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Interaction of spatial and temporal integration in global form processing

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Abstract

The mechanisms by which global structure is extracted from local orientation information are not well understood. Sensitivity to global structure can be investigated using coherence thresholds for detection of global forms of varying complexity, such as parallel and concentric arrays of oriented line elements. In this study, we investigated temporal integration in the detection of these forms and its interaction with spatial integration. We find that for concentric patterns, integration times drop as region size increases from 3° to 10.9°, while for parallel patterns, the reverse is true. The same spatiotemporal relationship was found for Glass patterns as for line element arrays. The two types of organization therefore show quite different spatiotemporal relations, supporting previous arguments that different types of neural mechanism underlie their detection.

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1. Introduction

Representation of the significant properties of the visual world requires the identification of large scale structures. Such structures are often implicit in the spatial relationships between local elements—for example, parallelism and contour continuation. The importance of the identification of large-scale visual structure has been recognized since the Gestalt psychologists; however, the mechanisms by which global structure is extracted from local pattern information are not yet well understood. Many physiological and psychophysical studies have investigated how the brain processes local pattern information (e.g., contour orientation) at the level of primary visual cortex (V1), and knowledge is accumulating on the nature of the complex representations in the occipito-temporal pathway that are used to identify objects. Between these two ends, the processes by which the brain transforms the low level local representations into high level global representations are largely unknown. These

intermediate processes may be studied by investigating the detection of structures that are simple, and do not raise the semantic aspects of object identification, but require operations on a large spatial scale compared to their component elements (“global form stimuli”). Here we study two such structures: concentric and parallel arrays of oriented line elements. The sensitivity of the human visual system to the global structure can be quantified in terms of coherence thresholds—the proportion of elements in an otherwise random array that need to conform to the structure in order for its organization to be detected (Atkinson et al., 1997; Wilson, Wilkinson, & Asaad, 1997). This measure is an analogue, for the form processing system, of the motion coherence thresholds, which are a well-established way of investigating extra-striate levels of processing in the visual motion system (Baker, Hess, & Zihl, 1991; Britten, Shadlen, Newsome, & Movshon, 1992; Newsome & Paré, 1988).

There is evidence from several sources that global forms with concentric structure tap some specific processes within human vision that are distinct from the processes involved in detecting parallel structure. It has been found that coherence thresholds for detecting concentric structure are lower

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than those for detecting parallel structure (Dakin, 1997, 1999; Kurki & Saarinen, 2004; Lewis et al., 2004; Wilson & Wilkinson, 1998; Wilson et al., 1997) and several studies have suggested the processing of concentric and parallel organization involves different degrees of spatial integration (Braddick et al., 1999; Wilson & Wilkinson, 1998; Wilson et al., 1997). The greater spatial summation seen for concentric structure suggests that this organization is processed at a relatively global level, while parallel structure is processed more locally (although see Dakin & Bex, 2002 for an alternative explanation that depends on cues from the edge of the pattern area). Further support for different underlying neural mechanisms comes from single unit studies that have found neurons in area V4 that are more sensitive to concentric, radial and hyperbolic gratings than to parallel gratings (Gallant, Braun, & Van Essen, 1993, 1996) and a recent fMRI study reporting that human V4 is activated more strongly by concentric gratings than by parallel gratings (Wilkinson et al., 2000).

Area V4 is able to pool information about local orientation signals across space because its receptive fields (in macaque) are 4–7 times larger than those in V1 (Desimone & Schein, 1987). Wilson and Wilkinson (1998) and Wilson et al. (1997) have therefore proposed that concentric structure is processed by specialized detectors in V4, while parallel structure is processed by complex cells in area V1/V2. An alternative view is that global form structure, whether the organization is concentric or parallel, may be processed by basically similar mechanisms (Dakin, 1997, 1999; Dakin & Bex, 2002). Such mechanisms could involve either specialized detectors with large receptive fields (e.g., V4 neurons) or an interactive process which integrates information among multiple local detectors (V1/V2 neurons). Psychophysically assessed spatial summation might reflect either kind of process. It would be helpful to have additional lines of argument on the level of processing at which either kind of organization is detected.

Arguments from spatial summation rest on the idea that, at successive stages of processing, convergence of inputs from the preceding level will in general act to increase the spatial area over which information is combined. A similar argument applies for time; in general successive stages of processing will increase rather than decrease temporal integration, so evidence that one process shows combination of information over a longer duration than another will indicate that the former is likely to be acting later in a sequence of processes. Thus, if concentric organization is more complex than parallel and is processed by later stages in the occipito-temporal pathway, concentric patterns might be expected to require longer temporal integration than parallel patterns. The studies of global form so far discussed used the same short stimulus durations, of the order of 150 ms, for both concentric and parallel patterns. However, the proper comparison of performance with the two pattern types ought to take account of the possibility that the same stimulus duration may not be optimal for both.

Furthermore, space and time may interact. Interactions between spatial and temporal integration in visual processing have been found in other domains. For example, in a study measuring thresholds for stimuli of different luminosities, critical duration was found to be shorter for larger stimuli (Roufs & Meulenbregger, 1967). The present study investigates whether, and how, spatial and temporal integration interact in the processing of global pattern information.

The data we report below shows that for large region sizes, the detection of concentric patterns has a shorter integration time than for parallel, suggesting that the apparently more complex concentric configuration is detected by a faster system. However, this relation is reversed for small region sizes. To allow comparison with other data in the literature, the main experiment using form coherence stimuli composed of short line segments was replicated with Glass patterns, and a similar pattern of results was observed. The two types of global processing therefore show quite different spatiotemporal relations, implying that the neural mechanisms involved have quite different properties and are unlikely to represent serial stages in the processing of form information.

2. Methods

2.1. Equipment

An IBM-compatible desktop computer controlled stimulus presentation and recorded subjects' responses. The programs for running the experiment were written in the Lua environment, version 5.0 (see <http://www.lua.org/> and Ierusalimsky, 2003). Stimuli were presented on an Eizo FlexScan T652-T color monitor driven by a Radeon 7000 graphics card at a refresh rate of 75 Hz. The screen resolution was 1280 × 1024 pixels. Subjects viewed the display from a distance of 0.5 m in a dimly lit room, and responded by pressing the left or right mouse buttons.

2.2. Stimuli

2.2.1. Form coherence stimuli (line elements)

Stimuli were arrays of 2530 short black line elements ($0.46^\circ \times 0.05^\circ$) presented against a white background (luminance 43 cd/m²) on a computer screen measuring $36.5^\circ \times 27.6^\circ$. Lines were drawn with sub-pixel accuracy and could be oriented at any angle from 0° to 180° in 1° steps. Each line element was placed within a grid of positions spaced at $0.8^\circ \times 0.8^\circ$ and randomly jittered by $\pm 0.16^\circ$ horizontally and vertically.

A concentric form was created by orienting the line elements, in a region surrounding the central fixation point, tangentially to virtual concentric circles (see Figs. 1A and B). A parallel form was created by orienting the line elements in the central region either vertically or horizontally (see Figs. 1C and D). The line elements outside the central form region were oriented randomly. The diameter of the central form region could be one of four sizes: 3°, 6°, 8.5° or 10.9°. Stimulus coherence was varied by replacing a proportion of the systematically arranged elements in the central region with randomly oriented elements (see Fig. 1B). The proportion of elements aligned according to the concentric or parallel organization defined the value of form coherence. A centrally located black fixation square measuring $0.35^\circ \times 0.35^\circ$ was present throughout the experiment.

2.2.2. Glass patterns

To compare this study to previous work, we tested two of the subjects with the same paradigm but using Glass patterns, setting stimulus parameters to match closely the stimuli used by Dakin and Bex (2002) and Wilson and Wilkinson (1998). Black dots were presented against a white back-

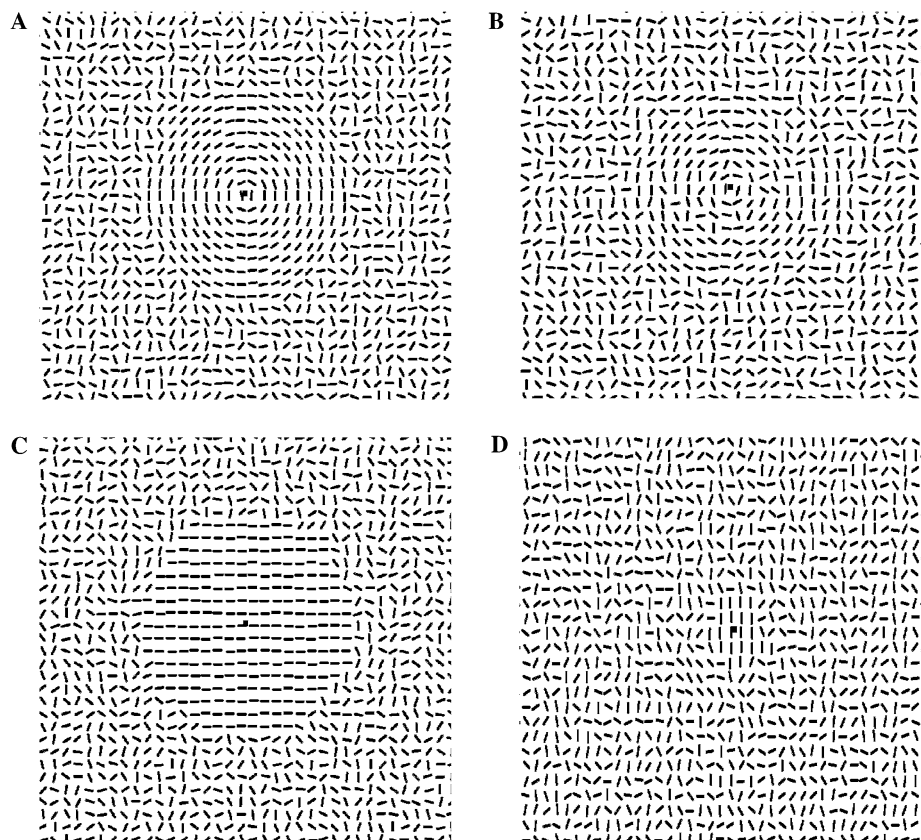


Fig. 1. Form coherence stimulus at different coherence levels and diameters. (A) 100% coherent concentric (10.9° diameter); (B) 60% coherent concentric (10.9°); (C) 100% coherent parallel (horizontal) (10.9°); (D) 100% coherent parallel (vertical) (3°).

ground on a computer screen measuring $36.5^\circ \times 27.6^\circ$ as before. Dots measured 0.08° square, dipole (dot pair) separation was 0.16° and dot density was set at 89.3 dipoles/deg². Dots were positioned with sub-pixel accuracy, and the orientation of dot pairs could take any value on a continuous distribution from 0° to 180° . Coherence levels were varied by replacing a proportion of the dipoles by randomly oriented dipoles. As in our other experiments (but not the earlier studies), the coherent region was surrounded by noise—i.e., randomly oriented dipoles, and its diameter was either 3° or 10.9° . Concentric Glass patterns were created by positioning dipoles randomly in the pattern but with the dipole orientation tangent to a circle centered on the pattern. Parallel Glass patterns were constructed in a similar way, by orienting dipoles either horizontally or vertically. The procedure of stimulus presentation was identical for both line element and Glass pattern stimuli, and is described below.

2.3. Procedure

The task was a two-interval forced choice and subjects had to indicate in which of the two intervals they saw a form appear. The two intervals in which the form stimulus could appear were preceded, separated and followed by masks, which consisted of arrays of randomly oriented line elements (or random dots in the Glass pattern experiment). The masks served to limit stimulus information from the global form to the defined interval. The durations of each interval were equal and were constant within a run, but between runs varied between 27 and 1733 ms. The duration of the first (pre-) mask was 400 ms; of the mask between intervals 800 ms and of the post-mask, 400 ms. The onset of the form stimulus was indicated by a short auditory tone. Tones occurred in both intervals but in only one interval did a form actually appear: in the non-target interval the display was composed entirely of randomly oriented line elements (or dipoles for the Glass pattern). After presentation of the 'post mask' the display became white (but the fixation square remained visible) and subjects responded by

pressing the mouse key to indicate in which interval they judged the form to be present.

In any one run, either parallel or concentric organization was used, and the runs were interleaved; subjects always knew which organization to expect. Within a 'parallel' run, vertically and horizontally oriented stimuli were presented in random sequence from trial to trial: this was intended to ensure that subjects had to detect the global organization, rather than monitoring the display for the presence of a particular orientation.

A Bayesian adaptive method—the ψ method (Kontsevich & Tyler, 1999)—was used to sample a range of coherence levels and converged on the level at which subjects gave 75% correct performance on the task. A single staircase consisted of 30 trials at a given combination of duration and stimulus diameter, and a single run comprised six staircases (one for each duration tested), of total duration ~ 9 min. The order of staircases (i.e., durations) presented within a run was randomized; however the stimulus diameter was kept constant within a run. Five runs were undertaken for each data point (i.e., for each combination of duration and stimulus diameter).

Critical durations for each stimulus diameter were determined by double-linear functions fitted to plots of log threshold vs. log duration. The functions were fit by a multi-phase linear regression fitting Java™ program created by Andrew Ganse of the University of Washington, USA. The program calculates slope, y -intercept, and total residual sum of squares for two conjoined lines best fitted to the data with least-squares.

2.4. Subjects

One of the authors (S1), one experienced observer (S4) and three naïve observers (S2, S3 and S5) were subjects in the experiments. For the experiment with random line elements, two subjects (S1 and S5) were tested on the full range of possible diameters of the form region and three further subjects were tested with the largest (10.9°) and smallest (3°) diameters.

For the Glass pattern experiment subjects S1 and S4 were tested with the 10.9° and 3° diameters.

All experiments were undertaken with the understanding and written consent of each subject.

3. Results

3.1. Temporal integration: Line element stimuli

Fig. 2 shows an example of the way in which integration time (critical duration) was derived from the data set for a particular subject, form organization, and region size. For all conditions, and all subjects, more variance was explained by fitting a double regression line to the data as compared to fitting a single regression line. The improvement in the r^2 value ranged from 0.003 to 0.203, with a mean improvement of 0.068.

Fig. 3 plots for each of the five subjects the critical durations for the smallest (3°) and largest (10.9°) region sizes. For the large region size, detection of the concentric structure shows a shorter integration time than detection of parallel structure. For the small region size this relation is reversed: temporal integration is longer for the concentric structure than for parallel. The figure shows that the detection of large concentric forms has a shorter critical duration than that of small concentric forms but the reverse is true for the parallel condition: critical duration increases with the area of the region. Analysis of variance (subject \times form type \times diameter ANOVA, with ‘subjects’ as a random factor) revealed a significant main effect of diameter ($F(1, 12) = 5.6$; $p = 0.036$) on critical duration, no main effect of form type ($F(1, 12) = 2.5$; $p = 0.14$), but a highly significant interaction of form type \times diameter ($F(1, 12) = 19.1$; $p = 0.001$).

Fig. 4 shows the full data from the two subjects who were tested on all four diameter sizes. Both subjects show critical duration rising with diameter for parallel structure, and falling with diameter for concentric structure. The functions cross over, with critical durations for the two types of pattern close to equal for a 6° diameter region. A

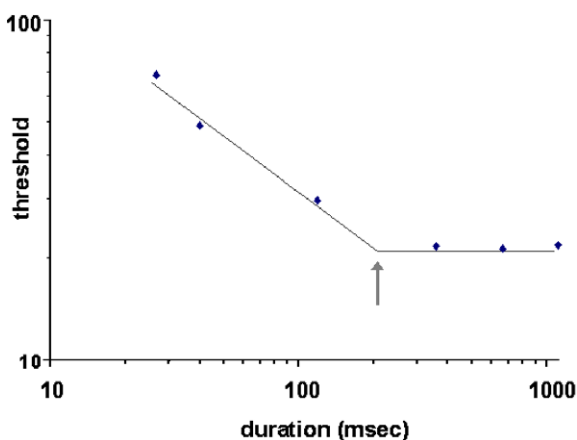


Fig. 2. Sample temporal integration function (for 6° diameter parallel stimulus, subject S1). Arrow indicates critical duration.

subject \times form type \times diameter ANOVA (with subject as random factor) of the data from these two subjects showed no main effect of form type ($F(1, 7) = 1.2$; $p = 0.31$) nor of diameter ($F(3, 7) = 2.6$; $p = 0.133$), but a significant interaction effect of form type \times diameter ($F(3, 7) = 7.0$; $p = 0.016$), see Fig. 4.

3.2. Glass patterns

Fig. 5 shows the data for the two subjects tested with Glass patterns. The general pattern is the same as that found for the line element displays: for both subjects tested, for large (10.9° diameter) patterns, critical durations were longer for parallel structure than for concentric structure but this relationship was reversed for small (3° diameter) Glass patterns. A subject \times form type \times diameter ANOVA (with subject as random factor) of these data showed no main effect of form type ($F(1, 3) = 2.55$; $p = 0.21$) nor of diameter ($F(1, 3) = 1.41$; $p = 0.321$), but a significant interaction effect of form type \times diameter ($F(1, 3) = 22.13$; $p = 0.018$).

3.3. Coherence thresholds

The data presented in Figs. 3–5 suggest that there will be no single answer to the question “which kind of global organization elicits maximum sensitivity?” since performance on parallel and concentric patterns varies differently as a joint function of spatial extent and duration. However, the asymptotic value of threshold as duration increases gives a measure that can be compared between the two tasks. Fig. 6A plots this value as a function of diameter, for the line element patterns for the two subjects whose data are shown in Fig. 4. Under the conditions of this experiment, performance for the parallel structure is consistently better than that for concentric (note, however, that this will not necessarily be true for shorter durations given the difference in temporal integration between the two types of display). However, Fig. 6B shows that this relation is reversed in the data obtained with Glass patterns: asymptotic thresholds are markedly lower for the concentric display, consistent with the results of Wilson and Wilkinson (1998).

Log-log fits to the two functions in Fig. 6A give a slope of -0.48 for log threshold vs. log diameter for the concentric pattern, and -0.85 for the parallel pattern.

4. Discussion

For each of the two forms of organization, our results show a spatio-temporal interaction, with temporal integration properties depending on the size of the pattern region. However, the nature of this interaction is quite different in each case: in concentric patterns, integration times drop as region size increases, while for parallel patterns, the reverse is true. Another way to express this result is that, for small regions, concentric detection shows a longer integration

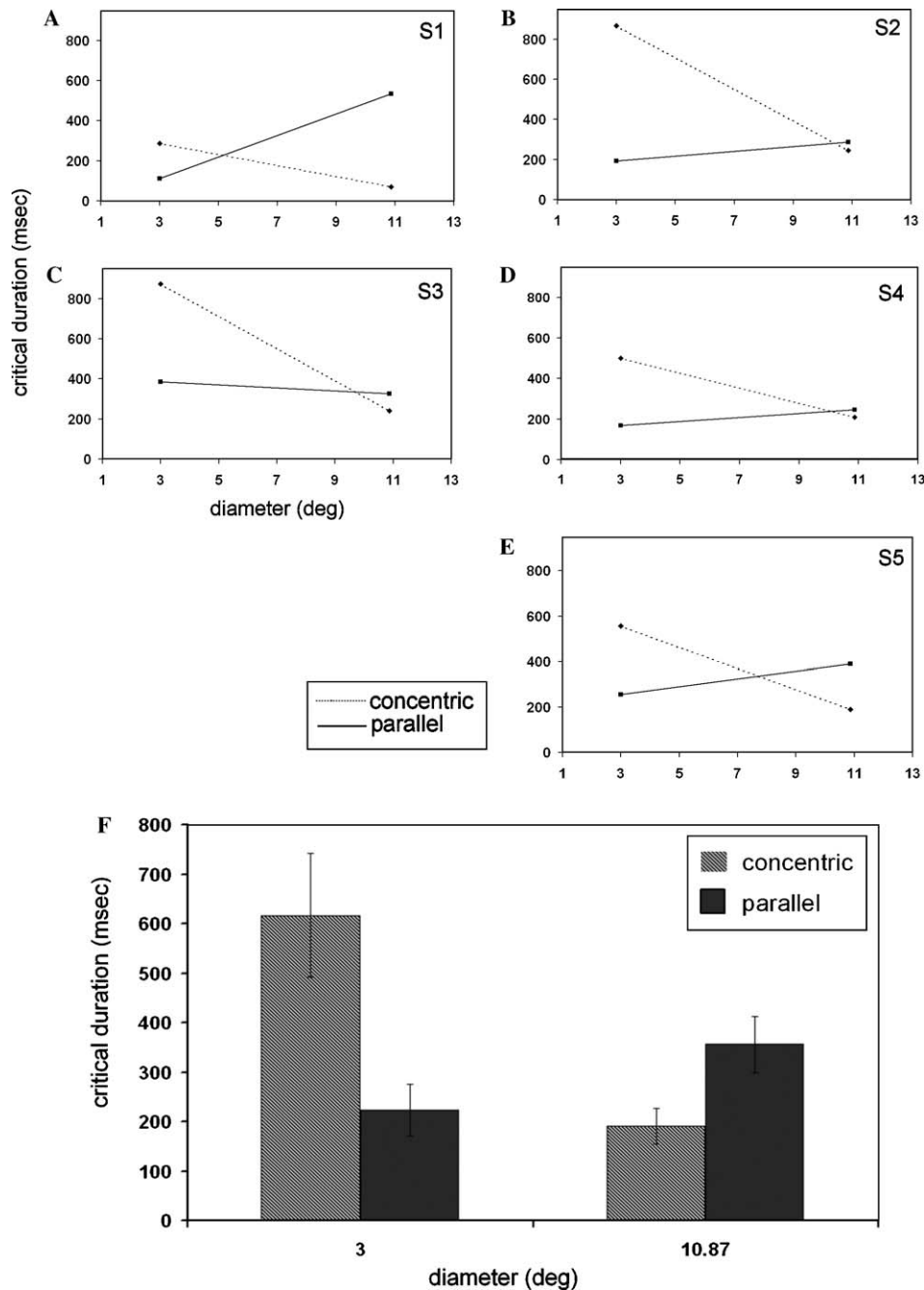


Fig. 3. (A–E) Plots of critical duration for 3° and 10.9° coherent form diameters for parallel and concentric conditions for individual subjects. (F) Group plots showing averaged data of all five subjects; error bars show standard error of the mean.

time than parallel, but this relationship is reversed for large regions. This difference in spatio-temporal properties argues for different neural mechanisms underlying the processing of concentric and parallel patterns.

How can we interpret these patterns of interaction? For the parallel condition the time to reach asymptotic performance increases with region size. This could be explained if a fast process, with short integration time, operated over a short spatial range, but a slower acting process integrated information over more spatially separated regions. We can suggest a relatively local, fast acting process that combines

parallel information over regions of a few degrees (possibly based on lateral interactions in V1). On this model, the system can only take advantage of information distributed over larger regions by involving a second-order process, which integrates signals for the local process and can do so over longer periods of time.

In contrast, the concentric patterns show primary temporal integration combining information over a region of at least 10°—i.e., this primary, fast-acting process is more global in spatial extent than for the parallel organization. The log-log gradient of threshold against diameter of

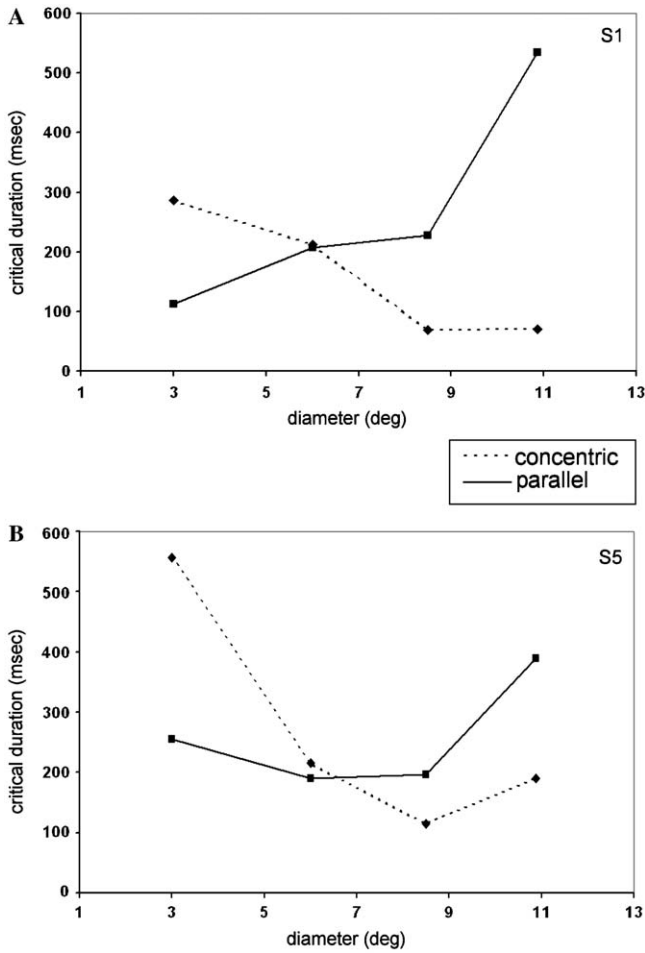


Fig. 4. Plots of critical duration for 3°, 6°, 8.5° and 10.9° coherent form diameters for parallel and concentric conditions for subjects (A) S1 and (B) S5. (Data for 3° and 10.9° also appear in Figs. 3A and E.)

approximately -0.5 , found for the concentric asymptotic results (see Fig. 6A) is consistent with linear summation of information over the area of the patch. The higher gradient found for parallel structure suggests that the summation process in this case is different, and non-linear.

It is also notable, that, for increasing sizes, the integration time for concentric structure decreases. This suggests an adaptive process that can extend temporal integration when the spatial extent of the information is reduced. This can perhaps be considered analogous to Kahneman and Norman's (1964) finding that temporal summation of luminance was task-dependent. It also resembles the data of Roufs and Meulenbregger (1967) which showed the critical duration for luminance summation to reduce with patch size, a finding that does not seem to have been followed up experimentally or theoretically.

It should be noted that, in our displays, the organized region was surrounded by random elements. Thus, obligatory pooling of information within a spatial integration region would have degraded performance for small region sizes. On the other hand, region size was constant within a run, so the subject could be aware of the region over which integration would be useful. There is some evidence for

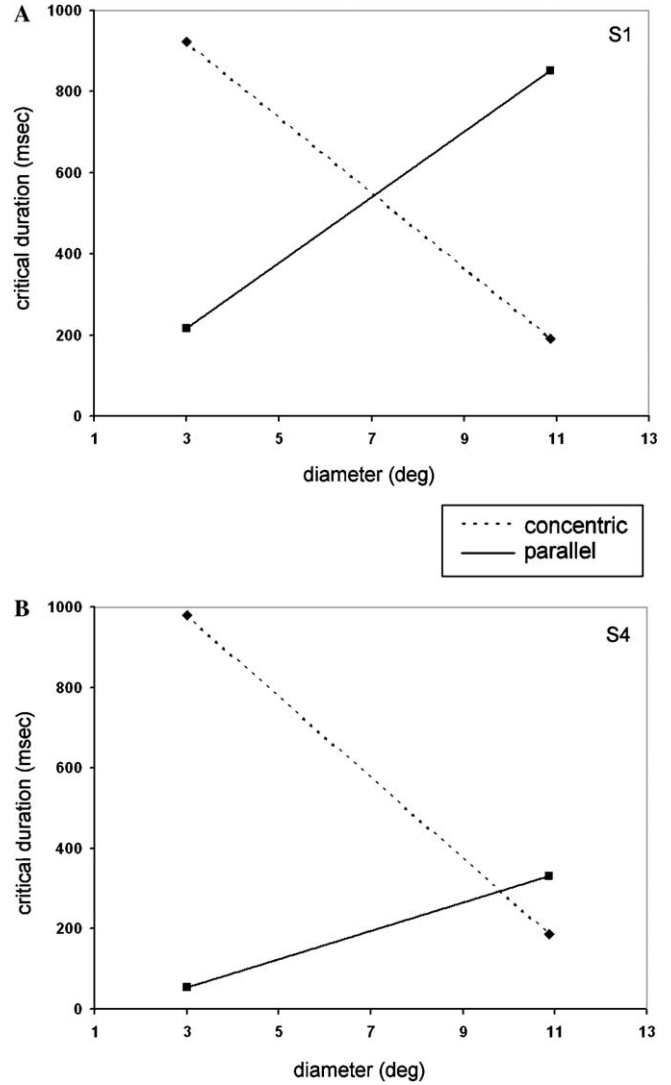


Fig. 5. Plots of critical duration for 3° and 10.9° diameter Glass patterns, for parallel and concentric conditions. (A) subject S1; (B) subject S4.

such obligatory pooling in orientation judgments (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) and in crowding phenomena for orientation and vernier discrimination (Levi, Klein, & Aitsebaomo, 1985; Westheimer & Hauske, 1975). The present data cannot distinguish between performance being lower with small patches because irrelevant information is integrated from the wider region, or simply because there is less of the relevant information available when the region is small. However, a speculative interpretation of the fall of integration time with region size for concentric patterns is that the process of selecting the relevant region for small patterns incurs a time penalty. On this argument, the penalty does not exist for parallel patterns because the intrinsic area of spatial integration is relatively small.

Whether or not these proposals are correct in detail, the pattern of our results implies radically different detection mechanisms for concentric and parallel structure, and supports previous suggestions (Kurki & Saarinen, 2004; Wilson & Wilkinson, 1998; Wilson et al., 1997) that specialized

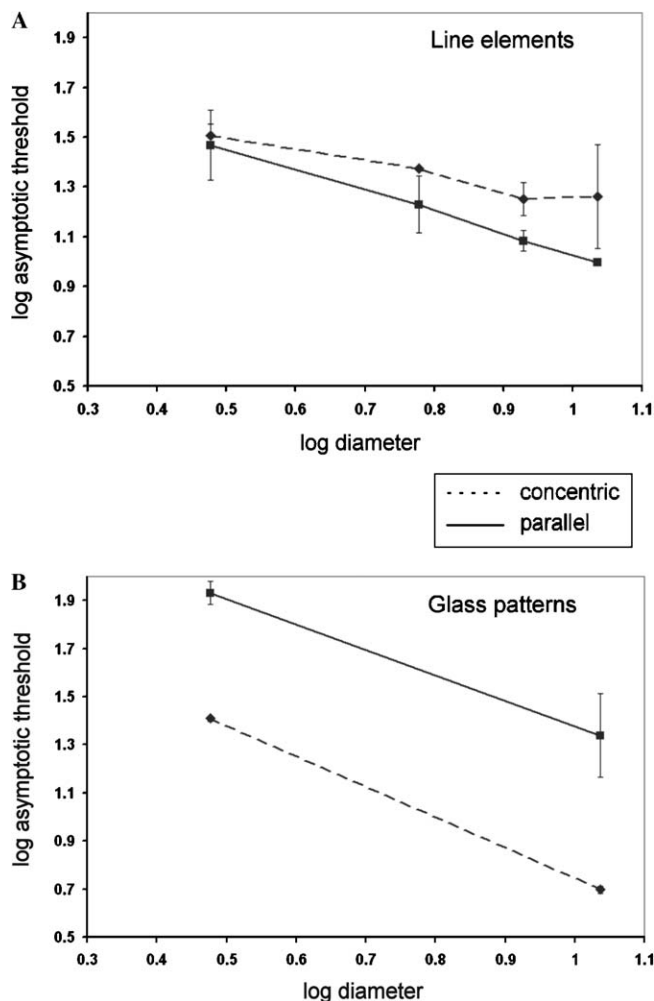


Fig. 6. Plot of asymptotic thresholds for different diameter sizes. Error bars show standard error of the mean. (A) Line element patterns (averaged data for subjects S1 and S5). (B) Glass patterns (averaged data for subjects S1 and S4).

global detectors exist for concentric structure, but not for parallel. The combination of information over large areas that occurs rapidly for concentric information is further support for the existence of such detectors, which, according to Wilson and Wilkinson (1998), form a second stage of processing, and are found in area V4. Indeed, some V4 neurons are known to be selective for curved contours, circular and concentric structure (Gallant et al., 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Kobatake & Tanaka, 1994). The large-scale integration of parallel structure involves mechanisms that are less efficient in temporal terms.

Receptive field sizes in V4 are approximately 3–5° at the fovea (Boussaoud, Desimone, & Ungerleider, 1991; Kobatake & Tanaka, 1994), however efficient temporal integration of concentric structure occurred up to diameters of 10.9° (we have not tested larger sizes). This may reflect V4 neurons representing more peripheral regions of the visual field. Alternatively, the processing responsible for this temporal integration may take place higher in the ventral visual

pathway—e.g., the human area homologous to macaque inferotemporal cortex (IT). IT neurons have receptive fields that are larger than in V4 and for some, concentric forms are the critical features for their activation (Kobatake & Tanaka, 1994).

The explanation suggested by Dakin and Bex (2002) for the differences in detection thresholds and spatial summation between parallel and concentric Glass patterns—that they are due to edge smoothness cues present only in concentric Glass patterns—does not find support in the present study. Our Glass patterns do not have strong edge smoothness cues as they are surrounded by random dipoles, and yet large differences in thresholds and spatial summation between the concentric and parallel patterns are still observed. Kurki and Saarinen (2004) also tested the ‘edge effect’ by fading out the contrast of dots at the edges of their Glass patterns but found no systematic effects on detection thresholds.

What are the constituent processes conferring sensitivity to concentric texture? At certain scales concentric forms also have locally parallel texture but they differ in many ways from parallel forms, e.g., in being made up (at higher coherence levels at least), of curved contours and closed contours (Kovacs & Julesz, 1993) and in having a more compelling global circular shape and symmetry. Further experiments are needed to determine which of these are the critical factors contributing to the global representation of form. It is also important to ask why specialized large-scale detectors might exist for concentric texture but not for parallel. In their fMRI study Wilkinson et al. (2000) showed that concentric structure activates the fusiform face area more effectively than does parallel structure, and half as well as actual faces, possibly because faces are themselves made up of roughly circular structures within other roughly circular structures (head, eyes, nostrils etc.). It may be that the extraction of concentric structure is one of the crucial intermediate stages in the processing of many important ecological features—not only faces—prior to complex object recognition at the highest stages of the ventral visual pathway. In contrast, ecologically significant use of parallel texture may be on relatively local scales—e.g., the use of texture gradients in determining surface orientation (Gibson, 1950) implies that texture density and orientation is determined over a small region that can be compared with other small regions elsewhere on the surface.

The proposal that sensitivity to concentric structure involves specialized global detectors does not necessarily imply that thresholds for concentric structure are lower than for parallel. In fact, our data show that asymptotic thresholds for our line element patterns are lower for parallel structure (Fig. 6A) over the whole range of pattern sizes (though not necessarily over the whole range of durations). Optimal sensitivity for the two types of mechanism occurs with different combinations of space and time, and the relationship between these different optimal values, considered in isolation, is not the most informative way to compare the underlying mechanisms.

It is noteworthy that the relationship between thresholds is different for Glass patterns (Fig. 6B, and see Wilson & Wilkinson, 1998) than for line elements. The most obvious difference between the two types of pattern is that in the Glass pattern, the potential pairings between dots in nearby dipoles creates a source of noise beyond the noise explicitly introduced when percentage coherence is reduced. This ‘correspondence noise’ becomes important given the high density of dipoles in the Glass patterns, and the fact that (unlike the line element patterns) there is no constraint to prevent dipoles from overlapping. These differences in signal to noise relationships may have had a differential effect on concentric and parallel patterns.

In conclusion, we argue that the different spatio-temporal patterns of performance between the two types of pattern provides a more secure basis for investigating the difference in underlying neural processing than does the comparison of level of performance on the two tasks.

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