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The effect of variability of unattended information on global and local processing: evidence for lateralization at early stages of processing

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Abstract

Visual objects can often be analyzed as hierarchical in structure, composed of local elements that are spatially arranged to form a global shape. The brain mechanisms involved in the analysis of hierarchical figures have been under considerable scrutiny in recent years, and one of the many interesting features that have emerged is that there is an asymmetry across the two hemispheres for global (right hemisphere) vs local (left hemisphere) processing. Event-related potentials (ERP) were used to examine selective attention to global or local levels of hierarchical figures to determine the stage of processing at which the asymmetry first emerges. Two conditions were tested, one in which unattended information was variable from trial to trial, and one in which it was not. The variability of unattended information influenced the lateralization of processing. Presentation of invariable, neutral distractors resulted in global/local processing asymmetries at early stages (P1). In contrast, presentation of variable, task-relevant distractors resulted in processing asymmetries that occurred at much later stages (N2). Our hypothesis is that lateralized enhancement of neural populations in extrastriate cortex results from both selective attention to locations in the visual field, as well as selective attention to global or local information. We suggest that unattended information that varies from trial to trial is processed in parallel with attended information, masking hemisphere biases for local vs global information at early stages of processing. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Object; Vision; Hemisphere; Extrastriate; Feedback; ERP

1. Introduction

In a now classic study, Navon [26] introduced a type of stimulus that simulates the hierarchical structure often found in natural objects, but allows better control over the content carried at each level (e.g. a large global letter is formed by the spatial arrangement of small local letters). There have been some very robust findings using these stimuli. For example, Navon found that subjects were faster to respond to global than local elements, and that inconsistent global information interfered with local processing but not vice versa. From these observations, Navon developed the global precedence hypothesis, the central idea being that the global level receives priority in perception. Furthermore, processing of global information begins before local information is available to the system [26,27]. Many investigators have interpreted global precedence to mean that the global and local levels are processed serially, however, evidence that speed of processing effects are dissociable from interference effects led to the idea that these two observations could not be taken together to imply serial processing [10,17].

Recent evidence from behavioural [1,12,14,16,40], brain-imaging [6,8–10], and neuropsychological studies [4,17,18], suggests that the mechanisms that subserve global/local processing operate in parallel systems in the right and left hemispheres (see [13] for a review).

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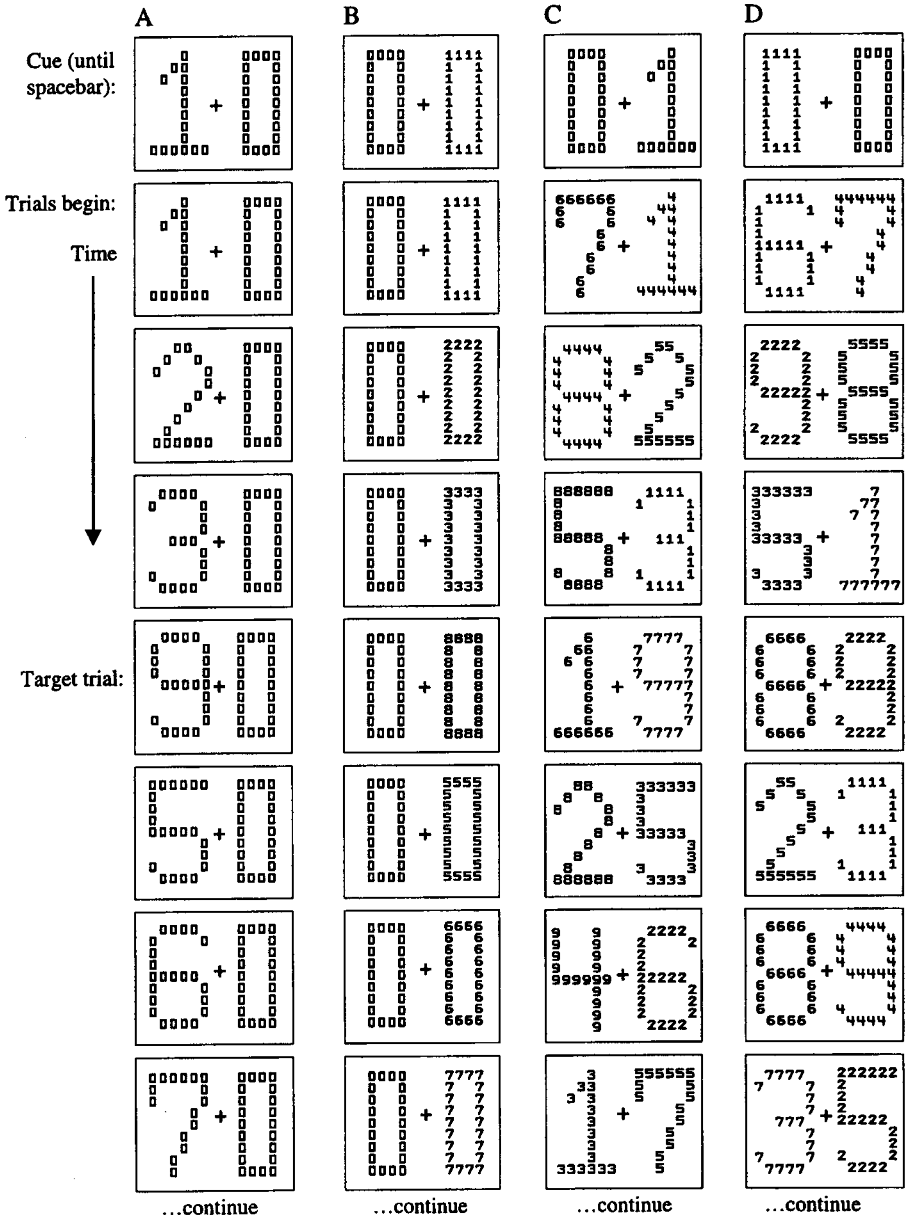

Fig. 1. The four columns are examples of the first seven (of 27) trials of four different block types. At the top of each column is shown the cue which indicates the Level (global or local) and Visual Field (LVF or RVF) to be attended. This cue remains on the screen until the spacebar is pressed to start the block of trials. At the attended level and visual field, digits are then presented in increasing sequence except for target trials to which a response is required. Column A: Global LVF attention with Invariable box-distractors (neutral boxes on every trial). Column B: Local RVF attention with Invariable box-distractors. Column C: Global RVF attention with Variable digit-distractors (digits which change from trial to trial). Column D: Local LVF attention with Variable digit-distractors. For each example, the fourth trial is an example of a target trial. The block types not shown are Global RVF and Local LVF (Invariable distractors), and Global LVF and Local RVF (Variable distractors).

While both hemispheres are capable of processing both global and local information, there is a bias for global processing in the right hemisphere (RH), and for local processing in the left hemisphere (LH).

Although the evidence for the hemispheric processing bias is compelling, the mechanisms underlying the lateralization are not well understood, and it is unclear at what stage the lateralization occurs. Some brain-imaging evidence exists for differentiation of global/local activity at processing stages as early as prestriate areas [6,8]. The prestriate cortical area has been identified as the generator location of the ERP component P1 [25], which occurs in response to visual stimuli with a peak latency as early as 80–100 ms. However, other evidence suggests that the lateralization of global/local biases does not occur until later stages of processing, indexed by a negative deflection in the ERP that occurs between 250 and 350 ms [9,10].

In the following experiment, we present data from two conditions, one which shows lateralization of global and local processing in extrastriate cortex (as indexed by the P1 component), and one which does not show lateralization until the later N2 component. Hierarchical figures constructed of digits were presented bilaterally. Participants selectively attended to either the global or local elements of either the left visual field (LVF) or the right visual field (RVF) figure. On each trial, at the attended level and position, digits were presented in a repeating sequence in ascending order, 1–9. At the selected level and position, participants monitored the ascending sequence of digits and responded each time an out-of-sequence digit was detected.

Most global/local studies employ detection tasks which involve small stimulus sets and a consistent mapping between target and response within a block of trials. For example, the target might be ‘H’ for all of the trials within a block [e.g. 9,29], and subjects respond when they detect a match between the expected and presented letter. In our task, there are a few important differences. First, the expected digit changes on each trial, and subjects do not respond to a match, but to a mismatch. Second, the relatively large target set also changes on each trial, because a target is any one of the eight out-of-sequence digits. We believe that the varied-mapping nature of our task requires a more controlled and complete processing of each attended item [cf. 39]. Third, the information carried at the unattended level is systematically controlled. In one condition, unattended items vary from trial to trial, consistent with most global/local paradigms reported in the literature, resulting in late lateralized global/local effects. In another condition, critical to our findings, unattended items do not vary from trial to trial, resulting in early lateralized global/local effects.

2. Method

2.1. Subjects

Twelve right-handed volunteers (nine females and three males) participated in the experiment for a small remuneration. Six of the volunteers were assigned to one experimental group (five females and one male in the Invariable box-distractor condition) and the remaining six were assigned to the other experimental group (four females and two males in the Variable digit-distractor condition). All subjects were right-handed as assessed by a subset of the handedness questionnaire outlined in Steenhuis and Bryden [43], and ranged in age from 23 to 38 years. All had normal or corrected-to-normal vision.

2.2. Stimuli

The hierarchical stimuli were global digits (1–9) constructed of local digits (1–9), producing 81 compound figures. These were used in the Variable digit-distractor condition. There were also global digits (1–9) constructed of neutral boxes, and neutral boxes constructed of local digits (1–9), producing another 18 compound figures. These were used in the Invariable box-distractor condition. A subset of the 99 hierarchical digit and box figures appears in the examples shown in Fig. 1. Global figures subtended a visual angle of 4.29° by 5.71° (width × height), and local figures subtended 0.38° by 0.57°. Stimuli were presented in pairs, centered vertically to the left and right of fixation, 2.29° of visual angle from the center of the fixation cross to the center of each compound figure. Stimuli were presented on a standard VGA computer monitor displaying 640 × 480 resolution with 60 Hz refresh rate. The testing room was dimly lit (approximately 30 cd/m^2) and the stimuli were presented white on a black background (approximately 15 and 0.3 cd/m^2, respectively). Timing of stimuli and response collection was controlled by MEL2 [38].

2.3. Procedure

Each experimental session was approximately 2 h in duration, including setup time. At the beginning of the session, participants received verbal instructions about the experimental procedure and the nature of the task. After the application of the electrodes, the participant was seated in front of a computer screen. A chin rest ensured that the distance between the subject and the computer screen, and so the retinal size of the stimulus, remained constant. Instructions were to remain fixated on the central cross for the duration of each block, and to maintain covert attention on the peripheral stimuli without eye movements. Two demonstration blocks of trials were presented, followed by six practice blocks. Finally, there were 72 test blocks of 27 trials; the duration of each block was 24.3 s.

During the demonstration blocks and practice blocks, participants were monitored closely and reminded of the importance of maintaining fixation. All of our subjects were psychology graduate students who were highly motivated and educated with respect to the importance of maintaining fixation, therefore we have confidence that this is not a concern. We also monitored eye movements with EOG electrodes placed beside and above the eyes.

Each block of trials began with a cue which remained on the screen until the subject initiated the

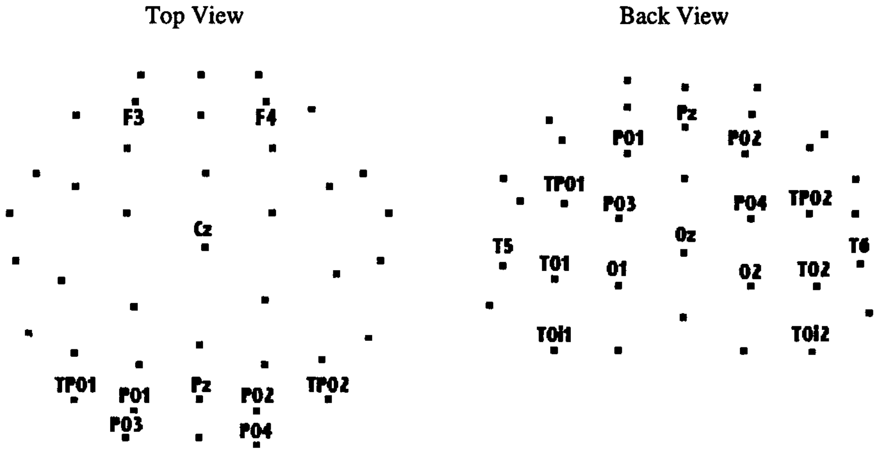

Fig. 2. Top View (left) and Back View (right) of 64 digitized electrode locations, fitted to a sphere. Note that locations near the edges of the sphere are not as close together as they appear, and that some of the lateral frontal electrode sites do not appear on these views. Electrodes were placed so that each electrode was as equidistant as possible from surrounding electrodes. Labeled electrodes are referred to in the text and figures, shown here at the frontal (F3/F4), central (Cz), occipital (Oz, O1/O2), temporal and temporal-occipital (T5/T6, TO1/TO2, TOi1/TOi2), parietal and parietal-occipital (Pz, PO1/PO2, PO3/PO4), and temporal-parietal-occipital (TPO1/TPO2) sites.

block by pressing the spacebar. The cue indicated the level (global or local) and visual field (LVF or RVF) to which attention should be directed for the duration of that block. The top row in Fig. 1 shows each of the four possible cues: Global LVF, Local LVF, Global RVF, and Local RVF attention. After the spacebar was pressed, the screen was cleared except for the central fixation cross. After a 1000 ms delay, the 27 trials began.

On each of the 27 trials, stimulus duration was 100 ms. Stimulus onset asynchrony (SOA) was selected randomly from a rectangular distribution ranging from 850 to 1050 ms. A random SOA was used to reduce the amount of distortion of ERP components due to averaging of overlapping epochs [44]. The fixation cross remained on the screen at all times.

The task involved monitoring an ascending sequence of digits (3 repetitions of 1–9) presented at the cued level (global or local) and visual field (LVF or RVF), and responding to targets by pressing a key with the right hand. A target was an out-of-sequence digit presented at the attended location. For example, given the sequence ‘1, 2, 3, 4, 8, 6, 7, 8, 9’ the first 8 is a target (see also the examples in Fig. 1). Targets were presented pseudo-randomly with the following constraints: (1) a target did not occur in the first or last two trials, and (2) two consecutive target trials did not occur. The probability of a target was 0.18. Instructions were to respond as quickly as possible without sacrificing accuracy. At the end of each block of trials, feedback was provided, including number of hits, misses, and false alarms, and the average response time for hits.

There were two between-subject conditions which differed in the nature of the distractors. In both conditions, the attended digits were presented in sequence from trial to trial (except for target trials). In the Invariable box-distractor condition, only the attended digit varied from trial to trial. The distractors in this case were always boxes (see two examples in Fig. 1, columns A and B), which were neutral in the sense that they never required a response in any of the conditions. In the Variable digit-distractor condition, the attended digit and all three distractor digits varied from trial to trial (see two examples in Fig. 1, columns C and D). The distractor digits were presented pseudorandomly with the following constraints: (1) a distractor digit did not equal the previous, current, or next in-sequence digit; (2) a distractor digit did not equal the target on the previous, current, or next trial; and (3) a distractor digit did not equal another distractor digit on the current trial.

2.4. EEG recording and method of analysis

Subjects were fitted with an elasticized cap mounted with 64 pure tin electrodes (ElectroCap International Inc.). The arrangement of electrodes in the custom-designed ElectroCap was such that each electrode was equidistant from surrounding electrodes; the array is illustrated in Fig. 2, which shows a top view and a back view of electrode placement after locations were digitized and fitted to a sphere for calculation of topographical maps. Eye movements and blink activity were monitored by leads placed supraorbitally and at the external ocular canthi. Each electrode was adjusted to maintain impedance below 5 kilo-ohms (kΩ) at scalp sites and below 10 kΩ at orbital sites. A continuous EEG was recorded from the 64 channel montage, referenced to the right mastoid and amplified by a cus-

Table 1
Means and standard errors of behavioural analysis of response times (ms) and accuracy. Accuracy is shown as proportion correct of target trials (hits/hits + misses)

	Global attention		Local attention	
	LVF (RH)	RVF (LH)	LVF (RH)	RVF (LH)
Variable digit-distractor group				
RT	561 (18)	568 (22)	591 (20)	582 (28)
Accuracy	0.89 (0.05)	0.90 (0.04)	0.83 (0.04)	0.84 (0.05)
Invariable box-distractor group				
RT	537 (23)	538 (25)	551 (18)	543 (22)
Accuracy	0.96 (0.02)	0.95 (0.02)	0.90 (0.05)	0.88 (0.02)

tom-built S.A. Instrumentation Bio-amplifier system. The recording bandwidth was 0.1–100 Hz and the signal was digitized at 400 Hz.

The EEG was segmented and averaged off-line. Epochs that contained eye blinks or other eye or muscle movement artifacts were discarded, making up approximately 10% of the epochs. Only epochs associated with correct behavioural responses were included in the averages. The data were digitally filtered using a low-pass 40 Hz filter and re-referenced using a distance-weighted Laplacian algorithm [11]. The topological maps were calculated from subtractions of global minus local voltage waveforms. Topologies were mapped using digitized electrode locations fitted to a sphere (Fig. 2). Spherical splines were used to interpolate the topological voltage maps [30].

Of the 64 electrodes (Fig. 2), the following electrode sites were selected for statistical analysis of component peaks and latencies. The labels correspond to the 10/20 system, including additional electrode sites named to reflect spatial relation to the 10/20 system sites. These sites were chosen based on differences between the conditions in the averaged waveforms and include frontal (F3/F4), central (Cz), occipital (Oz, O1/O2), temporal and temporal-occipital (T5/T6, TO1/TO2, TOi1/TOi2), parietal and parietal-occipital (Pz, PO1/PO2, PO3/PO4), and temporal-parietal-occipital (TPO1/TPO2) sites. At these sites, repeated measures analyses of variance (ANOVAs) were performed on the following components (ms time windows are shown in brackets): P1 (50–150 ms), N1 (100–200 ms), N2 (200–400 ms), and P3 (300–700 ms; target trials only). In addition to amplitude peaks and latencies, mean amplitudes within a time window were compared to determine statistical significance of differences between global and local processing in portions of the waveform for which a peak was not easily identifiable.

The factors that went into the ERP analyses for lateral electrode sites were attended Level (global vs local attention), attended Visual Field (LVF vs RVF attention), and Hemisphere of recording (left vs right electrode site). For central electrode sites, the factors Level and Visual Field were used. These sets of analyses were done separately for the Invariable (boxes) and the Variable (digits) distractor groups, and for target (P3) and non-target (P1, N1, and N2) trials.

3. Results

3.1. Behavioural results

Repeated measures ANOVA was used to examine the behavioural results for accuracy and RT, using the following factors: Level (global vs local attention), Visual Field (LVF vs RVF attention), and Invariable vs Variable distractor group as a between-subjects factor. Table 1 contains the means and standard errors for these data.

Both RT and accuracy were affected by attended Level. Over all, subjects were more accurate ($F(1,10) = 26.18$; $p < 0.001$) and faster ($F(1,10) = 8.24$; $p = 0.02$) to detect global targets than local targets. These behavioural results describe the classic observation of global processing dominance [26]. There was also a significant interaction between Level and Visual Field on RT ($F(1,10) = 9.68$; $p = 0.01$), in which local targets were detected more slowly when attention was directed to the LVF (Scheffé's test, $p < 0.01$). Although the difference between LVF and RVF attention for global targets was not significant (Scheffé's test, $p = 0.5$), the LVF disadvantage for local processing fits with a hypothesis of right hemisphere bias for global processing.

Although the mean RTs in each condition in the Invariable box-distractor condition were shorter than the corresponding means in the Variable digit-distractor condition (Table 1), the between-subject analysis comparing the two distractor groups revealed that differences were not statistically significant for accuracy or RT.

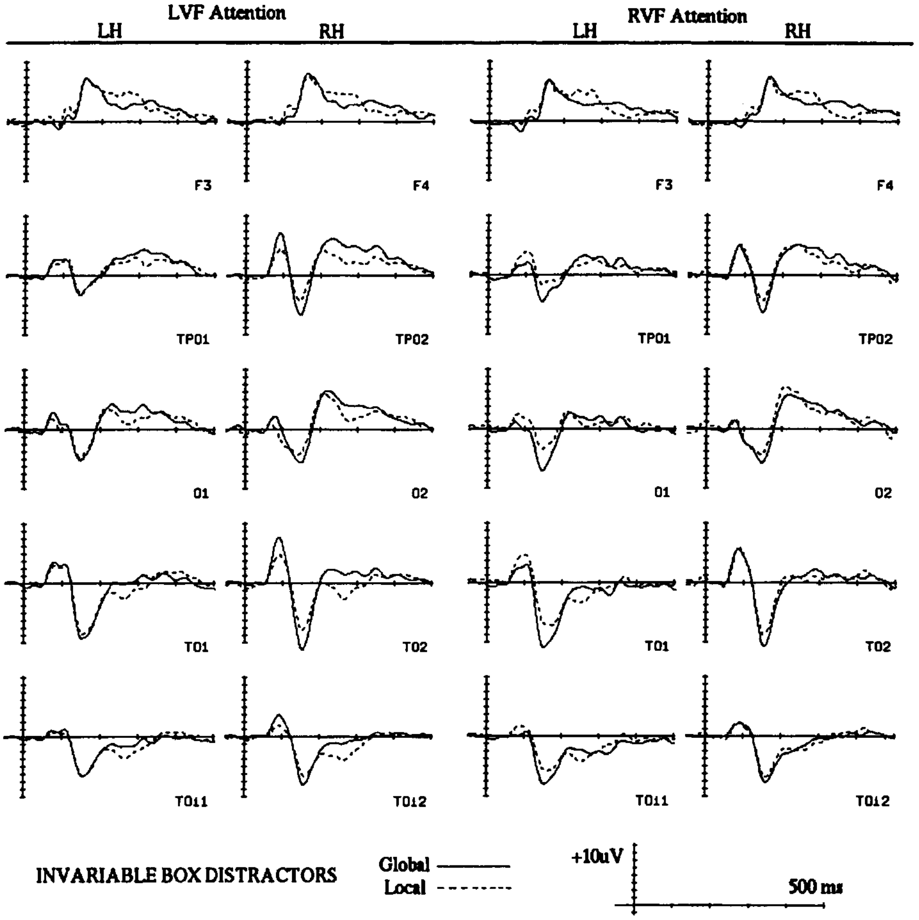

Fig. 3. Invariable box-distractor group. Global and local waveforms for LVF attention (left panel) and RVF attention (right panel), for frontal sites (F3/F4), temporal-parietal-occipital sites (TPO1/TPO2), occipital sites (O1/O2), temporal-occipital sites (TO1/TO2), and inferior temporal-occipital sites (TOi1/TOi2). Note the global/local difference in the P1 and the N1 that is greater over the RH sites for LVF attention, and over the LH sites for RVF attention. The global-P1 is larger than the local-P1 over RH sites for LVF attention. In contrast, the local-P1 is larger than the global-P1 over LH sites for RVF attention. The global-N1 is larger than the local-N1 over the contralateral hemisphere to the attended visual field.

3.2. ERP results

The waveforms from the global and local attention conditions are displayed for a small subset of the 64 electrode sites, for LVF (left panel) and RVF (right panel) attention, for the Invariable box distractor condition (Fig. 3), and the Variable digit distractor condition (Fig. 4). Waveforms comparing electrophysiological responses on target trials are displayed in Fig. 5 for the Invariable box distractor condition (top), and the Variable digit distractor condition (bottom). No significant differences in latency were found for any of the early components.

3.2.1. P1 component

3.2.1.1. Invariable box-distractor P1 amplitude. By far the largest and most lateralized effects on the amplitude of the P1 occurred for the Invariable box-distractor group. An interaction between Hemisphere of recording and Level described a larger local-P1 (compared to global) at LH sites (not significant; Scheffè's test; $p > 0.05$), and a larger global-P1 (compared to local) at RH sites (Scheffè's test; $p < 0.05$). This interaction was significant at the temporal sites (T5/T6; $F(1,5) = 12.06$; $p = 0.02$), temporal-occipital sites (TO1/TO2; $F(1,5) = 22.46$; $p < 0.01$), inferior temporal-occipital sites (TOi1/TOi2; $F(1,5) = 10.07$; $p = 0.02$), and temporal-parietal-occipital sites (TPO1/TPO2; $F(1,5) = 40.18$; $p < 0.01$). This is consistent with a hypothesis of a LH-local bias and a RH-global bias.

3.2.1.2. Variable digit-distractor P1 amplitude. At central sites (Oz), the global-P1 was larger than the local-P1 ($F(1,5) = 9.49$; $p = 0.03$). This was mostly evident when attention was also directed to the LVF, although statistically the Level × Visual Field interaction only approached significance ($F(1,5) = 6.44$; $p = 0.052$).

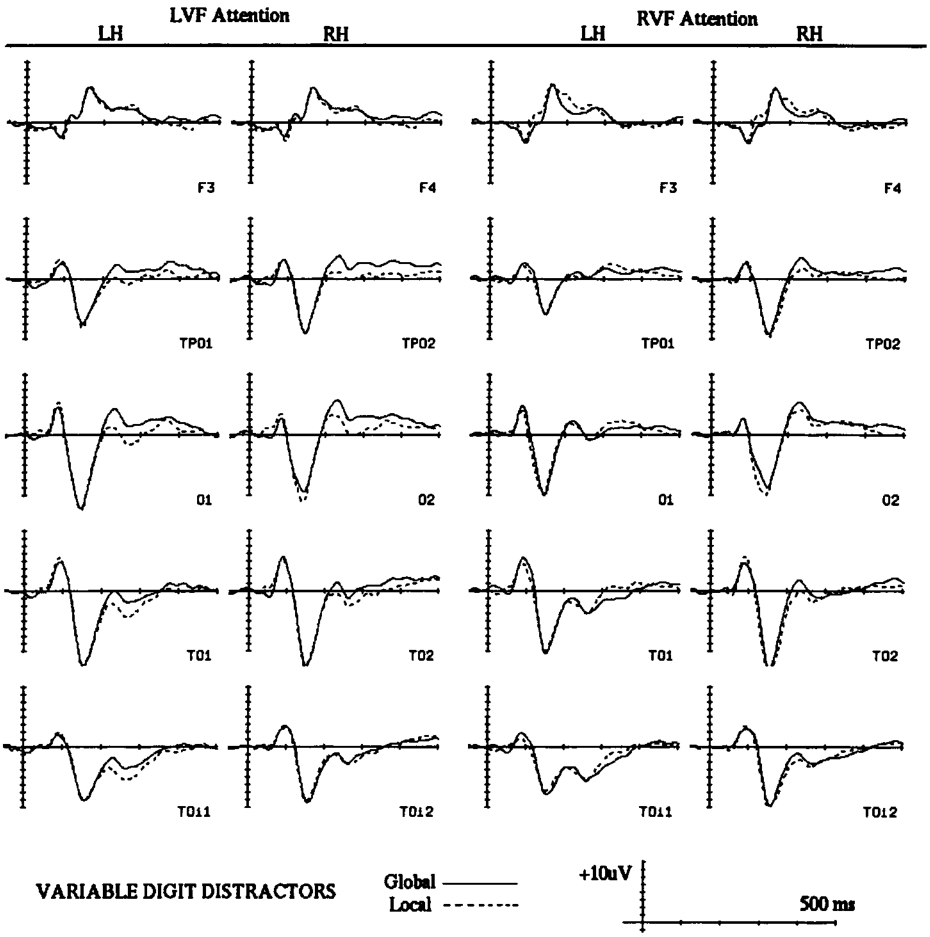

Fig. 4. Variable digit-distractor group. Global and local waveforms for LVF attention (left panel) and RVF attention (right panel). Note the absence of global/local differences in the P1 and the N1 compared to the Invariable box distractor condition, shown in Fig. 3.

None of the LH vs RH differences was significant. Given that the task is more demanding in the Variable distractor condition, one might hypothesize that global/local differences over posterior sites might be masked by frontal activity. However, there were no global/local differences in the early components over the frontal sites.

Fig. 6 illustrates the topological map of the P1 for the subtraction global minus local at 95 ms. All the topological difference maps were calculated using the Laplacian source derivation algorithm of Hjorth [11]. The global/local differences in the Variable digit-distractor condition were not lateralized. In contrast, in the Invariable box-distractor condition, the greater contralateral local-P1 during RVF attention is clearly contrasted with the greater contralateral global-P1 during LVF attention.

3.2.2. N1 component

3.2.2.1. Invariable box-distractor N1 amplitude. The largest effects of Level on the amplitude of the N1 occurred in the Invariable box-distractor condition. The N1 was greater for global attention than for local resulting in a main effect of Level at temporal sites (T5/T6; $F(1,5) = 7.63$; $p = 0.04$), temporal-occipital sites (TO1/TO2; $F(1,5) = 14.35$; $p = 0.01$), and temporal-parietal-occipital sites (TPO1/TPO2); $F(1,5) = 7.82$; $p = 0.04$). The global-local difference in the N1 amplitude also tended to be greater over the right hemisphere but the Hemisphere × Level interaction did not reach statistical significance. There was a Visual Field × Hemisphere interaction at frontal sites showing greater negativity over the left hemisphere, especially for RVF attention (F3/F4; $F(1,5) = 7.83$; $p = 0.04$). There were no Level effects at the frontal sites. Finally, the three-way Level × Visual Field × Hemisphere interaction was significant at parietal-occipital sites (PO3/PO4; $F(1,5) = 8.85$; $p = 0.03$), for which the global-N1 was greater over the hemisphere contralateral to the attended visual field, however this was only statistically significant for RVF attention at the LH site (Scheffé's test, $p < 0.05$).

3.2.2.2. Variable digit-distractor N1 amplitude. There was no effect of Level on amplitude of the N1 at any of the electrode locations. There were, however, latera-

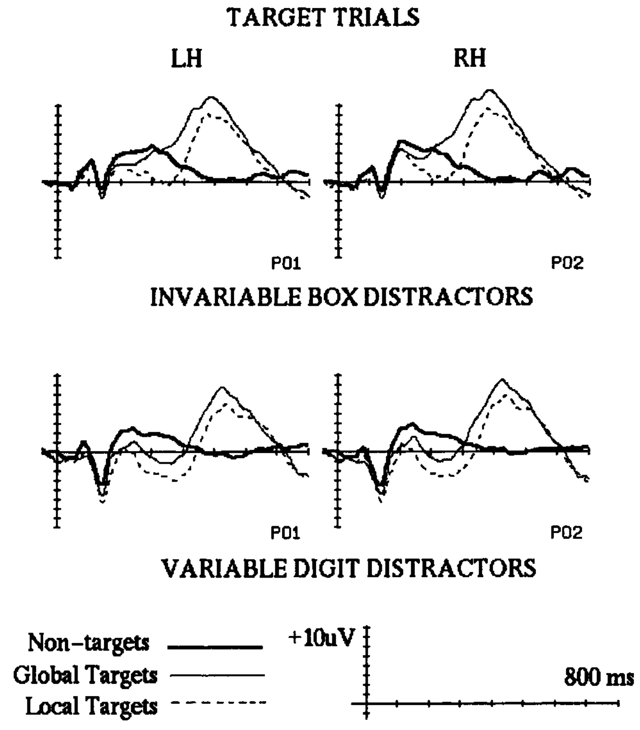

Fig. 5. Global and local waveforms at parietal-occipital sites (PO1/PO2) for target trials. Invariable box distractor condition (top), and the Variable digit distractor condition (bottom).

lized effects of attended Visual Field: at central electrode sites, LVF attention produced a larger N1, significant at electrode Oz ($F(1,5) = 16.26$; $p < 0.01$), and approaching significance at electrode Pz ($F(1,5) = 6.22$; $p = 0.054$). A Visual Field × Hemisphere interaction was significant at frontal (F3/F4; $F(1,5) = 6.75$; $p = 0.05$), temporal-occipital (TO1/TO2; $F(1,5) = 10.34$; $p = 0.02$), temporal-parietal-occipital (TPO1/TPO2; $F(1,5) = 9.08$; $p = 0.03$), and inferior temporal-occipital electrode sites (TOi1/TOi2; $F(1,5) = 6.73$; $p = 0.048$), for which the N1 was consistently greater over the right than the left hemisphere site for RVF attention. LVF attention did not produce this laterality in the N1 and there was no interaction with Level.

The topological difference maps illustrated in Fig. 7 show the contrast in lateralization between the two distractor conditions. Although there were lateralized effects due to LVF vs RVF attention in the Variable digit-distractor condition, only in the Invariable box-distractor condition was the lateralization based on significant differences in global/local attention.

3.2.3. N2 component

The N2 component was most identifiable over temporal-occipital sites, however, in some cases it did not have an easily identifiable peak. For this reason, statistical analyses for this component were done on the mean amplitude within a window. One analysis examined pairs of temporal, parietal, and occipital electrode sites using a 200–400 ms window. A second analysis examined the mean amplitude at the temporal-occipital sites TO1/TO2 and the frontal sites F3/F4 (where the N2 was most visually observable in the grand-averaged waveforms), within eight consecutive 25 ms windows between 200 ms and 400 ms.

3.2.3.1. Invariable box-distractor N2 amplitude. Global/local differences in the N2 were observed in the Invariable distractor group, where the local-N2 was greater (more negative) than the global-N2. A main effect of Level was found at parietal-occipital sites PO1/PO2 ($F(1,5) = 8.39$; $p = 0.03$), and temporal-parietal-occipi-

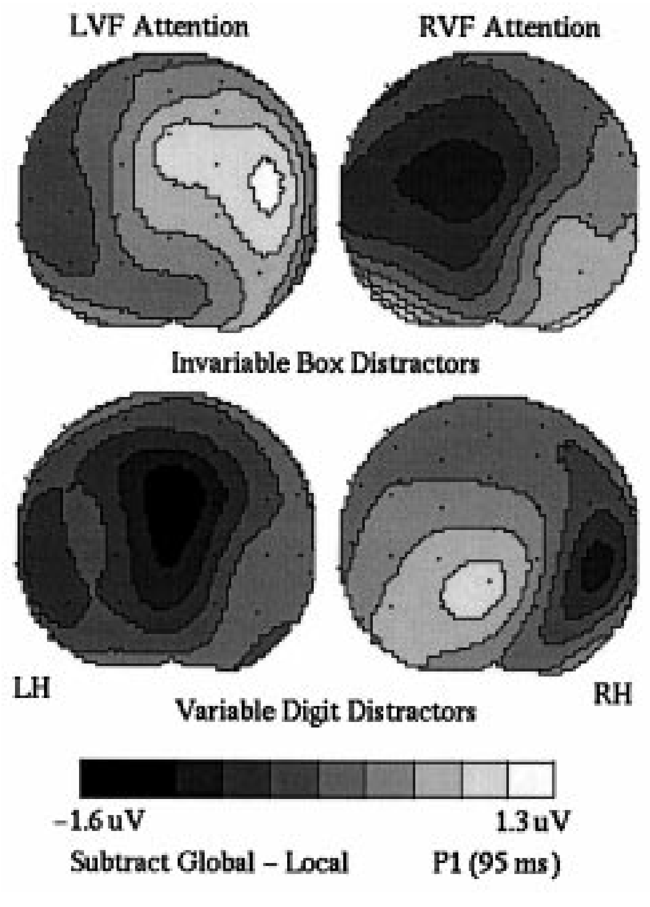

Fig. 6. Subtraction (global-local) topological maps at P1 (95 ms) for Invariable (top row) and Variable (bottom row) distractor groups, for LVF (left column) and RVF (right column) attention. Topological maps are calculated using the Laplacian source derivation algorithm of Hjorth [11]; the posterior view of the head is shown (LH on the left for each map). The P1 global/local differences in the Variable digit distractor condition (bottom row), showed primarily a greater global P1 when attention was directed to the LVF figure; there were no significant lateralized effects. In the Invariable box distractor condition (top row), the global/local differences were more clearly lateralized, showing a greater LH-local P1 (RVF attention) and a greater RH-global P1 (LVF attention).

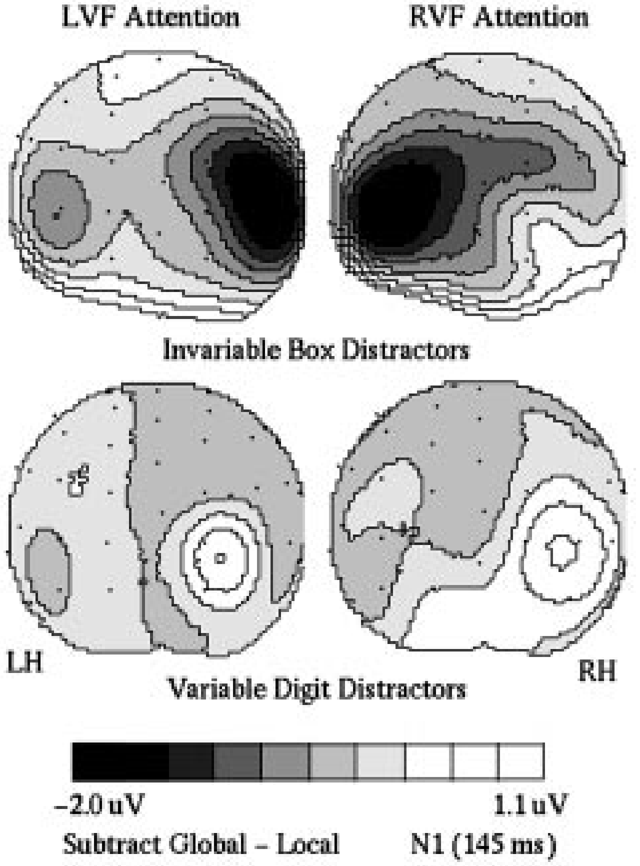

Fig. 7. Subtraction (global-local) topological maps at N1 (145 ms). There were no significant global/local N1 differences in the Variable digit distractor condition. In the Invariable box distractor condition, however, the global-N1 was larger than the local-N1, and tended to be so over the hemisphere contralateral to the attended visual field.

tal sites (TPO1/TPO2; $F(1,5) = 6.43$; $p = 0.05$). There was also an effect of Hemisphere of recording at PO3/PO4, describing the observation that the N2 over the LH site was consistently more negative than over the RH site ($F(1,5) = 8.45$; $p = 0.03$). The interaction between Level and Hemisphere was not significant.

The analysis at TO1/TO2 of mean amplitudes within 25 ms windows revealed a greater local than global-N2 between 250 ms and 300 ms (250–275 ms: $F(1,5) = 16.71$; $p < 0.01$; 275–300 ms: $F(1,5) = 10.82$; $p = 0.02$). Within the 225–250 ms and 300–325 ms windows, a Level × Visual Field interaction showed that the local-N2 was significantly larger than the global-N2 only when attention was directed to the LVF (225–250 ms: $F(1,5) = 11.43$; $p = 0.02$); 300–325 ms: $F(1,5) = 15.32$; $p = 0.01$).

The analysis at F3/F4 of mean amplitudes within 25 ms windows showed a reflection of the posterior global/local effects. There was an interaction between Level and Hemisphere of recording such that the local waveform was more positive than the global waveform between 225–250 ms and 275–300 ms, especially over the right hemisphere site (225–250 ms: $F(1,5) = 9.39$; $p = 0.03$; 275–300 ms: $F(1,5) = 12.83$; $p = 0.02$). This effect reversed at 300 ms, so that the global response was more positive than the local response, especially over the right hemisphere (300–325 ms: $F(1,5) = 8.64$; $p = 0.03$; 325–350 ms: $F(1,5) = 5.79$; $p = 0.06$; 350–375 ms: $F(1,5) = 11.77$; $p = 0.02$). There was a main effect of Level between 325 ms and 375 ms, reflecting a more positive local waveform compared to global (325–350 ms: $F(1,5) = 12.57$; $p = 0.02$; 350–375 ms: $F(1,5) = 6.39$; $p = 0.05$).

3.2.3.2. Variable digit-distractor N2 amplitude. Global-local differences were observed over temporal, parietal, and occipital sites. The local-N2 was more negative than the global-N2, and these differences were much more pronounced (over both left and right hemisphere sites) when attention was directed to the LVF compared to RVF attention. The Level × Visual Field interaction was significant at the temporal (T5/T6; $F(1,5) = 7.89$; $p = 0.04$) and temporal-occipital sites (TO1/TO2; $F(1,5) = 7.49$; $p = 0.04$). There were no significant differences between LH and RH sites.

Further analysis of mean amplitudes within 25 ms windows, at the TO1/TO2 sites, confirmed that the local-N2 was greater than the global-N2 for both LVF and RVF attention between 225 ms and 275 ms only (225–250 ms: $F(1,5) = 9.87$; $p = 0.03$; 250–275 ms: $F(1,5) = 9.11$; $p = 0.03$). From 325 to 400 ms, the local-N2 exceeded the global-N2 only when attention was directed to the RVF (325–350 ms: $F(1,5) = 9,10$; $p = 0.03$; 350–375 ms: $F(1,5) = 6.79$; $p = 0.048$; 375–400 ms: $F(1,5) = 8.67$; $p = 0.03$). This attentional asymmetry approached significance for the 275–325 ms region as well. Again, there were no significant differences between LH and RH sites.

The 25 ms window analysis was also performed at the frontal F3/F4 sites for the range 200–400 ms. There was an interaction between Level and Hemisphere of recording, showing a more negative-going global than local waveform between 225 ms and 250 ms, especially over the left hemisphere site (225–250: $F(1,5) = 27.67$; $p = 0.003$). There was also an interaction between Hemisphere of recording and Visual Field, in which the waveforms for both global and local attention were more negative-going for RVF attention over the RH site (275–300 ms: $F(1,5) = 8.57$; $p = 0.03$; 375–400 ms: $F(1,5) = 14.58$; $p = 0.01$).

Fig. 8 displays the topological subtraction maps for the N2 component at 250 ms. There were global/local differences for both distractor conditions, however, laterality effects differed. In the Invariable distractor condition, LVF attention appeared to produce a greater local N2 over the RH, contrasted with RVF attention which appeared to produce a greater local N2 over the LH. However, the Level × Visual

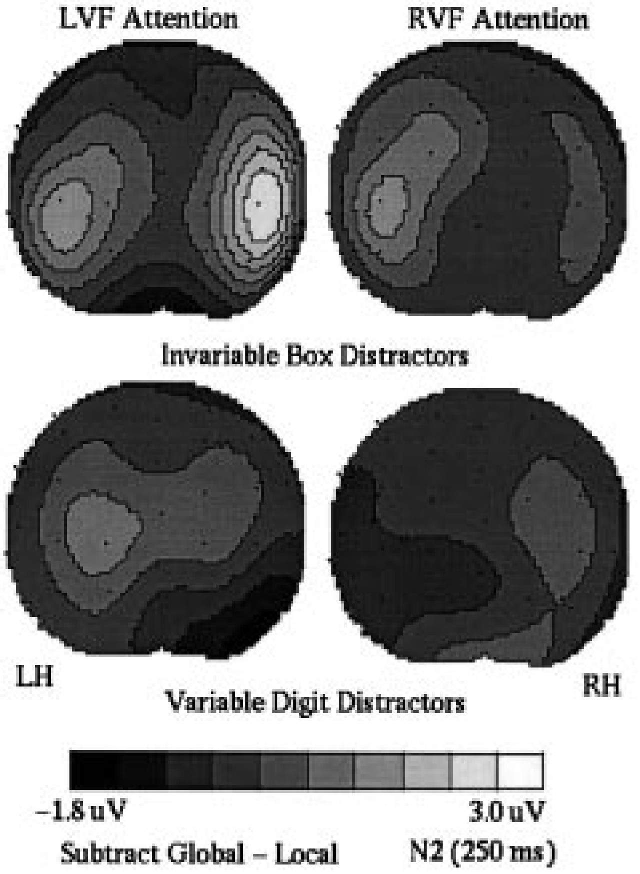

Fig. 8. Subtraction (global-local) topological maps at N2 (250 ms). There were global/local differences in both distractor conditions, with local-N2 greater than the global-N2. In the Invariable box-distractor condition, the local-N2 tended to be larger for LVF attention, and larger overall over LH sites. There were no significant LH/RH effects in the Variable digit-distractor condition.

Field × Hemisphere interaction was not significant. Overall, the local N2 was greater for LVF attention, and greater over the LH. The pattern was different for the Variable distractor condition, for which the local-N2 was greater than the global-N2, but the effect of Visual Field was less clear, and there were no significant Hemisphere effects.

3.2.4. P3 component

The P3 was examined for target trials only. This component was observed broadly but was maximal over parietal-occipital sites. Although no significant differences were found in the latency of the peak of the P3, the onset of the global-P3 obviously occurred earlier than the onset of the local-P3 (Fig. 5). To test the significance of this difference, we compared the mean amplitudes of the global and local waveforms measured at parietal-occipital sites (PO1/PO2; where the P3 was largest), within a series of 25 ms windows over the range of 300–600 ms. For example, the mean was calculated for each of the 12 25 ms windows between 300 ms and 600 ms for each subject and repeated measures ANOVAs were applied for the factors Level, Visual Field, and Hemisphere, as described above. In general, global attention elicited a larger P3 mean amplitude within the windows capturing the onset of the P3 than local attention primarily because of the earlier onset of the global-P3.

3.2.4.1. Invariable box-distractor P3 amplitude. The global-P3 peak amplitude was significantly more positive than the local-P3 at central site Cz ($F(1,5) = 10.53$; $p = 0.02$) and approached significance at Pz ($F(1,5) = 6.24$; $p = 0.05$). The analysis of mean amplitude within 25 ms windows was performed at PO1/PO2 as described above, and revealed that the global-P3 was greater than the local-P3, significant between 300 ms and 425 ms, and between 475 ms and 575 ms ($F(1,5) > 7$; $p < 0.05$).

3.2.4.2. Variable digit-distractor P3 amplitude. The global-P3 peak amplitude for this group was greater than the local-P3 at central sites (Oz: $F(1,5) = 13.66$; $p = 0.01$, Pz: $F(1,5) = 11.24$; $p = 0.02$), at parietal-occipital sites (PO1/PO2: $F(1,5) = 17.43$; $p < 0.01$), and at temporal-parietal-occipital sites (TPO1/TPO2: $F(1,5) = 9.77$; $p = 0.03$). The 25 ms window analysis of mean amplitude at PO1/PO2 produced the following. Global amplitude was higher than local and this was significant between 325 ms and 375 ms, and between 425 ms and 575 ms ($F(1,5) > 8$; $p < 0.05$).

4. Discussion

The purpose of this ERP study was to explore the temporal stages at which lateralized differences between global and local processing first appear, to provide insight into the mechanisms responsible for the lateralization. We used a selective attention task and examined ERP responses under two conditions, one in which unattended information varied from trial to trial (Variable digit distractors), and one in which unattended information was invariant across trials (Invariable box distractors). The results show clearly that the presence or absence of variability in the unattended elements has a significant impact on the stage at which a lateralized, electrophysiological distinction between global and local processing is first observed.

Each of the temporal components present in the averaged, stimulus-locked ERP is related to some stage of cognitive processing of the stimulus. Some agreement has been reached regarding the interpretations of these voltage deflections as they relate to activity in the underlying neuron populations. The early, exogenous components are assumed to illuminate the influence of visual-spatial attention as it facilitates processing of the attended global and local stimuli by inducing more synchronous firing within the active neuron populations [23]. The later-appearing, endogenous components are usually interpreted to be indexes of higher level cognitive processes [3], and changes in amplitude may provide an index of the energy devoted to a cognitive operation. Usually, waveforms from two or more conditions are compared for changes in latency, amplitude, and topological distribution across the scalp. When there are amplitude changes without changes in the topography of the components, one can hypothesize that there has been a change in the level of response from the same generators. However, when topological changes occur, this can be interpreted as the differential contribution of different neural generators [24].

In our experiment, lateralization of the global/local P1 depended on the variability at the unattended level. When information at the unattended level did not vary from trial to trial (Invariable box-distractor condition), global/local differences were revealed as early as the extrastriate P1. Consider that a briefly presented stimulus in the left or right visual field is input to the contralateral hemisphere. Specifically, when attention was directed to the stimulus in the LVF (RH), global attention elicited a larger P1 than local attention (over the RH). The opposite occurred when attention was directed to the stimulus in the RVF (LH), in which case local attention elicited a larger P1 than global attention (over the LH). This pattern is consistent with models which hypothesize LH-local and RH-global processing biases [4,17,35]. In contrast, when information at the unattended level varied from trial to trial (Variable digit-distractor condition), there were no lateralized differences between the P1s elicited by global vs local attention.

P1 is an exogenous, sensory component elicited by the onset of an object in the visual field, and has been localized to extrastriate generator sites [25]. The amplitude of the P1 can be modulated by attention which acts to facilitate early sensory processing at an expected location [21,23,37]. Thus, when relevant global stimuli are expected in the LVF (input to the RH), attention acts to enhance activity in the RH neuron populations biased for processing global information that is typically carried by lower spatial frequencies. Likewise, the neuron populations in the LH that are biased for processing local information typically carried by higher spatial frequencies are primed when relevant local stimuli are expected in the RVF (LH).

Does this mean that populations in extrastriate cortex are biased for global or local information (or low or high spatial frequencies)? The extrastriate areas are likely primed directly via spatial attention to visual field location [21,23,37], and may also be primed indirectly via feedback from areas that are biased for relative differences in spatial frequency [36,42]. The idea that prestriate areas might be primed via feedback from temporal-parietal areas that are biased for global or local information has been suggested by Fink and colleagues [6,8]. The enhancement that we observed may be an additive effect of two kinds of priming. The extrastriate areas are primed via selection for spatial location, in addition to feedback from temporal-parietal areas, which are primed via selection for a preferred range of (relative) spatial frequencies. In that case, selective attention for global information (typically carried by lower spatial frequencies) would prime activity in temporal-parietal areas of the RH, which would feedback to enhance activity in extrastriate areas of the RH, adding to the enhancement due to selection of the LVF figure, and resulting in a greater global than local P1 over the RH. Global attention to the RVF figure would not produce this enhancement in the LH because there would be no such additive effects. Conversely, selective attention for local information (typically carried by higher spatial frequencies) may prime populations in the LH, and attention to the RVF figure may help to enhance the activity in LH extrastriate cortex. The robust phenomenon of global processing dominance, evident in the behavioural responses and in the P3, may provide some insight into why the effect was so much larger for global attention.

Importantly, we only saw differences in the global vs local P1 components in the Invariable box-distractor condition. We believe that in the Variable digit-distractor condition, global and local processing of attended and unattended information occurred in parallel, so that lateralized biases may have been masked. Note that this Variable distractor condition is most similar to other studies, which have also shown no early lateralized global/local effects during selective attention [9].

The influence of spatial attention is also evident at subsequent ERP components. The N1 component is interpreted to be an index of the orientation of spatial attention to a task-relevant object [21,22]. In our study, there were no differences between the global-N1 and the local-N1 when unattended information varied from trial to trial, however, when the unattended information was invariant, the global-N1 was larger than the local-N1 over the hemisphere contralateral to the attended visual field.

Several analogies have been made to describe how attention acts to select for further processing a portion of the visual field that contains relevant information. These metaphors include a ‘spotlight’ of attention in which a facilitation of processing is extended to stimuli falling within the boundaries of the spotlight [31]. Others proposed a similar spotlight description but, rather than having discrete all-or-none boundaries, the size of the spotlight could be made to vary as required by task demands and stimulus characteristics [5]. In terms of global and local processing, the difference in N1 amplitude may be brought about by attention to global or local features as resulting from sizing of an attentional window to accommodate the relative sizes of the global or local forms. When subjects attended to the global level, a hypothetical attentional window was sized to accommodate the larger global form where relevant information was located. When subjects attended to relevant information at the local level, spatial attention acted to reduce the size of the window because local elements occupy a smaller portion of the visual field. Thus, the greater amplitude of the global-N1 in the Invariable box-distractor condition may be a result of a larger attentional window.

Why, then, are the global and local-N1 amplitudes not different in the Variable distractor condition? It is possible that the variance at the unattended global level, during local attention, is enough to grab processing resources for the global as well as the local elements, in essence maintaining the global-sized attentional window in both global and local attention conditions. Even when subjects attended to the local level, variability occurring at the global level may have drawn attention. Another way of thinking about this is that there is some failure of selective attention when distracting information varies from trial to trial.

The N2 component is thought to be an endogenous component and has been hypothesized to be sensitive to stimulus evaluation and classification processes [3,24]. In our task, when attention was directed locally, the peak of the N2 was consistently more negative than it was for globally directed attention, and this was especially so for LVF attention. When distractors were invariable over time, although the peak of the local-N2 was fairly obvious, the global-N2 was difficult to identify. It is possible that the N2, in this study, provides a measure of a process by which information is classified as having a global or local source. When attending to the dominant global level, and the local distractors are invariant boxes, there may be very little processing required to separate global from local sources. When attending to the local level, however, even though the global distractors are invariant boxes, there is still some work required to extract the non-dominant local information from the compound figure.

In the Variable digit-distractor condition, both global and local N2 peaks were clearly identifiable. In the context of the above hypothesis, when information at the unattended level varies over time, more work is required to determine the source of the information, whether attending to global or local elements. Note also that, in the Variable distractor condition, the N2 is the earliest component for which there is any significant interaction between global/local and LVF/RVF attention.

As mentioned in the introduction, results from brain-imaging studies have been somewhat conflicting with regard to the processing stage at which lateralized differentiation of global/local activity occurs. The pattern of lateralization in most of these studies is consistent with the LH-local and RH-global biases suggested by behavioural and neuropsychological literature [e.g. 17]; but they differ in the processing stages at which the lateralization is observed. Although some PET studies have shown lateralized differences to occur in extrastriate areas [6,8], other brain-imaging studies suggest that lateralized differences do not occur until much later stages [9,10].

For example, in a PET study of normal subjects, Fink et al. [6] demonstrated that selective attention to local elements resulted in greater activity in the inferior occipital cortex of the LH, and selective attention to global elements resulted in greater activity in the lingual gyrus of the RH. However, Heinze and Münte [10], in an ERP study using a divided attention paradigm, in which subjects identified a target that could appear at either the global or local level on any trial, the first ERP component to show lateralization of processing was the N2, a negative component observed approximately 250 ms after stimulus onset. This component was larger over the left hemisphere for local targets, and larger over the right hemisphere for global targets. Importantly, no differences were found between local and global processing at earlier components that would indicate differences as early as suggested by Fink et al. [6].

Moreover, Heinze et al. [9] examined both ERP data (selective and divided attention tasks) and PET data (selective attention task). In contrast to Fink et al. [6], the PET data revealed no significant laterality differences between global and local processing. The early visual components of the ERP in the selective attention task showed that the global P1 was greater in amplitude than the local P1, but this effect was not lateralized and was interpreted to be a result of the relatively larger attentional window required for global vs local selective attention. The amplitude of the N2 (260–360 ms) was not different for global and local selective attention. In the divided attention task, consistent with Heinze and Münte [10], there were no global/local differences in the early ERP components. However there were lateralized effects observed in the N2 component, which was greater in amplitude for local attention over left temporal-occipital sites, and tended toward greater amplitude for global attention over right temporal-occipital sites.

Proverbio et al. [32] also found early global/local differences in the amplitude of the N115, a component that appears in response to bright, high frequency visual patterns [45]. The global/local differences became apparent in a contrast between congruent and incongruent distractor conditions. It was asymmetric in the sense that the amplitude of the N115 was reduced for local targets when the global distractors were incongruent vs congruent, but this interference effect did not occur for global targets. The effect was hypothesized to be due to dominance of global over local information [32]. Importantly, consistent with Heinze et al. [9], these early differences were not lateralized.

Hemispheric differences in processing global and local information can be predicted in terms of their *relative* spatial frequencies [18,33]. To explain the asymmetric allocation of processing, a model has been proposed in which a range of spatial frequencies is selected (via attentional processes), the absolute spatial frequencies within that range are converted to relative values, and finally, processing of the relative high and low spatial frequencies within that range is distributed across the two hemispheres to optimize processing [see 13]. Heinze et al. [9] use this model to explain their data in the following way. During divided attention, the range of spatial frequencies that define both global and local elements are distributed across the two hemispheres to optimize performance, resulting in the observed asymmetries in the N2 component. During selective attention, however, a smaller range of spatial frequencies is first selected, consisting of either the lower spatial frequencies when attending to global elements, or the higher spatial frequencies when attending to local elements. This smaller range of spatial frequencies is then distributed across the hemispheres, resulting in more equal processing and no observed asymmetries.

We also used a selective attention task, but showed lateralized differences at early stages of processing, indexed by the extrastriate P1. If the lack of processing asymmetry in the selective attention condition in the Heinze et al. [9] paper were a result of the narrow range of attended spatial frequencies, then one would not predict processing asymmetries in our task, which also required selective attention. This would especially be the case in the Invariable box-distractor condition, in which the only information that varied from trial to trial was within the narrow range of attended spatial frequencies.

However, this is not what we observed. Our hypothesis for this discrepancy involves the presence vs absence of the variability at the unattended level. Importantly, the early lateralized global/local differences occurred only in the Invariable box-distractor condition. It is possible that such early lateralization is a result of the influence of temporal-parietal regions feeding back to affect processing in early extrastriate areas, as suggested by Fink et al. [6], and the additive effect this might have with selective attention to the left or right visual hemifields. It may be important that the stimuli used by Heinze et al. [9] were presented at central fixation.

When information at the unattended level varied from trial to trial, as it did in our Variable digit-distractor condition, and in both divided and selective conditions in the Heinze and Münte [10], and Heinze et al. [9] studies, we did not observe lateralization at early stages, consistent with their observations. When attending to real world stimuli, unattended information that varies across time may be potentially relevant, even if the task at hand requires directed attention. We suggest that there is substantial processing of any information that varies from trial to trial, including information presented at the ignored level during selective attention conditions [41]. At early stages of processing, this may engage the left and right hemispheres more equally, so that activity does not appear to be lateralized.

The difference in the stage at which we observe lateralization relates closely to the idea that there is a difference in salience of the relevant stimulus level between the Invariable and Variable distractor conditions. Fink et al. [7] demonstrated early lateralized differences for global and local attention that depended on the perceptual salience of the stimulus levels. For their particular stimuli, they defined salience as a function of relative spatial frequency. For example, when attention was directed to the local level of a stimulus consisting entirely of relatively low spatial frequencies, left inferior occipital cortex was preferentially activated. In contrast, when attention was directed to the global level of a stimulus consisting of relatively high spatial frequencies, the right lingual gyrus showed more activation. This interaction was explained by a hypothesis that the global form was more salient in the stimulus consisting entirely of high spatial frequencies, and that the local form was more salient in the stimulus consisting entirely of low spatial frequencies [7]. Clearly, the stimuli in our Invariable box-distractor condition have this same quality, that the invariable nature of the distractors makes the global digits more salient when local items are boxes, and makes the local digits more salient when global items are boxes. Our results in that condition are consistent with the direction and early stage of lateralization shown by Fink et al. [7]. The additional work load in the Variable digit-distractor condition, reflected at the later stage indexed by the N2 component, may be attributable to the fact that neither global nor local information is more salient than the other, and it becomes more difficult to extract the relevant information from the compound figure. An empirical question is whether it is possible that stimulus manipulations (e.g. a longer stimulus duration) that alter the salience of global or local items in the Variable digit-distractor condition would result in the observation of lateralization at earlier stages.

The dissociation between the Variable and Invariable distractor conditions supports the hypothesis that there are at least two different mechanisms operating to produce hemispheric asymmetries at different temporal stages. The idea of multiple mechanisms involved in the analysis of hierarchically structured information is not new, and is consistent with many reports showing a dissociation between speed or efficiency of processing on one hand, and interference between global and local information on the other [15,17–19,28,33,35,36]. How these mechanisms act to produce the observed hemispheric asymmetries is still not clear, and there is some debate over whether spatial frequency is a critical factor for selection of global vs local information at early stages of processing [20,34]. Our results lend insight into these issues by suggesting a mapping between observed behavioural dissociations and lateralized ERP components at different stages. We show that when attention is easily allocated (Invariable box-distractors), lateralization occurs early in processing (P1), and may reflect the mechanism that produces the perceptual advantages associated with speed of processing in the two hemispheres, usually global precedence [1,16,28,32]. When attention is not so easily allocated (Variable digit-distractors), both global and local information receive processing at early stages, and the observed asymmetry occurs much later (N2). The late lateralized component may reflect the mechanism involved in producing interference effects that occur between local and global levels [2,15–17,28,29,35,41].

When we form a percept of the whole, we do not lose the individuation of the parts. Both parts and the whole are available to us. Recognition of a teapot does not require that we first determine specific parts, in fact, the handle may be hidden from view. As we manoeuvre to grasp the handle, lift the teapot, and aim the spout toward a cup, we must maintain information about the parts. However, it is just as important to maintain the spatial configuration of the whole or we may misjudge the distance between the handle and the spout. It is not clear that, during divided attention, we are actually attending to both parts and wholes simultaneously, or whether we need to switch between global and local representations. Lateralization at later stages during divided attention may be an indication of asymmetric activity as attention actually switches between global and local elements. Again, the lateralized difference at the N2 may be related to determining the source, local or global, of the relevant information.

Results from these experiments support the notion that global and local levels of a hierarchical stimulus are processed in parallel by separate mechanisms. The presence or absence of variability at the unattended level had a significant effect on behavioural and electrophysiological correlates of global/local processing and underscores the role of visual selective attention in the processing of these stimuli. When distractor variability was absent, the influence of visual selective attention was apparent very early in the processing of the levels. However, distractor variability, indicating the presence of potentially relevant information at the unattended level, may have resulted in some degree of parallel processing of that level as well. In essence, the presence of variability at the unattended level resulted in a failure of selective attention. It is biologically adaptive to be susceptible to a degree of distractibility if the result is to alert the organism to potentially important stimuli that occur at a location other than the attended location, or outside the selected range of spatial frequencies.

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