PERGAMON

Vision Research 40 (2000) 1293–1300

Vision Research

www.elsevier.com/locate/visres

Feature-based integration of orientation signals in visual search

Stefano Baldassi [a], David C. Burr [a,b,*]

[a] *Istituto di Neurofisiologia del CNR, Via S. Zeno 51, Pisa 56127, Italy*
[b] *Dipartimento di Psicologia, Università di Firenze, Florence, Italy*

Received 5 August 1999; received in revised form 19 January 2000

Abstract

We have measured orientation discrimination in the presence of a variable number of neutral distracters for two distinct tasks: *identification* of the orientation of a tilted target and *location* of its position. Both tasks were performed in the presence of visual noise of variable contrasts. Under a range of conditions, subjects could identify the direction of target tilt at thresholds well below those necessary to locate its position. The location thresholds showed only weak dependency on set-size, consistent with a stimulus uncertainty of parallel search of the output of independent orientation analysers, while the identification thresholds showed a much stronger dependency, varying with the square root of set-size over a wide range noise contrasts. The square root relationship suggests perceptual summation of target and distracters. Manipulating the spread of visual noise suggests that the summation is feature-based, possibly operating on the outputs of first-stage orientation analysers. Pre-cueing the target eliminates the effects of set-size, showing that the summation is under rapid attentional control; the visual system can choose between high performance over a limited area and poorer performance over a much larger area. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Orientation discrimination; Attention; Visual noise; Visual search

---

1. Introduction

An important issue in visual science is the extent to which selective attention to a target can increase the speed and accuracy with which the target is detected and analysed. Under some conditions cueing attention may have little effect, while under others the effects are very large indeed, both in speed and in accuracy. One of the more common techniques to study the effects of cueing is the ‘visual search’ paradigm, where observers are required to make some perceptual judgement about a *target* in the presence of a variable number of neutral *distracters* (for review see Wolfe, 1996). When cueing is important, performance in the uncued conditions depends on the number of distracters. The reduction in performance has often been assumed to imply serial processing through mechanism of limited capacity (Neisser, 1963; Treisman, 1982; Bergen & Julesz, 1983), although the serial-parallel dichotomy has recently come under serious question (Duncan, 1989; Duncan & Humphreys, 1989; Cheal & Lyon, 1994; Joseph, Chun & Nakayama, 1997; Eckstein, 1998; Nakayama & Joseph, 1998; Palmer, Verghese & Pavel, 2000).

The vast majority of studies of visual search measure reaction times, but some studies measure psychophysical thresholds, such as orientation or length discrimination, and have demonstrated very large effects of cueing and of distracter number (Palmer, Ames & Lindsey, 1993; Morgan, Ward & Castet, 1998). These experiments are particularly interesting, as threshold measures are easier to interpret quantitatively, and can be related more readily to other psychophysical results and known neurophysiological mechanisms.

Various explanations have been suggested for the effects of set-size. One of the more common suggestions is that cueing reduces the spatial uncertainty of target location (Palmer et al., 1993; Palmer, 1994; Solomon, Lavie & Morgan, 1997). This is a purely statistical advantage resulting from the intrinsic variability (internal noise) in the representations of visual stimuli; the more representations to choose from, the greater the probability that random variations cause a non-target to be wrongly chosen as target. This approach has proven quantitatively accurate under several conditions

---

[*] Corresponding author. Tel.: +39-050-559711; fax: +39-050-559725.

E-mail address: dave@in.pi.cnr.it (D.C. Burr)

PII: S0042-6989(00)00029-8

(Palmer et al., 1993; Palmer, 1994; Solomon et al., 1997) but has been challenged under others (Morgan et al., 1998). Another possible explanation is that of perceptual integration, where signal information is combined at a perceptual stage, leading to a stronger set-size dependency. The possibility was rejected by Palmer (1994) but strongly supported by Morgan et al. (1998) for orientation discrimination. Specifically they claim that the effect of distracters in an orientation discrimination task can be explained by high process of perceptual integration, limited by a central noise source.

The use of visual noise has proven particularly useful in vision research (e.g. Pelli, 1985, 1990; Heeley, Buchanan-Smith, Cromwell & Wright, 1997). Adding external noise to the stimulus can provide much information about the mechanisms involved in the analysis of the stimulus, and in estimating the amount and the site of internal noise within the visual system. These techniques have recently been applied to the study of attention (Lu & Dosher, 1998; Lee, Itti, Koch & Braun, 1999), providing useful information about the nature and location of mechanisms governing visual attention.

This study examines further the effects of attention on visual resolution, by measuring orientation discrimination in the presence of visual distracters and visual noise. Orientation discrimination is a particularly useful task, as it is reasonably well understood, with simple and plausible theories relating discrimination to the orientation selective cells of primary visual cortex (Regan & Beverley, 1985). It is also a useful task as humans have an internal standard of vertical, and readily detect small deviations from it (Buchanan-Smith & Heeley, 1993). We measure orientation discrimination thresholds for two different tasks: for identifying the direction of target tilt, and for locating the position of the target. Under some conditions subjects can identify the target tilt with threshold well below those necessary to locate its position, suggesting that the orientation of a target can be identified correctly without know where the target is. The results suggest that identifying the direction of target tilt depends on perceptual summation of orientation signals by second-stage integration, while thresholds for location are well predicted by position uncertainty. Measurements with visual noise suggests that the primary noise source is early, in the orientation detectors themselves, rather in the central integrator.

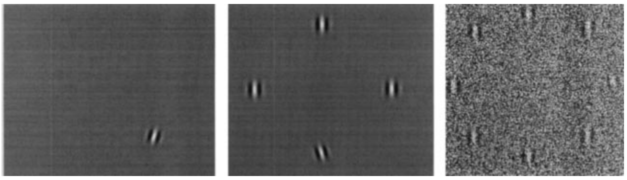
Fig. 1. Examples of the stimuli used in this study. The left-hand figure shows the target alone, tilted 8° clockwise. The central figure has three vertical distracters (set-size 4), with the target cued by a small peripheral spot displayed 20 ms before the target. The right-hand figure shows an uncued target with seven distracters (set-size 8), with superimposed binary visual noise of 35% contrast. Subjects fixated a central spot, and the grating came on for 100 ms. Throughout any given session, set-size, cueing condition and noise level remained constant.

2. Methods

Two young adults with normal or corrected vision served as observers. One was naïve of the aims of the experiment.

A small grating patch, tilted slightly off vertical, was briefly displayed for 100 ms at 5° eccentricity, either alone or in the presence of a variable numbers of iso-eccentric and equi-spaced vertical distracters (illustrated in Fig. 1). The patches comprised gratings of 2 cyc/deg, 50% contrast, curtailed with a two-dimensional Gaussian window of space constant 0.5°. The mean luminance of the screen was 20 cd/m^2. For many conditions, binary visual noise of variable contrast was added to the display, illustrated in Fig. 1C. The size of each noise pixel was 0.05°. No mask followed stimuli presentation.

On separate sessions, subjects were asked either to *identify* the direction of tilt of the target grating (clockwise or anticlockwise), or to *locate* its position on the screen. For some sessions of the identification discrimination, the position of the target was indicated to the observer by a *cue*, a small (0.25°) high contrast black dot displayed near the target 20 ms before it appeared, disappearing with the stimuli onset.

All measurements were made with a multiple alternative forced choice paradigm. For tilt identification, subjects pressed one of two response keys corresponding to clockwise or anticlockwise tilt. For location discrimination they pressed a key corresponding to the position of the target on the numeric keyboard of a standard PC keyboard, so the number of alternatives varied with set-size. Practice sessions preceded threshold measurement in order to minimise finger and proximity errors. Auditory feed-back for errors was provided in both tasks. Orientation of the tilt varied from trial to trial to home in near threshold, following the adaptive QUEST routine (Watson & Pelli, 1983). The QUEST routine was repeated five to six times, intermingling conditions, yielding 150–180 responses per subject per condition. The final estimate of thresholds for each condition was obtained by fitting a cumulative Gaussian to the percent correct judgements at each orientation:

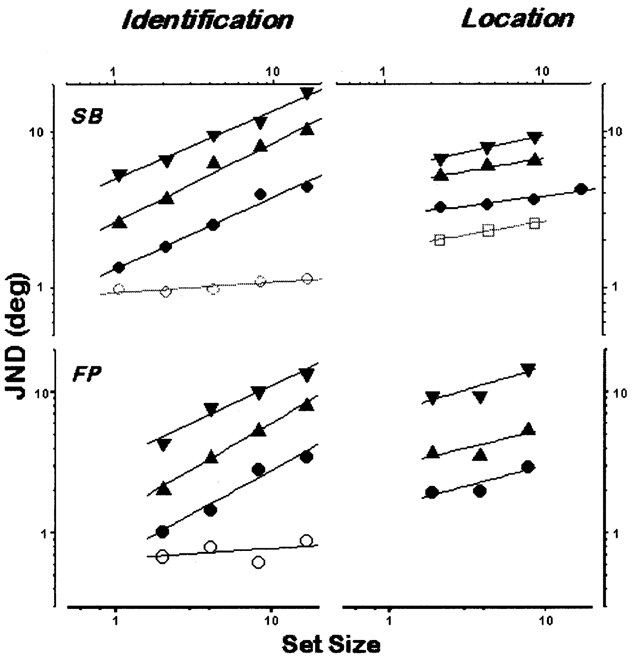

Fig. 2. Orientation discrimination thresholds for identifying the orientation of the target (left) or for locating its position (right) as a function of set-size, for subjects SB and FP. The open circles show results for the cued condition for identification (no noise), the filled symbols for uncued stimuli at various noise levels: circles no noise, upright triangles 17%, inverted triangles 34% noise. The open squares of subject SB show results for location when the target was always tilted clockwise, simplifying the task. Although the absolute thresholds are lower, the slope remains similar to the others (0.18). The values of the slopes of the conditions are plotted in Fig. 3.

$$p_\theta = \gamma + \frac{1-\gamma}{\sigma\sqrt{2\pi}} \int e^{(-\ln^2(\theta/\theta_0))/2\sigma^2}\, d\theta \qquad (1)$$

γ is the guessing rate (0.5 for identification and the inverse of set-size for location discrimination). θ is orientation and σ the standard deviation that determines the steepness of the curve. θ_0 is orientation threshold, corresponding to the point of inflection of the sigmoid curve, always half way between guessing level and perfect performance. Both θ_0 and σ were determined by best fit.

3. Results

3.1. Effect of set-size on identification and location

The effects of variable number of neutral distracters on orientation discrimination, with various levels of visual noise, are shown in Fig. 2. Thresholds for identifying tilt direction are shown on the left and for locating the tilted target on the right. The various curves with filled symbols indicate results in which the target was not cued, for different levels of visual noise. For tilt identification, thresholds depended strongly on set-size. At all levels of noise, the slope of the threshold versus set-size curves was around 0.5 on logarithmic co-ordinates, indicating a square root relationship. The thresholds for locating the target also depended on set-size, but the log–log dependency was much shallower, around 0.2. It is also interesting to compare the absolute levels of the two conditions. For some conditions, the thresholds for identification were considerably lower than for location, showing that subjects could discern the orientation of a target without knowing which of the stimuli contained the orientation cue.

The open circles show identification thresholds for ‘cued’ targets. Here the distracters had very little effect on thresholds. This shows that subjects could effectively ignore the distracters and direct their attention to the target, if the target was indicated (in agreement with many other studies (Palmer et al., 1993; Carrasco & Yeshurun, 1998; Morgan et al., 1998)). As the cue was displayed only 20 ms before the target, its efficacy shows that attention can be directed quite quickly.

The open squares show discrimination thresholds for one subject for locating a target that was known to be tilted clockwise. This simplified the task, as the subject could search for the most clockwise stimulus rather than searching for the most tilted stimulus. Thresholds were lower for this condition, but the slope of the curve remained the same.

Fig. 3 summarises the effect of set-size for the two tasks, plotting the logarithmic slope of the threshold versus set-size functions (like those of Fig. 2) as a function of noise contrast. For both subjects, the set-size dependency for identification was clearly different from that for location, and both were independent of noise level. For identification, the slopes were consistently around 0.5, implying a square root relationship. For location the slopes are far less, averaging around 0.2. The slope for the ‘always clockwise’ target is shown by an open triangle, similar to that of the other condition.

3.2. Theoretical predictions

A square root dependency on distracter number suggests an integration mechanism: the discrimination task may be performed simply by summing the noisy output of local orientation detectors, possibly normalising the result to calculate mean orientation. The theoretical signal-to-noise (S/N) level for such an integrator is readily calculated. The signal is simply the sum of the orientations (θ_i) for all k stimuli. As the distracters have orientation zero the sum is equal to the target orientation θ_t:

$$S = \sum_{i=1}^{k} \theta_i = \theta_t \qquad (2)$$

We may simplify the noise analysis by supposing three separate noise sources: the external noise added to the stimulus (N_{ext}), the intrinsic noise of each local orientation detector (N_{int}) and a central noise source at the level of the integrator (N_{cent}), that does not vary with set-size. The total noise N can be calculated by summing the variances of each noise source (see for example Pelli, 1990):

$$N = \sqrt{k(N_{\mathrm{int}}^2 + N_{\mathrm{ext}}^2) + N_{\mathrm{cent}}^2} \qquad (3)$$

Assuming signal-to-noise ratios (S/N) to be constant at threshold, an integrator model predicts threshold values of target orientation:

$$\theta_{\mathrm{t}} \propto \sqrt{k(N_{\mathrm{int}}^2 + N_{\mathrm{ext}}^2) + N_{\mathrm{cent}}^2} \qquad (4)$$

Alternatively, a mechanism that averages rather than sums orientation values (normalising both signal and noise by dividing by k) predicts:

$$\theta_{\mathrm{t}} \propto \sqrt{k(N_{\mathrm{int}}^2 + N_{\mathrm{ext}}^2) + k^2 N_{\mathrm{cent}}^2} \qquad (5)$$

Over the range where $N_{\mathrm{cent}}^2 < < N_{\mathrm{int}}^2 + N_{\mathrm{ext}}^2$ the central noise can be effectively ignored so both the integrator and averaging models (Eqs. (4) and (5)) predict:

$$\theta_{\mathrm{t}} \propto k^{0.5} \qquad (6)$$

giving a logarithmic slope of 0.5, as observed at all levels of noise (Fig. 3).

The fact that the slope of the set-size functions does not vary with external noise levels suggests that under these conditions the central noise N_{cent} was not a significant limiting factor for orientation thresholds. Otherwise one would expect N_{cent} to dominate at low but not at high values of external noise, changing the slopes of the functions. The exact effect on the slope would depend on whether one assumes the straight summation of Eq. (4) (where it should drop to 0) or the averaging of Eq. (5) (where it should increase to 1); but both equations predict a systematic noise-dependent change of slope, while none is apparent in the data of either subject in Fig. 3.

Note also that the prediction of log–log slope of 0.5 is different from that of 0.8 predicted by Palmer et al. (1993), as they assume that subjects must also locate the position of the target. Our results (lower thresholds for discrimination than for detection) suggest that location of target position is not necessary. This idea is supported by observer reports, claiming to do the task on a ‘global sense of tilt’, without identifying which grating was tilted. It is also consistent with the fact that identification thresholds can be half those for location under the same conditions.

The location results are well predicted by target uncertainty. Several such models have been elaborated in detail to explain set-size effects (e.g. Shaw, 1980; Palmer et al., 1993; Verghese & Stone, 1995), all predicting log–log slopes of around 0.25, consistent with the results shown here. Simply put, if there exists a mechanism searching the output of orientation detectors for the most tilted stimulus, then increasing the number of distracters will increase the chance that the noisy output of at least one distracter will be more tilted than that of the target.

3.3. Tilted distracters

The suggestion of different mechanisms for discrimination and location leads to a clear prediction: tilting the distracters should affect the two tasks differently. Tilting them in the same direction as the target should aid identification (by increasing the summed orientation signal) but should hinder the location task (reducing the orientation contrast between target and distracter). Tilt in the opposite direction to the target should have the reverse effect on the two tasks.

To test this prediction, the distracters were caused to tilt away from the vertical, by a constant proportion of the target tilt. In a given session, the distracters could be tilted in the same direction (positive tilt factor) or

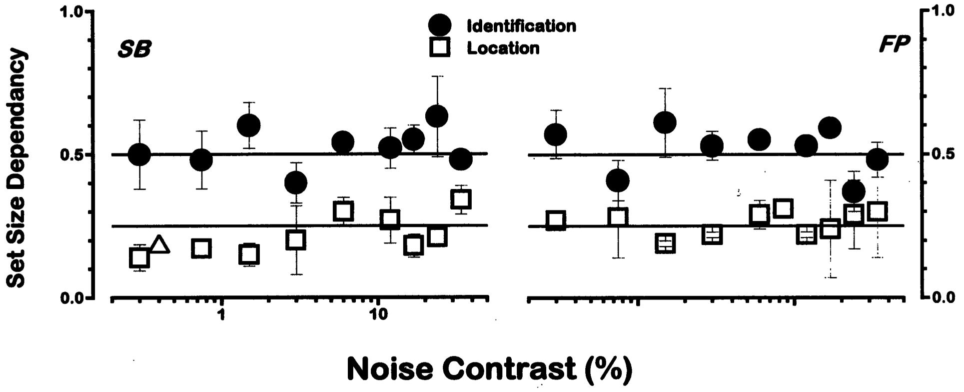

Fig. 3. Set-size dependency, given by the log–log slope of the threshold versus set-size functions, for the two tasks at various levels of noise. The filled symbols represent the identification task, open symbols localisation (with error bars showing the error of the linear fit). The open triangle (for SB) shows the slope of the condition when the target was always tilted clockwise. The horizontal lines show the theoretical predictions for the two tasks (see methods).

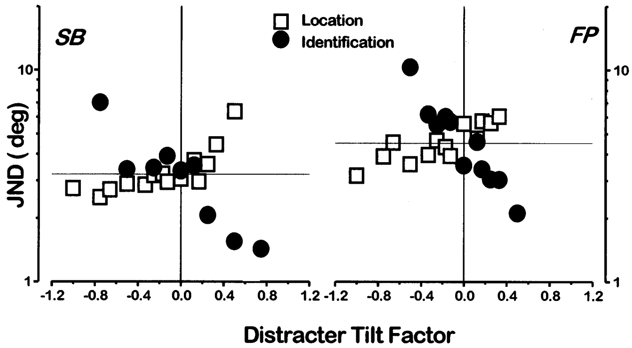

Fig. 4. The effect of tilted distracters on thresholds for the two different tasks. The 'distracter tilt factor' refers to the amount of tilt of the distracters, relative to the target tilt. For a value of 1 they were all identical to the target, at −1 they were tilted by the same amount in the opposite direction as the target and at 0 they were all vertical. The distracter tilt varied with the target tilt from trial to trial, as the QUEST program homed in on threshold. The distracters were tilted off vertical either in the same (positive) or opposite (negative) direction as the target, randomly interleaved within a given session. For any given session, the amount of tilt was always a constant proportion of that of the target, varying from trial to trial with the target. The results show that tilt in the same direction aided identification and hindered location, while opposite direction had the opposite effect.

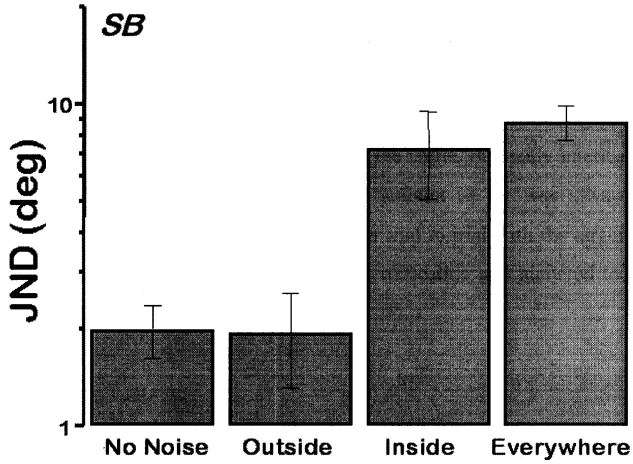

Fig. 5. Orientation discrimination thresholds for target identification in the presence of three distracters, under four conditions of noise: no noise; noise (34% contrast) confined to fall outside the stimuli (noise free radius 1°); confined to fall on the stimuli, within a Gaussian window 1.5 times that of the stimuli; or over the entire screen. It is clear that only noise on the stimuli had any detrimental effect.

the opposite direction (negative tilt factor), randomly interleaved from trial to trial. The distracter tilt factor was the amount of tilt compared with the target tilt: a factor of one had the same tilt as the target, −1 the opposite. The magnitude of the tilt also varied from trial to trial, remaining a fixed proportion of the target tilt (that changed with the QUEST routine). Note that any factor less than one was below the individual threshold under that particular condition.

The results are shown in Fig. 4. As predicted, tilting the distracters had different effects for the location and identification tasks. Tilt in the same direction aided the identification task (presumably by adding to the average tilt) while hindering the location task (presumably by decreasing tilt contrast). Conversely, tilt in the opposite direction hindered identification while aiding location.

3.4. Feature- or space-based integration?

If there do exist integration mechanisms for identification, how do they operate? Do they simply sum over a given spatial region, or combine the output of local analyses of the grating patches? To investigate this, we repeated measurements with a set-size of four under four different conditions of added noise: no-noise, noise over the entire screen, noise confined to the grating patches and noise everywhere except the grating patches. The results (Fig. 5) show that noise outside the grating patches had virtually no effect, although it covers an area much greater than that covered by the gratings. Only noise falling on the grating patches affected thresholds. This clearly points to a second-stage integration of specific visual features, rather than a global integration over a given region of space.

4. Discussion

The results of this study all suggest that visual search for orientation tasks in the presence of distracters can be well explained by parallel processing: either integration for tilt identification, or parallel search for location of the tilted target. The dependency on set-size is quantitatively predictable in both tasks, resulting simply from the effects of early neural noise in the orientation detection process: there is no need to assume that the dependency on set-size reflects serial processing, or some bottleneck of limited capacity. The suggestion that identification is achieved by pooling the outputs of detectors is supported by subject report, by the lower threshold for orientation than location discrimination and, most significantly, by the effects of tilting the distracters: tilt in the same direction decreased thresholds, while that in the opposite direction increased them. If the position of the target is 'cued' 20 ms before its appearance, the distracters have no effect, showing that the integration pool is under attentional control.

The idea that orientation discrimination can operate on an average of orientation signals has been suggested previously by Dakin and Watt (1997), and taken up in the context of visual search by Morgan et al. (1998). However, the current integration model for identification has a major difference. Morgan and colleagues inferred a central limiting noise source at the level of the integrator, both from the steepness of the set-size effects and the weak summation effects for multiple targets of the same tilt. However, our results suggest that the primary noise source is in the peripheral detectors themselves. The robust data showing square root relationships over a very wide range of conditions does not support a central noise source. Furthermore, a major central noise source would predict that the set-size dependency should vary with the external noise level of the stimulus, as the external noise source will effectively sum with early neural noise, and must dominate at some stage (see Eqs. (4) and (5)). However, the slopes of the set-size functions showed no noise dependency whatsoever (Fig. 3), as expected by both summation and averaging mechanisms. The reason for the discrepancy between our data and those obtained by Morgan for short duration displays is not clear at this stage. One possibility is that in the summation task of Morgan et al., the thresholds were so low that they were dominated by a central noise source or thresholding mechanism. Indeed we have preliminary data that this may be the case, with evidence for summation at high but not low noise levels.

As mentioned earlier, our results are consistent with both simple integration and with averaging, given that thresholds seem to be dominated by early noise sources that will also be scaled by any averaging process. It is therefore difficult to choose between these two possibilities. On the one hand, an averaging mechanism is appealing, as this would give an estimate of average orientation texture (Dakin & Watt, 1997). On the other hand it could be inefficient to reduce signal amplitude before combination with the major noise source.

The current study shows that different tasks can activate different mechanisms. The location task could not be mediated by an integration mechanism, as this would necessarily destroy positional information. However, these results are perfectly consistent with parallel search of the noisy output of the independent orientation detectors, with the slight dependency of set-size an inevitable statistical side effect of noisy detectors (Palmer et al., 1993; Verghese & Stone, 1995). It may at first glance seem strange that thresholds are higher for location than for identification. The most likely explanation for this is that for the location task, subjects had to locate the most tilted stimulus, without knowing the direction of tilt, so there were in effect two unknowns. Identification, on the other hand, was a single task, judging whether the target was more or less clockwise. The extra uncertainty could easily explain the poorer performance with few distracters. Indeed, when the task was changed so the direction of tilt was known, location thresholds were always below identification thresholds. The slope, however, remained shallow.

Other mechanisms have been suggested for the action of attention on perceptual tasks. For example, with a different paradigm for manipulating attention, Lu and Dosher (1998) and Lee et al. (1999) have independently shown that manipulating the level of attention can alter the gain and selectivity of early visual mechanisms. However, this could not explain the current results, as it predicts different effects at different noise levels. The changes in selectivity and gain should act to exclude the added noise, producing shallower curves at high noise levels.

Dependency on set-size is usually taken as the signature for serial rather than parallel processing. This idea originated with studies measuring reaction times, where the increase in reaction time with additional stimuli is presumed to reflect an increase 'search time' in the serial search, but is readily adapted to threshold measures, assuming a limited central processing capacity (see Wolfe, 1996 for review). However, the serial-parallel dichotomy has recently been challenged by several researchers (e.g. Eckstein, 1998; Nakayama & Joseph, 1998). Similarly, this study shows that a strong dependency on set-size need not imply serial processing, but is entirely predictable by a very simple parallel processing mechanism, provided the limiting noise source is early: increasing set-size increases the number of mechanisms involved, hence the total noise source.

Previous studies on the effects of set-size on identification have been ambiguous: some have observed strong set-size effects, others none at all. For example, a weak set-size effect was also shown by Palmer et al. (1993, 1994) measuring orientation thresholds for both small ellipses and short lines, using two different measurement procedures (yes/no and 2IFC). One possibility for the difference between their results and ours could lie in the stimuli used. Doherty and Foster (1999) have also showed different set-size effects for identification of short and long lines: strong set-size effects for short lines (that they interpret to suggest serial processing), but weak set-size effects for long lines, suggesting parallel processing. These results could be accounted for by the integration model of Eq. (4), if the dominant noise source were to vary from peripheral to central. Short lines (like our vignetted gratings) have relatively high thresholds, so the dominant noise source will be early (N_{int}), and this increases with the square root of set-size. Thresholds for long lines are much lower, so the central noise N_{cent} may dominate, and this is independent of set-size. This idea is readily testable: adding external noise (N_{ext}) to the display will cause the early noise to dominate, inducing a set-size effect in long lines.

One may also ask whether the present results can be generalised for stimulus dimensions other than orientation. There is a good deal of evidence that the dependency of set-size in visual search varies considerably with the type of discrimination. For example, luminance and colour discriminations can show very little set-size effect under some conditions (Bonnel, Stein, & Bertucci, 1992; Verghese & Nakayama, 1994), while contrast discriminations tend to show greater effects (Solomon et al., 1997). This may imply that different mechanisms are involved in different tasks. Alternatively, it may imply that the primary noise source for those tasks is central rather than peripheral. If N_{cent} of Eq. (2) were large compared with N_{int}, there would be no set-size dependency. Again this idea is easily testable; adding external noise N_{ext} should cause the early noise to dominate, creating a set-size effect.

Noise falling outside the grating patches did not affect thresholds, ruling out the possibility of a simple global integration across the whole field. This suggests the action of 'second-stage' mechanisms, working on the output of primitive orientation detectors, and under voluntary attentional control. With a similar experimental design, Morgan and Parkes (1999) have shown that orientation discrimination does not depend on the spatial phase of the distracters, also pointing to second-stage rather than simple integration. These results are consistent with the idea that attention is focussed on visual 'features' rather than to a general region of space (Duncan, 1984; Duncan & Nimmo-Smith, 1996; Roelfsema, Lamme & Spekreijse, 1998; Treue & Martinez Trujilo, 1999). However, although the integration may be featured-based and clearly 'second-stage', it is not necessary that it *occur* at a higher level of analysis; only that it be *controlled* by higher top-down processes. For example, the integration may be mediated by the long-range horizontal interactions of primary visual cortex, connecting cortical cells of similar orientation (Gilbert, 1985). Recent studies suggest that the strengths of these interactions may be under attentional control (Ito, Westheimer & Gilbert, 1998).

References

Bergen, J. R., & Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. *Nature*, *303*, 696–698.

Bonnel, A.-M., Stein, J.-F., & Bertucci, P. (1992). Does attention modulate the perception of luminance gratings? *Quarterly Journal of Experimental Psychology*, *44A*, 601–626.

Buchanan-Smith, H., & Heeley, D. (1993). Anisotropic axes in orientation perception are not retinotopically mapped. *Perception*, *22*, 1389–1402.

Carrasco, M., & Yeshurun, Y. (1998). The contribution of covert attention to the set-size and eccentricity effects in visual search. *Journal of Experimental Psychology*, *Human Perception and Performance*, *24*(2), 673–692.

Cheal, M., & Lyon, D. R. (1994). Allocation of attention in texture segregation, visual search and location-precueing paradigms. *Quarterly Journal of Experimental Psychology*, *47A*, 49–70.

Dakin, S. C., & Watt, R. J. (1997). The computation of orientation statistics from visual texture. *Vision Research*, *37*, 3181–3192.

Doherty, L. M., & Foster, D. H. (1999). Limitations of rapid parallel processing in the detection of long and short oriented line targets. *Spatial Vision*, *12* (4), 485–497.

Duncan, J. (1984). Selective attention and the organisation of visual information. *Journal of Experimental Psychology General*, *113*, 501–517.

Duncan, J. (1989). Boundary conditions on parallel processing in human vision. *Perception*, *18*, 457–469.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychology Review*, *96*(3), 433–458.

Duncan, J., & Nimmo-Smith, I. (1996). Objects and attributes in divided attention: surface and boundary systems. *Perception and Psychophysics*, *58*, 1076–1084.

Eckstein, M. (1998). The lower visual search efficiency for conjunctions is due to noise and not serial attional processing. *Psychological Science*, *9*, 111–118.

Gilbert, C. D. (1985). Horizontal integration in the neocortex. *Trends in Neuroscience*, *8*, 160–165.

Heeley, D. W., Buchanan-Smith, H. M., Cromwell, J.A., & Wright, J. S. (1997). The oblique effect in orientation acuity. *Vision Research*, *37* (2), 235–242.

Ito, M., Westheimer, G., & Gilbert, C. D. (1998). Attention and perceptual learning modulate contextual influences on visual perception. *Neuron*, *20*(6), 1191–1197.

Joseph, J. S., Chun, M. M., & Nakayama, K. (1997). Attentional requirements in a 'preattentive' feature search task [see comments]. *Nature*, *387*(6635), 805–807.

Lee, D. K., Itti, L., Koch, C., & Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *Nature Neuroscience*, *2*(4), 375–381.

Lu, Z. L., & Dosher, B. A. (1998). External Noise distinguish attentional mechanisms. *Vision Research*, *38*(9), 1183–1198.

Morgan, M. J., & Parkes, L. (1999). Orientation discrimination is improved both by collinear and non-collinear flanking stimuli. *Perception*, *28*, 39d.

Morgan, M. J., Ward, R. M., & Castet, E. (1998). Visual search for a tilted target: tests of spatial uncertainty models. *Quarterly Journal of Experimental Psychology*, *51A*, 343–370.

Nakayama, K., & Joseph, J. (1998). Attention, pattern recognition, and pop-out in visual search. In R. Parasuraman, *The attentive brain* (pp. 279–298). Cambridge, MA: MIT Press.

Neisser, U. (1963). Decision time without reaction time: experiments in visual scanning. *American Journal of Psychology*, *76*, 376–385.

Palmer, J. (1994). Set-size effects in visual search: the effect of attention is independent of the stimulus for simple tasks. *Vision Research*, *32*, 1703–1721.

Palmer, J., Ames, C. T., & Lindsey, D. T. (1993). Measuring the effect of attention on simple visual search. *Journal of Experimental Psychology*, *Human Perception and Performance*, *19*, 108–130.

Palmer, J., Verghese, P., & Pavel, M. (2000). The psychophysics of visual search. *Vision Research*, *40*, 1227–1268.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America*, *A2*, 1508–1532.

Pelli, D. G. (1990). The quantum efficiency of vision. In C. Blakemore, *Vision: coding and efficiency* (pp. 3–24). Cambridge: Cambridge University Press.

Regan, D., & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America*, *A2*, 147–155.

Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, *395*, 376–380.

Shaw, M. L. (1980). Identifying attentional and decision making components in information processing. In R. S. Nickerson, *Attention and performance VIII* (pp. 277–296). New Jersey: Hillsdale.

Solomon, J. A., Lavie, N., & Morgan, M. J. (1997). Contrast discrimination functions: spatial cuing effects. *Journal of the Optical Society of America A*, *14*, 2443–2448.

Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology Human Perception and Performance*, *8*(2), 194–214.

Treue, S., & Martinez Trujilo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*, 575–579.

Verghese, P., & Nakayama, K. (1994). Stimulus discriminability in visual search. *Vision Research*, *34*(18), 2453–2467.

Verghese, P., & Stone, L. S. (1995). Combining speed information across space. *Vision Research*, *35*, 2811–2823.

Watson, A. B., & Pelli, D. G. (1983). QUEST: a bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*, 113–120.

Wolfe, J. M. (1996). Visual search. In H. Pashler, *Attention*. London: University College London Press.