelling closed coherent figure, which, regardless of how linking is achieved, should be provocative for the mechanisms or processes involved. In a final experiment, stimulus elements created a vertical contour whose local orientations were either aligned with the contour, or were randomised.

Our second main assumption was that, if linking is achieved through contrast-disturbing interactions, then this should affect the detectability of a contrast increment applied either to the entire stimulus or just a single element. Together with our first assumption (above), this predicts that contrast increment thresholds should be different for our coherent and incoherent stimuli. However, we found that spatial configuration had no systematic effect on contrast increment detection. In sum, our data are inconsistent with the idea that perceptual linking is achieved through constrained local interactions that disturb local representation of contrast in suprathreshold conditions (H_1 and H_2). These results raise two questions: (i) How can the present results be reconciled with earlier work that suggested evidence for interactions? (ii) What other methods might vision use to achieve linking?

4.1 *Constrained local interactions*

Our general conclusion (above) is not inconsistent with some of the previous psychophysical work on spatial interactions. Work by Bonnef and Sagi (1998) and Polat and Sagi (1993, 1994) (see section 1) has led to the suggestion that facilitatory interactions enhance local representations of contrast. But this might be a purely (near to) threshold effect (H_3), in which case it is possible that the purpose of these interactions might be to enhance the representation of low-contrast contours rather than to achieve linking per se. This is consistent with a recent report by Chen and Tyler (2001), who found that the psychophysical effects of fixed-contrast flankers changed from facilitation to inhibition when the pedestal contrast of a centrally placed test patch was increased above detection threshold. Williams and Hess (1998) used a contrast-matching task to assess the effect of flanking elements on perceived contrast of a centrally placed low-contrast test patch and found no effect. This and other results led Williams and Hess to question the usefulness for contour integration of the interactions proposed by Polat and Sagi.

Closer to our experiments (particularly experiment 2), Kovács and Julesz (1993, 1994) used a contrast-discrimination paradigm. Unlike in our experiments, Kovács and Julesz (1993, 1994) found configurational effects which they supposed were due to local interactions. It is unclear how their results fit with ours, but differences between the stimuli might be important. For example, in experiments 1 and 2, our stimuli did not contain contours as such but arrangements of stimulus elements that produced a coherent closed figure (figure 1b). Similarly, Kovács and Julesz (1993, 1994) used multiple Gabor stimuli containing a closed figure but one defined by a closed contour; their experimental effects were related to the position of a test patch relative to this contour. It is possible that some subtle difference between the stimuli meant that those used by Kovács and Julesz (1993) tapped a different type of linking mechanism from the one investigated here. For example, in their experiments, higher-order detectors selective for

spatial configurations such as circles (Gallant et al 1996; Wilson and Wilkinson 1998) might have interacted with (earlier) contrast-encoding elements to emphasise figure-ground boundaries through local contrast enhancement (Hupe et al 1998). Certainly, cells in V1 have been found to show response enhancement in the latter part of their spike train for figure-ground texture borders (eg Lee et al 1998), consistent with some of the psychophysical results of Kovács and Julesz (1993). If these effects are specific to figure-ground mechanisms and inoperative on local texture elements, then our stimuli might be immune from them because, in one sense, all of our multiple-element stimuli contain a figure of luminance-modulated elements against an unmodulated background. Clearly, further experiments are required to resolve this issue psychophysically.

4.2 *Linking does not disturb the local suprathreshold contrast code*

Our results challenge the view that element linking is achieved through a local mechanism or process that either enhances or suppresses the local contrast code, at least at moderate contrasts and above. In one respect, it is not surprising that vision does not work in this way. For example, as pointed out by Meese and Georgeson (1996b), if it did, then perception of contrast and the implementation of linking would be confounded. This possibility was tested by Hess et al (1998), who found that the introduction of contrast jitter in displays containing multiple and randomly oriented Gabor patches (Field et al 1993) did not affect an observer's ability to detect a 'snake-like' path of patches within the stimulus. Whereas experiments 1 and 2 in the present paper have addressed more general ideas about element linking, the work of Hess et al (1998) provides similar evidence regarding the specific case of contour linking and its indifference to the local contrast code. The results of experiment 3 and Levi and Klein (2000) (see experiment 3) provide further support for this.

4.3 *How is linking achieved in vision?*

The results reported here and by Hess et al (1998) do not rule out the possibility that linking is achieved through interactions of some kind; our main point is that they do not disrupt the local contrast code. It is feasible that vision contains units with similar stimulus selectivities but very different functional roles. Two putative classes of mechanism have been referred to by Meese and Georgeson (1996b) and Meese (1999) as data units (or data filters) and control units. The basic idea is that phase-preserving data units (eg simple cells) carry information about local stimulus structure (contrast, phase, spatial frequency, and orientation) in a population code (Meese and Georgeson 1996a), and that each unit has an associated control unit (eg a complex cell), responsible for linking and segmentation. In this scheme, interactions take place only between the control units, protecting the data units from disturbances that would disrupt their spatial code (including contrast). One version of this general idea was presented by Meese (1999) in the context of linking (binding) spatial filter elements in the Fourier domain across spatial frequency and orientation (Georgeson 1992; Meese and Georgeson 1996a; Georgeson and Meese 1997). However, whether vision contains functionally distinct data and control units is at present unknown.

Another possibility is that contrast and linking codes could be multiplexed by means of a sophisticated temporal code with common hardware (eg von der Malsburg and Schneider 1986; Castelo-Branco et al 2000). One specific example is that codes for contrast and contour might be carried by different parts of the spike train in single cells (Lamme 1995), be they simple or complex. The initial part of the spike train, reflecting the feedforward signal, might contain the contrast code whereas the later part, reflecting lateral interactions and feedback from higher areas, might carry the code for contour (Hess and Field 1999). There is physiological support for this proposal from the work of Lamme (1995), Zipser et al (1996), Lee et al (1998), and Lamme et al (1999).

5 Conclusions

Our contrast-discrimination results suggest that element linking is not generally achieved through local interactions that interfere with a local contrast code. Other possibilities for linking include: (i) higher-order mechanisms, (ii) the coexistence of two sets of units, one of which carries information about spatial structure including contrast, and the other information about element linking, and (iii) a temporal code that multiplexes a contrast code and an element-linking code. This conclusion is consistent with earlier evidence for interactions at contrast detection threshold (Polat and Sagi 1993, 1994; Bonnef and Sagi 1998; Usher et al 1999; Polat 1999; Saarinen and Levi 2001) which might reflect other processes such as those involved in enhancing the representation of low-contrast stimuli.

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