

The locus of attentional effects in texture segmentation

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Cuing covert spatial attention can increase spatial resolution. Here we pinpointed the specific locus of this effect using texture segmentation. At the level of visual cortex, texture segmentation theoretically involves passage of visual input through two layers of spatial linear filters separated by a pointwise non-linearity. By manipulating the textures to differentially stimulate first- or second-order filters of various scales, we showed that the attentional effect consistently varied with the latter. These psychophysical results further support the hypothesis that attention increases resolution at the attended location and are consistent with an effect of attention at stages as early as the primary visual cortex.

Although many studies demonstrate that attending to a specific location improves performance on a variety of visual tasks, how and where this improvement takes place have been a subject of debate for over 30 years^{1–15}. Previous studies provide psychophysical evidence that attention can sharpen spatial resolution^{1–3}; here we explored the locus of this attentional effect using texture segmentation. The psychophysical (behavioral) evidence of this attentional effect can be related to the processing of visual information in primary visual cortex^{16–18}.

Previous experiments involved manipulating covert spatial attention (selective processing of visual information at a given location without eye movements to that location) in a stimulus-driven fashion via a transient peripheral precue. These results prompted the ‘resolution hypothesis’, namely, that attention can aid performance by increasing spatial resolution at the attended location^{1–3}. Such a hypothesis is supported by the finding that attention improves performance in both acuity and hyperacuity tasks, even when a suprathreshold target (a Landolt square or a vernier stimulus) is presented without distractors². Similarly, in an orientation-discrimination task, attention increases sensitivity across the contrast-sensitivity function when a suprathreshold target is presented alone (in the absence of distractors or masks) without location uncertainty. (Observers’ performance in a target-localization task is perfect.) These conditions ensure that the mechanisms of decisional factors or external noise reduction are not responsible for the attentional benefit⁴. Moreover, in a visual search task, attention improves performance more for peripheral than for central targets, implying that attention can reduce resolution differences between the fovea and the periphery³. The resolution hypothesis is also consistent with studies suggesting that attention affords a finer-scale analysis of the stimuli. When distractors are present in a visual search task, precueing target location reduces orientation thresholds to levels measured without distractors¹¹. In addition, a line is judged shorter when attention is directed to its location, presumably because it is processed by smaller ‘attentional receptive fields’¹².

In a critical test of the resolution hypothesis, we explored the effects of attention on a basic texture segmentation task for which

performance was expected to be diminished by heightened resolution¹. In this task, performance peaks at mid-periphery, dropping toward more central or farther peripheral locations. Presumably, performance drops because spatial linear filters, tuned to a specific band of spatial frequency and orientation^{19,20}, are too small at the fovea or too large at the far periphery for the scale of the texture (where resolution is too high or too low, respectively^{21–23}). Moreover, enlarging or decreasing the texture scale shifts the peak of performance to correspondingly farther or nearer eccentricities. This is because processing the enlarged texture requires larger filters, which are prevalent at farther eccentricities, whereas processing the decreased texture requires smaller filters, which are prevalent at the fovea^{21–23}.

We found that directing attention to the target location enhances performance where the resolution is too low for the texture scale (periphery), but impairs performance where the resolution is already too high (fovea). Furthermore, attention impairs performance over a wider range of eccentricities for larger than for smaller texture scales. This differential effect occurs because the mismatch between the texture scale and the size of the filters extends farther toward the periphery for the larger texture scale. Given that the pattern of the attentional effect depends on both the scale of the texture and target eccentricity, and that the properties and response of the filters change as a function of eccentricity and stimulus scale, the findings suggest that attention operates on these spatial filters. Specifically, these results suggest that attending to a location is similar to reducing the size of the corresponding filters¹.

However, the level of visual processing at which these attentional effects take place is not known. Several models of texture segmentation consider that, in visual cortex, the visual input passes through two layers of spatial linear filters separated by a pointwise nonlinearity^{23–29}. Whereas the first-order filters perform a local analysis of spatial frequency and orientation, the second-order filters, which are of a larger scale and tuned to lower frequencies, perform a more global analysis on the output of the first-order filters plus the intermediate nonlinearity. This idea is common to many computational models of texture segmenta-

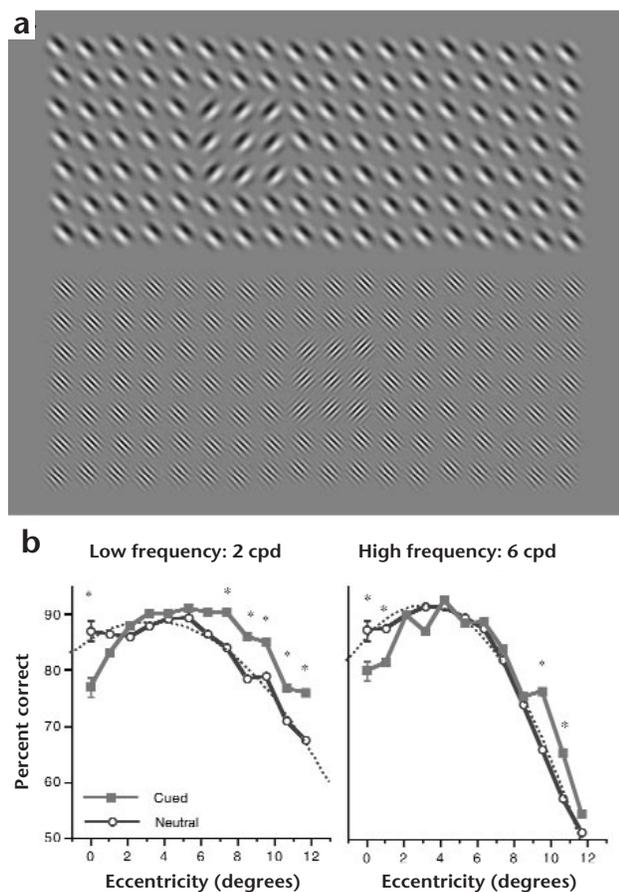


Fig. 1. Stimuli and results of experiment 1. (a) First-order texture displays. Top, 'low-frequency' texture with 2 cpd Gabor patches; bottom, 'high-frequency' texture with 6 cpd patches. (Only 18 of the 31 columns are shown.) (b) Observers' performance in experiment 1 as a function of cueing condition and target eccentricity. The attentional effect was the same regardless of the Gabor frequency (left, low frequency; right, high frequency). In both cases, a significant interaction emerged; accuracy was higher for cued trials (squares) than neutral trials (circles) at more peripheral eccentricities, but accuracy was lower at central locations (0° – 2°). Second-order polynomials (dotted line) were fitted to data for neutral conditions. Error bars give \pm s.e. for each condition. * $p < 0.05$ according to LSD *post-hoc* comparisons.

tion^{23–29}, even though their specific instantiation of these processing stages may differ. (Some authors propose that a global component enters only at the decision-making stage³⁰.) Working from the assumption of two layers of filters, we investigated whether previously reported attentional effects¹ could reflect a change in either of these two stages of filtering. The texture used in that study comprises broadband stimuli (line segments) that activate filters of various preferred spatial frequencies or scales; furthermore, manipulation of the scale by changing the viewing distance affects relevant factors for both filtering levels (for instance, microelements' size and spacing). To identify the specific level at which attention exerts its effect, here we used narrow-band stimuli that activated only filters of a specific scale, thus selectively manipulating either the first-order (experiments 1 and 4) or the second-order (experiments 2 and 3) content of the textures. Because second-order filters are tuned to a lower frequen-

cy than first-order filters^{23–29}, the spatial frequencies for the second-order textures are necessarily lower than those for the first-order textures. The two different spatial frequencies we used in each of the four experiments ensured the activation of filters of different scales.

RESULTS

Experiment 1

This experiment examined whether covert attention could operate on first-order filters. We used two textures whose microelements were narrow-band Gabor patches (2 cycle per degree 'low-frequency' versus 6 cpd 'high-frequency' stimuli; Fig. 1a). These two textures were identical, apart from the threefold (± 1.6 octave) difference between the patches' spatial frequency, which ensured that their processing required first-order filters of different scales^{19,20,27,31–33}. The task was a two-alternative forced-choice task. Observers had to indicate the interval containing a target composed of patches with orthogonal orientation to the background elements (Fig. 1a). On the cued trials, a peripheral cue indicated the display onset and the target location (Fig. 2). This cue always indicated the location where the target would appear but conveyed no information regarding the correct response^{1–4}. On the remaining trials, a neutral cue indicated the display onset but not the target location; it could appear in a number of locations. Peripheral cues direct attention in an automatic, transient, stimulus-driven fashion, with a maximum attentional effect at a stimulus-onset asynchrony of about 100–120 ms (ref. 34). If attention operated on first-order filters, precueing target location should have a differential effect on these textures. Given that processing the low-frequency texture requires filters of a larger scale, performance should peak at a farther eccentricity, and attention should impair performance in a larger range of eccentricities with the lower-frequency texture.

Accuracy was higher in cued than in neutral trials at peripheral locations, but lower at central locations (Fig. 1b). More importantly, the pattern of results was independent of the microelements' spatial frequency: first, a second-order polynomial fit revealed that, for the neutral trials, performance peaked at a similar eccentricity for both textures (low frequency, 3.5° ; high frequency, 3.1°). This suggests that the central performance drop was not mediated by the characteristics of the first-order filters. Second, for both textures, attention impaired performance in the same range of eccentricities (0 – 2°). This suggests that attention did not operate on the first stage of linear filtering. Although the attentional benefit started at a farther eccentricity for the high- than for the low-frequency texture, this result was opposite in direction from that predicted by the idea that attention operates on first-order filters. At peripheral locations, the steeper performance drop for the high- than for the low-frequency texture (which follows the resolution decrement as a function of eccentricity^{19,20,35}) was present for both cueing conditions, implying that this finding was not related to the operation of attentional mechanisms.

Experiment 2

To assess whether attention operated on the second-order filters, in this experiment we manipulated second-order filters of different scales while keeping constant the first-order frequency of both textures (5.33 cpd). The second-order textures²⁷ were composed of Gabor patches of the same spatial frequency (5.33 cpd) but different orientations (Fig. 3a). The target Gabor patches were arranged like a checkerboard, and the background patches in horizontal stripes. Because these two regions differed

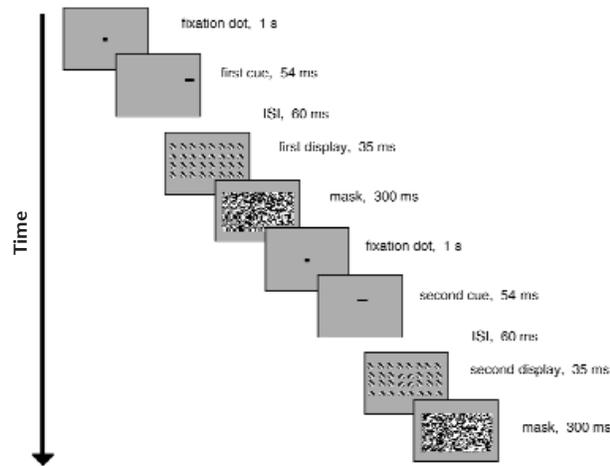


Fig. 2. Sequence of events in a single trial.

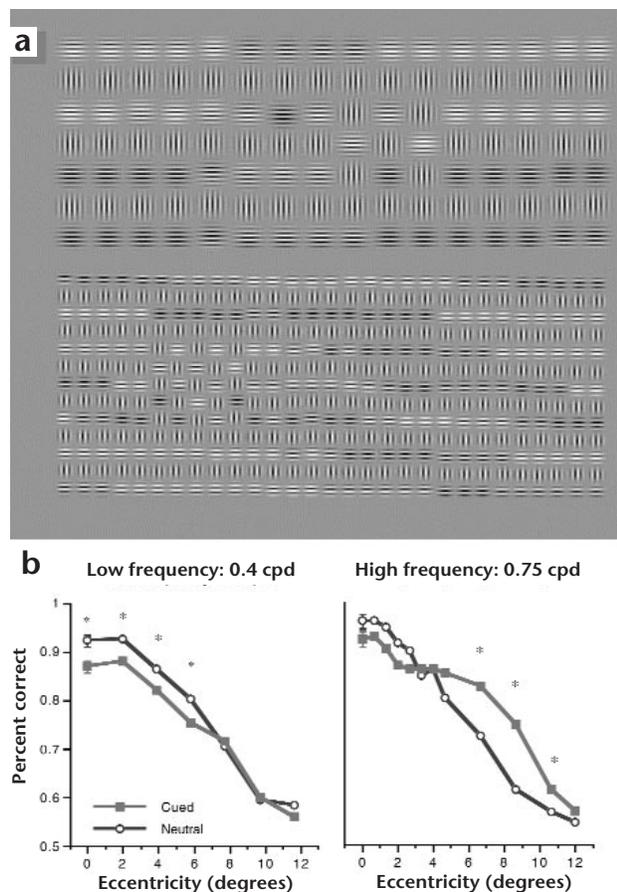


Fig. 3. Stimuli and results of experiment 2. (a) Second-order texture displays. Top, 'low-frequency' second-order texture (0.4 cpd). Bottom, 'high-frequency' second-order texture (0.75 cpd). (b) Observers' performance in experiment 2 as a function of cueing condition and target eccentricity. The attentional effect differed when the second-order content was varied: attention impaired performance in a greater range of eccentricities for the low (left) than the high (right) frequency textures (0–7.76° versus 0–3.33°), and an attentional benefit emerged only for the 'high frequency'. Error bars, \pm s.e.; * $p < 0.05$.

only in the microelements' layout, the local analysis of first-order filters is similar for both regions, and texture segmentation requires the activation of second-order filters. To activate second-order filters of different scales, the two textures differed in their second-order frequency, 0.4 cpd ('low') versus 0.75 cpd ('high'). If attention could operate on the second-order filters, attending to the target location should have differentially affected performance.

The attentional effect differed for the two textures in the predicted way: attention impaired performance over a greater range of eccentricities for the low- than for the high-frequency textures (0–7.76° versus 0–3.33°; Fig. 3b); this effect was statistically significant only for the low-frequency textures. In addition, whereas attention benefited performance significantly from 6° of eccentricity for the high-frequency texture, its effect was not significant for the low-frequency texture. In all, in contrast to experiment 1, the pattern of the attentional effect depended on the texture spatial frequency that activated second-order filters of different scales. Therefore, attention seems to operate at the second stage of linear filtering.

In addition, the finding that performance peaked at the fovea, rather than at mid-periphery (Fig. 3b, neutral functions), suggests that the central performance drop may not have been due to a mismatch between the scale of the texture and second-order filters. Instead, it may have been mediated by interfrequency inhibition; mechanisms tuned to high spatial frequencies inhibit mechanisms tuned to low spatial frequencies²¹. This hypothesis is supported by two previous findings: removing high-frequency information from the display eliminates the central performance drop (K. Morikawa, *Invest. Ophthalmol. Vis. Sci.* 38, 2986, 1997), and sensitivity to low spatial frequencies remains constant at the fovea and periphery^{19,20,35}.

Experiment 3

To examine whether this conclusion applies to other 'second-order' textures, in experiment 3 we used Gabor modulations of a band-limited, isotropic carrier noise (Fig. 4), which activate second-order filters³⁶. The observers' task was to detect the presence of the Gabor modulation. When the target's spatial frequency is lower than that of the carrier noise, the stimulus does not contain Fourier energy at the Gabor frequency; hence, the target is visible only to the second-order mechanisms^{24,25,36}. To activate second-order filters of different scales, the two textures differed in the Gabor's spatial frequency; frequencies were 0.25 cpd ('low frequency'; Fig. 4a) versus 1 cpd ('high frequency'; Fig. 4b). To keep constant the textures' first-order content, the carrier noise frequency was 2 cpd for both textures.

In consonance with experiment 2, attention significantly impaired performance at central locations for the low frequency (0–2.25° eccentricity, Fig. 4d) but not for the high frequency (Fig. 4e). Furthermore, a significant attentional benefit emerged at a farther eccentricity for the low frequency (6°, Fig. 4d) than for the high frequency (3°, Fig. 4e).

Experiment 4

To further examine whether attention affected the first-order filters, in this experiment we used the same type of textures as in experiment 3 (ref. 36), but instead of varying the spatial frequency of the Gabor modulator (second-order content), we varied the carrier noise frequency (first-order content). The Gabor frequency in the 'high-frequency noise' texture was kept at 1 cpd ('high frequency' in experiment 3), but the carrier

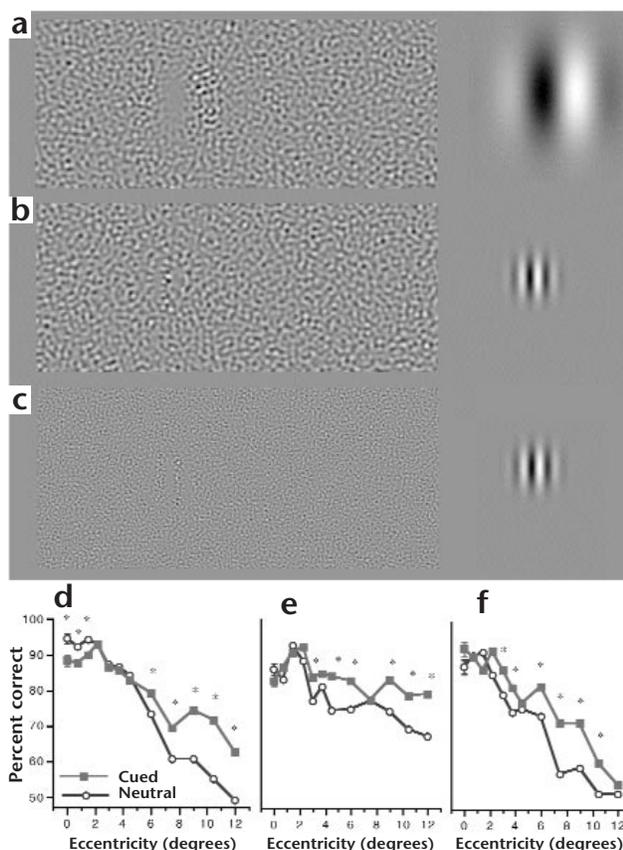


Fig. 4. Stimuli and results of experiments 3 and 4. (**a–c**) First and second-order texture display distinctions. The left panels depict the texture displays and the right panels the Gabor modulators. The central frequency of the Gabor modulator was either 0.25 cpd ('low frequency', **a**) or 1 cpd ('high frequency'; **b**, **c**). The central frequency of the carrier noise was either 2 cpd (**a**, **b**) or 4 cpd (**c**). The first-order content was the same for (**a**) and (**b**), whereas the second-order content was the same for (**b**) and (**c**). (**d–f**) Observers' performance in experiments 3 and 4 as a function of cueing condition and target eccentricity. Note that the attentional effect differed when the second-order content was varied (**d** versus **e**). Attention impaired performance at the central locations for the low-frequency texture (**d**) but not for the high-frequency texture (**e**). An attentional benefit emerged at 3° of eccentricity for the high-frequency texture (**e**), but only at 6° for the low-frequency texture (**d**). In contrast, performance was similar when the first-order content was varied (**e** versus **f**). For both textures, attention did not impair performance at the central locations, and the attentional benefit emerged at 3°. Error bars, \pm s.e.; * $p < 0.05$.

noise frequency was increased from 2 cpd to 4 cpd (Fig. 4c) to ensure the activation of first-order filters of a different scale. If attention indeed operated at the second rather than the first stage of linear filtering, the attentional effect should have been similar for both textures, regardless of the octave difference in their noise frequency.

As predicted, for both textures attention did not impair performance significantly at any eccentricity, and the attentional benefit started at the same eccentricity (3°, Fig. 4e and f). (The lack of a significant attentional effect at 12° of eccentricity for the high-frequency texture was probably due to performance

that was already at the level of chance.) This finding supports the conclusion of the first three experiments: attention affected the second but not the first stage of filtering.

DISCUSSION

The findings of all four experiments, which used different texture patterns and stimuli that either were (experiments 1 and 2) or were not (experiments 3 and 4) followed by a mask, indicate that attention operates at the second stage of filtering, possibly through the reduction in size of second-order filters. This reduction could be accomplished in two ways. First, attention may, in effect, reduce the size of receptive fields at the attended area. This hypothesis is compatible with physiological studies demonstrating that attention contracts a cell's receptive field around the attended stimulus^{15,37–39}. Alternatively, attention may reduce filter size by increasing the sensitivity of the smallest receptive fields at the attended area¹⁰, which in turn may inhibit the sensitivity of the larger receptive fields at the same area. Consequently, the overall sensitivity of the attended region would shift toward higher spatial frequencies. The latter alternative is consistent with our hypothesis that the central performance drop may be mediated by interfrequency inhibition²¹. Such interference may result from a normalization process occurring across channels and operating on the output of second-order filters. This process divides the response of each individual filter by the total response of a set of spatially overlapping filters of different frequencies and orientations^{26,40–43}.

This normalization process could also explain the central performance drop found in previous studies^{1,21,22} that used broadband stimuli (lines) that activate filters of different scales, many nonoptimal for the task. When the output of high-frequency non-optimal filters is entered into the normalization process, the final response of the optimal filters is weakened. This 'response inhibition' at central locations, where sensitivity to high-frequency information is highest,^{19,20} could be responsible for the central performance drop. In contrast, the lack of a central drop in experiments 2–4 may reflect the fact that the narrow-band Gabor stimuli only activated filters with optimal frequency, whose final response was not diminished by the normalization process. In the case of experiment 1, the central drop may be due to the non-optimal, second-order filters activated by the non-optimal spacing of the Gabor microelements⁴⁴. Similarly, by including filters of a smaller scale, attention may affect the outcome of the normalization process. For targets at central locations, the output of small, non-optimal filters would weaken the response of the larger, optimal filters, and attention would hinder performance. Conversely, for peripheral targets, where the average filter size is larger, the smaller-scale filters brought about by attention are closer to optimal and would improve performance. This sort of attentional mechanism could explain previous findings¹ as well the results we describe here.

This study showed that covert attention could affect early stages of visual processing^{1–4,10–14,45}, and that, in texture segmentation, attention could operate as early as the second stage of linear filtering. This hypothesis is consistent with physiological evidence showing that responses capable of underlying segregation occur in V1 (refs. 16–18). The attentional effects found here suggest a link between task performance (behavior) and physiological studies demonstrating, by means of either single-cell recording^{46–47} or fMRI^{48–50}, attentional modulation of activity in area V1.

Attention consists of multiple independent but interactive systems. Attentional facilitation in visual tasks may reflect a combination of mechanisms such as signal enhancement, external noise reduction and decisional factors, depending on task and stimuli^{1–15}. In this study, we concentrated on the attentional mechanism operating on simple texture segmentation. Alternative accounts of attention, such as noise reduction or changes in decisional factors^{6–9} cannot explain our findings here because they predict that attention always helps and never hinders performance. The experimental conditions and findings of this study suggest that, in this texture segmentation task, attention operates through increased resolution at the level of the second-order filters.

To conclude, our results here using narrow-band stimuli lend further support to a previous study showing that attending to target location helps texture segmentation when the spatial resolution is too low, but hinders segmentation when the resolution is already too high¹. These findings also provide convergent evidence for our resolution hypothesis^{1–3}. More importantly, our selective manipulation of the first-order (experiments 1 and 4) or the second-order (experiments 2 and 3) content of the textures allowed us to pinpoint the specific level at which covert attention exerted its effect in these segmentation tasks. The results of all four experiments indicate that this attentional effect in texture segmentation occurs at the level of the second-order filters. The range of eccentricities at which attention either improved or impaired performance was consistently affected by the second-order spatial frequency of the textures. This finding indicates that in texture segmentation, covert attention could increase spatial resolution by reducing the scale of the second-order filters.

METHODS

General procedure. Each temporal interval of a two-alternative, forced-choice task began with a central fixation dot followed by a cue of 54 ms. On half the trials a 'peripheral cue'—a black horizontal bar ($0.3^\circ \times 0.7^\circ$)—appeared 0.3° above the target location (Fig. 2). On the remaining trials a neutral cue—two horizontal lines ($0.3^\circ \times 31^\circ$)—appeared above and below the display. After an interstimulus interval (ISI) of 60 ms, the texture was displayed for an average of 35 ms for the low-frequency textures and 60 ms for the high-frequency textures (display duration ranged from 27 ms to 67 ms, and was adjusted for individual observers to keep overall performance at 75% correct). The average display duration did not differ among experiments. A random-dot mask followed the stimulus in experiments 1 and 2. The order of the 120 practice trials as well as that of the 768 experimental trials was randomized. The short time between cue onset and display offset (< 180 ms) precluded eye movements. The experimental protocol was approved by the New York University Committee on Activities Involving Human Subjects, Office of Sponsored Programs.

Experiment 1. A $3^\circ \times 3^\circ$ target texture, composed of 3×3 narrow-band Gabor patches of 2 cpd or 6 cpd (each subtending 1° of visual angle, oriented at 45° or 135°) was embedded in a background texture composed of 203 patches (7 rows \times 29 columns, subtending $7.5^\circ \times 31^\circ$) of the same spatial frequency whose orientation was orthogonal to the target (Fig. 1a). The target appeared equally often in each interval and was centered at any of 23 possible locations along the horizontal meridian.

Experiment 2. Stimuli were the same as in experiment 1, except for the following. The two texture displays (Fig. 3a) were composed of vertical and horizontal Gabor patches of the same spatial frequency (5.33 cpd). In the 'low-frequency' texture (0.4 cpd, second order) a $3.6^\circ \times 3.6^\circ$ 'checkerboard' target texture was composed of 3×3 patches, each subtending 1.2° of visual angle. In the 'high-frequency' texture (0.75 cpd, second order) a $3.3^\circ \times 3.3^\circ$ 'checkerboard' target was composed of 5×5 patches, each subtending 0.66° of visual angle. The target was embedded in a 'horizontal-stripes' background texture composed of 275 (low-frequency) or 945 (high-frequency) patches (subtending $13^\circ \times 30^\circ$ or $14^\circ \times$

30° of visual angle, respectively). The target was centered at any of 13 (low-frequency) or 23 (high-frequency) possible locations along the horizontal meridian.

Experiments 3 and 4. The $30.5^\circ \times 10^\circ$ texture display was created by multiplying a Gabor function with a band-limited carrier noise³⁶. The central frequency of the Gabor modulator was either 0.25 cpd ('low-frequency'; Fig. 4a) or 1 cpd ('high-frequency'; Fig. 4b and c). Their size differed because a smaller 1 cpd Gabor would have been too small to detect, whereas a larger, 0.25 cpd Gabor would have covered a too wide range of eccentricities. The carrier noise consisted of an isotropic, single-octave-wide band, with a central frequency of 2 cpd (Fig. 4a and b) or 4 cpd (Fig. 4c).

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1. Yeshurun, Y. & Carrasco, M. Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* **396**, 72–75 (1998).
2. Yeshurun, Y. & Carrasco, M. Spatial attention improves performance in spatial resolution tasks. *Vision Res.* **39**, 293–305 (1999).
3. Carrasco, M. & Yeshurun, Y. The contribution of covert attention to the set-size and eccentricity effects in visual search. *J. Exp. Psychol. Hum. Percept. Perform.* **24**, 673–692 (1998).
4. Carrasco, M., Penpeci-Talgar, C. & Eckstein, M. Spatial covert attention increases contrast sensitivity along the CSF: Support for signal enhancement. *Vision Res.* **40**, 1203–1215 (2000).
5. Posner, M. I. Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3–25 (1980).
6. Kinchla, R. A. Attention. *Annu. Rev. Psychol.* **43**, 711–742 (1992).
7. Prinzmetal, W., Amiri, H., Allen, K. & Edwards T. Phenomenology of attention: 1. color, location, orientation, and spatial frequency. *J. Exp. Psychol. Hum. Percept. Perform.* **24**, 1–22 (1998).
8. Sperling G. & Doshier B. A. in *Handbook of Perception and Human Performance* Vol. 1 (eds. Boff, K. R., Kaufman, L. & Thomas, J. P.) 1–65 (Wiley, New York, 1986).
9. Shiu L. & Pashler, H. Spatial attention and vernier acuity. *Vision Res.* **35**, 337–343 (1995).
10. Balz, G. W. & Hock, H. S. The effect of attentional spread on spatial resolution. *Vision Res.* **37**, 1499–1510 (1997).
11. Morgan, M. J., Ward, R. M. & Castet, E. Visual search for a tilted target: Tests of spatial uncertainty models. *Q. J. Exp. Psychol. A* **51**, 343–370 (1998).
12. Tsal, Y. & Shalev, L. Inattention magnifies perceived length: The attentional receptive field hypothesis. *J. Exp. Psychol. Hum. Percept. Perform.* **22**, 233–243 (1996).
13. Lee, D. K., Itti, L., Koch, C. & Braun, J. Attention activates winner-take-all competition among visual filters. *Nat. Neurosci.* **2**, 375–381 (1999).
14. Lu, Z. L. & Doshier, B. A. External noise distinguishes attention mechanisms. *Vision Res.* **38**, 1183–1198 (1998).
15. Desimone R. & Duncan J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193–222 (1995).
16. Purpura, K. P., Victor, J. D. & Katz, E. Striate cortex extracts higher-order spatial correlations from visual textures. *Proc. Natl. Acad. Sci. USA* **91**, 8482–8486 (1994).
17. Lamme, V. A. F. The neurophysiology of figure-ground segregation in primary visual cortex. *J. Neurosci.* **15**, 1605–1615 (1995).
18. Lamme, V. A. F., Van Dijk, B. W. & Spekreijse, H. Organization of texture segregation processing in primate visual cortex. *Vis. Neurosci.* **10**, 781–790 (1993).
19. DeValois, R. L. & DeValois, K. K. *Spatial Vision* (Oxford Univ. Press, New York, 1988).
20. Graham, N. *Visual Pattern Analyzers* (Oxford Univ. Press, New York, 1989).
21. Gurnsey, R., Pearson, P. & Day, D. Texture segmentation along the horizontal meridian: nonmonotonic changes in performance with eccentricity. *J. Exp. Psychol. Hum. Percept. Perform.* **22**, 738–757 (1996).
22. Kehler, L. Central performance drop on perceptual segregation tasks. *Spat. Vis.* **4**, 45–62 (1989).
23. Kehler, L. The central performance drop in texture segmentation: a simulation based on a spatial filter model. *Biol. Cybern.* **77**, 297–305 (1997).
24. Bergen, J. R. & Landy, M. S. in *Computational Models of Visual Processing* (eds. Landy, M. S. & Movshon, J. A.) 253–271 (MIT Press, Cambridge, Massachusetts, 1991).
25. Sutter, A., Beck, J. & Graham, N. Contrast and spatial variables in texture

- segregation: testing a simple spatial-frequency channels model. *Percept. Psychophys.* **46**, 312–332 (1989).
26. Graham, N., Beck, J. & Sutter, A. Nonlinear processes in spatial-frequency channel models of perceived texture segregation: Effects of sign and amount of contrast. *Vision Res.* **32**, 719–743 (1992).
 27. Graham, N., Sutter, A. & Venkatesan, C. Spatial-frequency and orientation-selectivity of simple and complex channels in region segregation. *Vision Res.* **33**, 1893–1911 (1993).
 28. Malik, J. & Perona, P. Preattentive texture discrimination with early vision mechanisms. *J. Opt. Soc. Am. A* **7**, 923–932 (1990).
 29. Kingdom, F. A. A. & Keeble, D. R. T. A linear systems approach to the detection of both abrupt and smooth spatial variations in orientation-defined textures. *Vision Res.* **36**, 409–420 (1996).
 30. Rubenstein, B. S. & Sagi, D. Spatial variability as a limiting factor in texture discrimination tasks: implications for performance asymmetries. *J. Opt. Soc. Am. A*, **7**, 1632–1643 (1990).
 31. DeValois, R. L., Albrecht, D. G. & Thorell, L. G. Spatial frequency selectivity of cells in macaque visual cortex. *Vision Res.* **22**, 545–559 (1982).
 32. Solomon, J. A. & Pelli, D. G. The visual filter mediating letter identification. *Nature* **369**, 395–397 (1994).
 33. Stromeyer, C. F., Klein, S. & Sternheim, C. E. Is spatial adaptation caused by prolonged inhibition? *Vision Res.* **17**, 603–606 (1977).
 34. Jonides, J. in *Attention and Performance* Vol. IX (eds. Long, J. B. & Baddeley, A. D.) 187–204 (Erlbaum, Hillsdale, New Jersey, 1981).
 35. Robson, J. G. & Graham, N. Probability summation and regional variations in contrast sensitivity curves across the visual field. *Vision Res.* **21**, 408–418 (1981).
 36. Sutter, A., Sperling, G. & Chubb, C. Measuring the spatial frequency selectivity of second-order texture mechanisms. *Vision Res.* **35**, 915–924 (1995).
 37. Moran, J. & Desimone, R. Selective attention gates visual processing in the extrastriate cortex. *Science* **229**, 782–784 (1985).
 38. Luck, S. J., Chelazzi, L., Hillyard, S. A. & Desimone, R. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77**, 24–42 (1997).
 39. Reynolds, J. H. & Desimone, R. The role of neural mechanisms of attention in solving the binding problem. *Neuron* **24**, 19–29 (1999).
 40. Graham, N. & Sutter, A. Spatial summation in simple (Fourier) and complex (Non-Fourier) texture channels. *Vision Res.* **38**, 231–257 (1998).
 41. Heeger, D. J. Model for the extraction of image flow. *J. Opt. Soc. Am. A* **4**, 1455–1471 (1987).
 42. Grossberg, S. & Mingolla, E. Neural dynamics of perceptual grouping: textures, boundaries, and emergent features. *Percept. Psychophys.* **38**, 141–171 (1985).
 43. Foley, J. M. Human luminance pattern-vision mechanisms: Masking experiments require a new model. *J. Opt. Soc. Amer. A* **11**, 1710–1719 (1994).
 44. Sagi, D. Detection of an orientation singularity in Gabor textures: effect of signal density and spatial-frequency. *Vision Res.* **30**, 1377–1388 (1990).
 45. Joseph, J. S., Chun, M. M. & Nakayama, K. Attentional requirements in a 'preattentive' feature search task. *Nature* **387**, 805–807 (1997).
 46. Motter, B. M. Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* **70**, 909–919 (1993).
 47. Ito, M. & Gilbert, C. D. Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* **22**, 593–604 (1999).
 48. Brefczynski, J. A. & DeYoe, E. A. A physiological correlate of the 'spotlight' of visual attention. *Nat. Neurosci.* **2**, 370–374 (1999).
 49. Gandhi, S. P., Heeger, D. J. & Boynton, G. M. Spatial attention affects brain activity in human primary visual cortex. *Proc. Natl. Acad. Sci. USA* **96**, 3314–3319 (1999).
 50. Martinez, A. *et al.* Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nat. Neurosci.* **2**, 364–369 (1999).