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Modulation of Brain Activities by Hierarchical Processing: A High-Density ERP Study

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Summary: The present study investigated how attention to global or local levels of hierarchical patterns modulates brain activities by recording high-density event-related brain potentials (ERPs) evoked by hierarchical stimuli. 120-channel recordings of ERPs were obtained from subjects while they detected targets at global or local levels of hierarchical stimuli displayed in the left or the right visual field. We found that attention to local stimulus features enhanced posterior P1 and N2 components, with the N2 enhancement showing a left hemisphere predominance regardless of stimulus positions. Difference was also seen in the distribution of the frontal P2. Reaction times were slowed when global and local levels of stimuli were incompatible, and an interference effect was observed on anterior N2 amplitudes and latencies. Three-dimensional current distributions showed common sources over the posterior cortex between 80-230 ms and a contralateral frontal source between 300-400 ms for global and local conditions. However, an additional ipsilateral frontal focus between 230-350 ms was found specially for local processing. The results corroborate the findings of previous ERP studies, and suggest that the frontal lobe is particularly important for the selective processing of local parts of a global structure.

Key words: Hierarchical pattern; Event-related brain potentials; Current density; Brain tomography.

Introduction

A large number of objects in the visual world are hierarchical, i.e., a global object is composed of distinct independent local objects. To address the relationship between global and local processing of this type of hierarchical stimuli, Navon (1977) employed a paradigm using compound letters, e.g., global letters made up of local letters. In tasks requiring subjects to discriminate global or local letters respectively, Navon found that reaction times (RTs) to global letters were longer than RTs to local ones. Global letters interfered with responses to local ones, but not vice versa. Based on these findings, Navon put forward a global precedence hypothesis asserting that the processing of global properties precedes that of local properties in visual perception.

Subsequent studies have shown that RTs and interference effect do not always display a global advantage. The global advantage could be reduced and a local advantage was even observed when specific properties of compound stimuli varied, such as visual angles, stimulus positions in the visual field, density of local elements, spatial frequency components of compound stimuli, strength of perceptual grouping of local elements, and selection effort involved in the discrimination of local stimuli (Badcock et al. 1990; Grice et al. 1983; Han and Chen 1994; Han and Humphreys in press; Han et al. in press; Hughes et al. 1990; Kinchla and Wolfe 1979; Lagasse 1993; Lamb and Robertson 1988; Lamb and Yund 1993, 1996; Martin 1979; Pomerantz 1983). The results of these behavioural studies give rise to great interests of exploring brain mechanisms of hierarchical processing.

Neuropsychological research suggests that different cortical regions are specialized for global/local processing (see Robertson and Lamb 1991 for a review). For example, patients with right hemisphere lesions, when asked to draw Navon-type stimuli from memory, tended not to produce the global shape but did reproduce local elements; the opposite pattern occurred with left hemisphere damaged patients (Delis et al. 1986). Other studies found that patients with lesions in the right temporal and parietal cortex responded faster to local than to global targets whereas patients with lesions in the left temporal and parietal cortex showed an abnormally global RT advantage (Lamb et al. 1989, 1990; Robertson et al. 1988, 1993). Brain activities of normal subjects in association with hierarchical processing have been studied recently with

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positron emission tomography (PET). Fink et al. (1996) measured regional cerebral blood flow (rCBF) of normal subjects when they named compound letters. Increases in relative rCBF in the right lingual gyrus was observed when subjects named global letters of visual compound stimuli, whereas increases in relative rCBF in the left inferior occipital cortex was found when subjects named local letters. The results of lesion and PET studies suggest that a subsystem composed of occipital, temporal and parietal lobes in the right hemisphere dominates global processing whereas a subsystem of the homologous areas in the left hemisphere dominates local processing. However, since patients' results exhibit final output of impaired cognitive process, and measures of rCBF show integration over several seconds (Kim et al. 1997; Kwong 1995), it is difficult for these studies to provide information about accurate time course of neural activities between the onset of stimuli and subject's responses (usually several hundred milliseconds).

The character of high temporal resolution makes the measurement of event related brain potentials (ERPs) particularly useful for studying time courses of cognitive processes. ERPs have been employed to investigate differences in brain activities associated with hierarchical processing. For example, Heinze and Münte (1993) recorded ERPs from subjects when they responded to targets which appeared at global or local levels of compound letters with equal probability (a divided attention paradigm). They found that a posterior N2 component exhibited an earlier onset and a higher amplitude to local targets than to global targets when RTs showed local advantage. Heinze et al. (1994) further showed that the N2 amplitude was higher to local than to global targets over the left hemisphere, whereas over the right hemisphere, the N2 amplitude was about the same for both global and local targets. They suggested that the posterior N2 component was an index of early global/local target perception. More recently, Han et al. (1997) recorded ERPs associated with identifying the global and local levels of non-linguistic compound stimuli (global arrows made up of local arrows) in a selective attention task. They required subjects to discriminate orientations of global or local arrows in separate blocks of trials. They found that, in line with behavioural results which showed a global advantage, the identification of local stimuli elicited longer peak latencies of the anterior N2 and parietal P3 components relative to the identification of global stimuli. The anterior N2 and P3 latencies were longer when stimuli at the global and local levels were inconsistent than when they were consistent. The incongruency between global and local levels also made the amplitudes of the posterior N2 and P3 more negative. This interference effect on the posterior N2 and P3 amplitudes and P3 latencies was stronger on the local level than on the global level. More important, Han et al. found that the amplitude of an early occipital P1 component was modulated by attention to the global and local levels of compound stimuli, being larger in the local condition than in the global condition. ERPs have been also used to compare the prevalence of the global or the local level at the perceptual or the later stages (Proverbio et al. 1998; Ridderinkhof and van der Molen 1995) and to reveal the mechanisms of attentional shift between global and local level of compound stimuli (Kotchoubey et al. 1997).

The first objective of this study was to confirm Han et al.'s (1997) finding that the early occipital P1 component was modulated by attention to global or local levels of compound stimuli, but using compound letters this time. Previous studies using divided attention paradigm (Heinze and Münte 1993; Heinze et al. 1994) did not show any difference in P1 amplitudes evoked by global and local stimuli. They employed hierarchical stimuli made up of global letters whereas non-linguistic stimuli were used in Han et al's (1997) work. Is the modulation of P1 amplitude a special effect for non-linguistic compound stimuli or a general effect for all sorts of compound stimuli including compound letters? In addition, compound stimuli were displayed in the centre of the visual field in the previous studies (Han et al. 1997; Heinze and Münte 1993; Heinze et al. 1994). In the current study, however, compound stimuli were presented in the left visual field (LVF) or the right visual field (RVF). This is helpful to compare the difference in processing dominance of global and local levels between the two hemispheres since it has been known that stimuli in the LVF are first projected to the right occipital cortex and stimuli in the RVF are first projected to the left occipital cortex.

The second aim of the present work was to localize brain activities, indexed by electric current foci computed from scalp recorded ERPs, in relation to hierarchical processing with the aid of a high spatial resolution EEG/ERP system. Previous ERP studies have provided less spatial information about brain activities associated with global and local processing because of the limitation of the number of electrodes used to record ERPs (e.g., Heinze et al. recorded ERPs from 10 electrodes; Han et al. recorded ERPs from 29 electrodes). In the current study, ERPs from 120 channels were recorded while subjects detected global or local targets in separate blocks of trials. In addition to voltage topography of ERPs related to global and local processing, the related sources of electric activities inside the brain were computed using a method called LORETA (low resolution electromagnetic tomography, Pascual-Marqui et al. 1994; Pascual-Marqui and Michel 1994; Lantz et al. 1997). On the basis of the findings from animal studies that neighbouring neurones are most likely to be active synchronously and simultaneously (Gray et al. 1989; Silva et al. 1991), LORETA assumes that currents change little between adjacent regions of the brain. Mathemati-

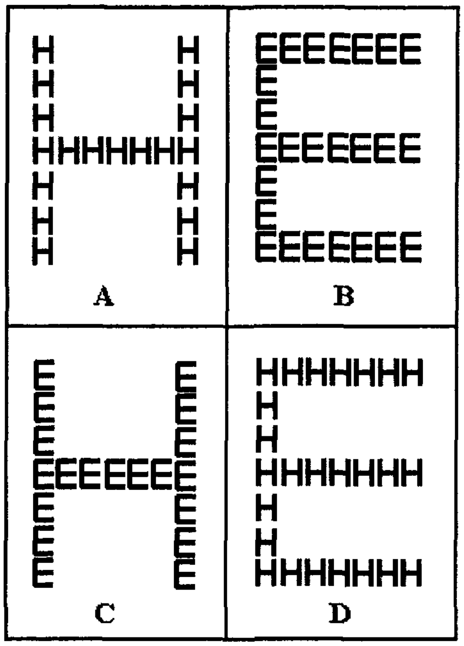

Figure 1. The compound stimuli used in the present study. Each stimulus served as global and local targets in different blocks of trials. For example, in a global task in which "H" was defined as a target, stimuli A and C served as targets whereas stimuli B and D were standard stimuli. In a local task in which "E" was defined as a target, stimuli B and C served as targets whereas stimuli A and D were standard stimuli.

cally, it computes the smoothest of all possible 3-dimensional (3D) current distributions, and thus obtains a unique and optimal 3D distribution of current density in a three shell spherical head model (Rush and Driscoll 1986). This 3D distribution of current source density provides information about the most likely locations of the ERP generators. LORETA does not demand a pre-assumption of the number of sources, and thus is advantageous for localizing ERPs related to cognitive processes without prior knowledge. As little has been known about sources of electric activities in the brain contributing to ERPs associated with global and local processing of compound stimuli (particularly at the late stages of hierarchical processing), LORETA is specially useful for estimating the sources of brain activities in hierarchical processing.

Methods

Subjects

Ten healthy undergraduate students (all male; right-handed; aged between 20 to 24 years) participated in this experiment as paid volunteers. All had normal or corrected-to-normal vision.

Stimuli

The stimuli, which were white on a black background, were presented on a computer-controlled video monitor placed 57 cm from the subject eyes. A fixation cross, subtending 0.3 x 0.2° of visual angle, was continuously visible in the center of the monitor as stimuli were flashed in the LVF and the RVF in random order. Each stimulus pattern consisted of a global letter made up of local letters in 7 x 7 matrix (see figure 1). The global and local letters subtended an angle of 3.3 x 5.6° and 0.4 x 0.6°, respectively. The distance between the fixation cross and the center of each compound stimulus was 2.9°. The background had a luminance of 0.02 cd/m^2. The compound patterns composed of local letter "E" (global letter "E": 0.82 cd/m^2, global letter "H": 0.78 cd/m^2) were slightly brighter than those composed of local letter "H" (global letter "H": 0.46 cd/m^2, global letter "E": 0.53 cd/m^2). The stimulus displays were presented for a duration of 200 ms. The intervals between stimulus displays were randomized between 600 - 1000 ms.

Procedure

A selective attention paradigm was adopted in the present study. While maintaining fixation of their eyes on the fixation cross, subjects were instructed to detect the presence of global or local targets by pressing a key on a response pad with the right-hand or the left-hand thumbs. Global letters ("H" and "E") and local letters ("H" and "E") served as targets in separate blocks of trials. Each block consisted of 100 trials. After 50 practice trials, a total of 600 trials were presented for each type of targets. A target letter occurred randomly in 20% of the trials. The presentation sequence of different types of targets was counterbalanced across subjects. Half of the subjects responded to target letter "H" with the left hand and responded to target letter "E" with the right hand. This arrangement was reversed for the other subjects.

ERP recording and Analysis

The electroencephalographic (EEG) activity was recorded with a 128-channel EEG/ERP equipment (Neuroscan Inc.). The current 120-channel montage is shown in figure 2. Each electrode was named with a number from 1 to 120. Electrodes 2, 18, 36, 73, 92, 105, 113 and 119 were arranged along the midline of the skull. Other electrodes were located approximately symmetrically at the two sides of the skull. The typical distance between two neighbouring electrodes was about 2 cm. The skin resistance of each electrode was made less than 5 kohms by injecting conducting gel with a blunt needle through the top of each electrode. The position of each electrode was measured with a probe for sensing the 3D

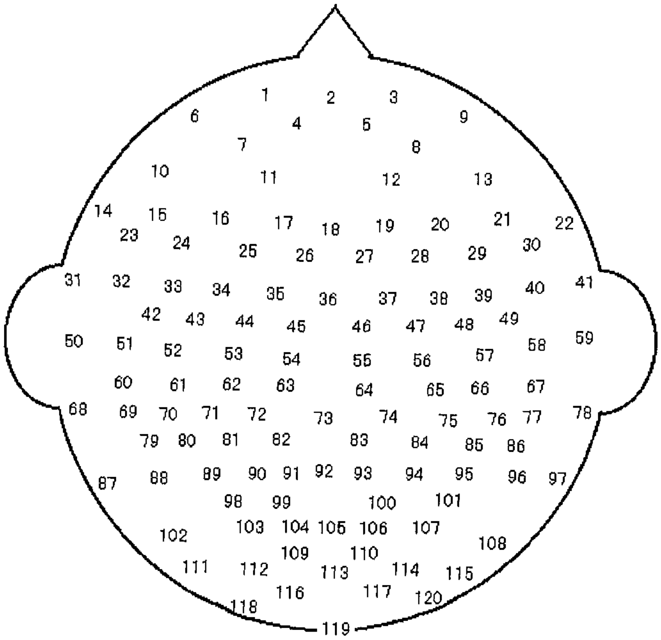

Figure 2. The diagram of 120-channel scalp montage used in the present study.

position of the probe tip with respect to a magnetic field source in the head support.

The average of the left and right earlobes was used as reference. Eye blinks were monitored with electrodes located below the left and right eyes. The horizontal electro-oculogram (EOG) was recorded from electrodes placed about 1.5 cm lateral to the left and right external canthi to measure eye movements. EEG was amplified with a gain of 15000 times by using a band pass of 0.1-40 Hz (1/2 amplitude cutoffs) digitized on-line at a sampling rate of 256 samples per second and stored on a hard drive. The ERPs to targets and standard stimuli were averaged separately off-line using a computer program that extracted epochs of EEG beginning 200 msec before stimulus onset and continuing for 1200 msec. Trials containing eye blinks, eye movements, muscle potentials exceeding a threshold of $\pm 75\ \mu v$ at any electrode, or incorrect behavioural responses were excluded from the averages. For the standard stimuli, the posterior P1, N1, and N2 were measured and analyzed at Electrodes 103 and 107; the frontal P2 was measured at electrodes 14 and 22. The anterior N2 was measured at electrodes 34 and 38. Target elicited P3 was measured at electrodes 90 and 94. The baseline for these measures was the mean voltage of a 200 ms pre-stimulus interval and the latency was measured relative to the stimulus onset.

Reaction times (RTs) were subjected to a repeated measure analysis of variance (ANOVA) with globality (detecting global or local targets), consistency (letters at the global and local levels were consistent or inconsistent), and hemifield (stimuli were presented in the LVF or the RVF) as independent variables. The peak latencies and amplitudes of ERP components were subjected to ANOVAs with globality, consistency, hemifield, and electrode position (on the left or right hemisphere) as independent variables.

To obtain information about cortical distributions of the ERP components and the difference between the ERPs in global and local conditions, topographic maps of the distribution of voltage over the scalp were constructed. The present work also calculated tomography of current source density with the average of all electrodes as a reference. The LORETA algorithm computes first an inverse operator based on the assumptions of maximal smoothness on a fixed lattice with input of the positions of each electrode and averaged ERPs at each electrode. The resolution of this 3D grid was set as 0.01m in the present study. After the calculation of inverse operators was complete, tomographic images during a specific time range were drawn to exhibit sharp foci at parallel horizontal brain slices viewed from the top of the head. A three shell spherical head model was adopted for the LORETA analysis, in which the ratio (inner skull radius)/(outer skull radius /(head radius) was fixed at 0.87/0.92/1.0 (Rush and Driscoll 1986). The coordinate system for presenting LORETA images was defined as follows. The origin was at the midpoint of the left and right preauricular points. The +X-axis is defined by the directed line from the origin through the nasion. The +Y-axis is defined by the directed line from the origin through the left preaauricular. The +Z-axis is defined as the directed line from the origin towards the top of the head perpendicular to the XY plane. The program for calculating tomography of current density was provided by a software called EMSE (ElectroMagnetic Source Estimation) written by Greenblatt (1995).

Results

Performance

False alarm rates were 0.1% and 0.025% respectively for global and local distractors. Accuracies were 97.5% and 94.6% respectively for global and local targets. No trade-off was found between RTs and accuracies. The results of RTs are shown in table I. The responses to global targets were faster than those to local ones ($F(1,9)=58.95$, $p<0.0005$). RTs were shorter when global and local letters were consistent than when the two levels were inconsistent ($F(1, 9)=60.97$, $p<0.0005$). The global interference over the local targets was stronger than vice versa ($F(1, 9)=156.48$, $p<0.0005$). The interaction of hemifield × globality was significant ($F(1, 9)=6.006$, $p<0.035$),

Table I. Mean reaction times (Standard deviation) (ms) to global and local targets in the left and right visual fields (n=10).

	global target		local target	
	consistent	inconsistent	consistent	inconsistent
right visual field	436 (63.9)	429 (60.8)	468 (53.5)	521 (41.7)
left visual field	437 (51.3)	433 (52.6)	483 (48.6)	538 (42.24)

reflecting the fact that global RT advantage in the LVF was larger than that that in the RVF.

ERP Waveforms

Grand averaged ERPs to compound stimuli were characterized by sequences of peaks that varied in morphology according to scalp location as illustrated in figures 3 and 4. Both global and local stimuli elicited a posterior P1(80~130 ms), N1(140~200 ms), and N2(250 ~ 330 ms), an anterior P2 (200 ~ 280 ms), a central negatively-going component N2 (230 ~ 340 ms), and a P3 (370 ~ 670 ms) over parietal sites. These components were present for both target and standard stimuli, but the ERPs to target stimuli were characterised by the P3 enhancement.

Table II shows the mean peak latencies and amplitudes of the posterior P1, N1, N2, and the anterior P2 evoked by standard stimuli. The P1 peak latencies were shorter at the contralateral than at the ipsilateral electrodes in both global and local conditions (F(1, 9)= 135.6, p<0.0005). The P1 amplitudes recorded at the left hemisphere were larger than those recorded at the right hemisphere (F(1, 9)=11.60, p<0.008). The P1 amplitudes were enlarged in the local condition relative to the global condition (F(1, 9)= 7.70, p<0.02). The posterior N1 showed shorter latencies (F(1, 9)= 88.86, p<0.0005) and higher amplitudes (F(1, 9)=18.60, p<0.002) at the contralateral than at the ipsilateral sides in both global and local conditions. The

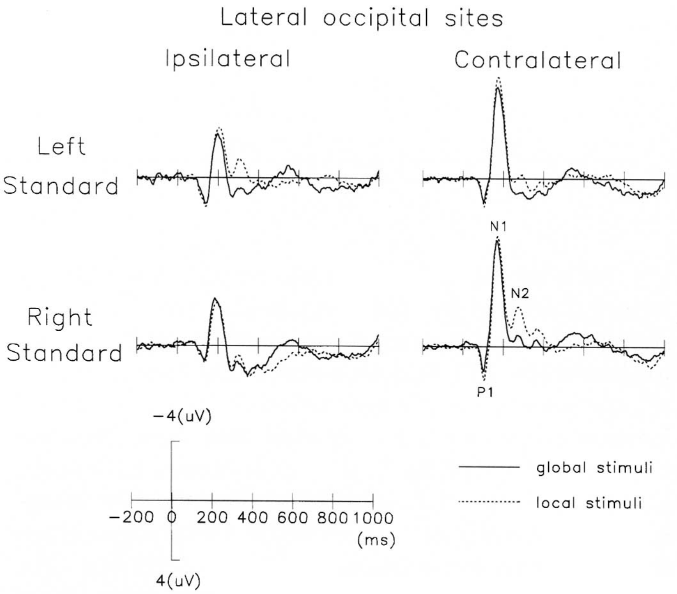

Figure 3. Grand averaged ERPs elicited by standard stimuli in global and local conditions at occipital electrodes. The waveforms are presented separately as a function of whether detecting global or local targets. The ERPs associated with consistent and inconsistent stimuli were collapsed. Note that negative is plotted upwards.

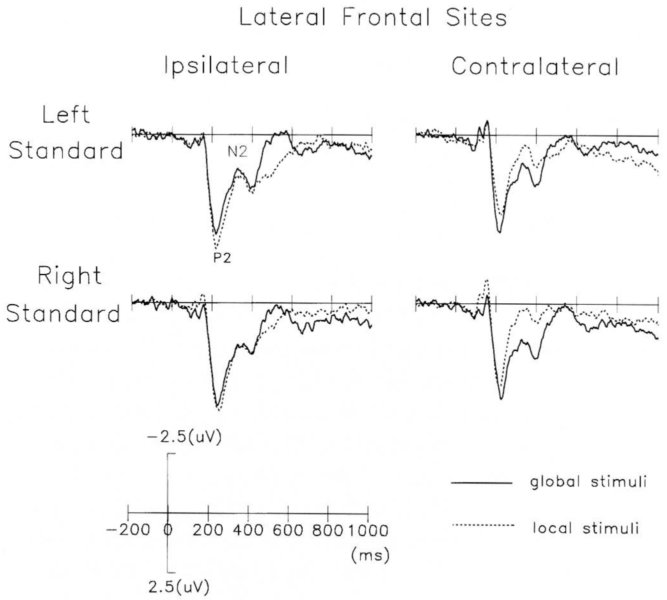

Figure 4. Grand averaged ERPs elicited by standard stimuli in global and local conditions at frontal electrodes. The waveforms are presented separately as a function of whether detecting global or local targets. The ERPs associated with consistent and inconsistent stimuli were collapsed.

Table II. Latencies and amplitudes of the P1, N1, P2 and posterior N2 evoked by standard stimuli (n=10).

Stimulus position	left visual field		right visual field	
Electrode	left	right	left	right
P1 latencies (ms)				
global	128	103	101	118
local	129	102	103	118
P1 amplitudes (μV)				
global	2.96	1.86	2.61	1.25
local	3.33	1.93	3.50	1.83
N1 latencies (ms)				
global	190	166	171	177
local	192	167	167	178
N1 amplitudes (μV)				
global	-3.58	-6.18	-8.66	-4.34
local	-4.20	-7.07	-9.15	-3.96
Posterior N2 latencies (ms)				
global	265	294	286	264
local	275	287	288	273
Posterior N2 amplitudes (μV)				
global	-0.75	-0.77	-1.42	-0.49
local	-2.28	-1.64	-2.66	-0.92
P2 latencies (ms)				
global	220	214	211	227
local	227	205	207	232
P2 amplitudes (μV)				
global	3.66	3.82	3.17	4.23
local	5.18	3.23	2.46	4.97

posterior N2 latencies were shorter at the ipsilateral than at the contralateral electrodes (F(1, 9)=5.05, p<0.05). This posterior N2 was enhanced in the local condition relative to the global condition (F(1, 9)=12.6, p<0.006). This difference was stronger at the left than at the right hemisphere regardless of stimulus position (F(1, 9)=6.54, p<0.03). The P2 latencies were shorter at the contralateral than at the ipsilateral electrodes (F(1, 9)=13.6, p<0.005). The P2 latency asymmetry was more stronger in the local condition than in the global condition, indicated by a significant three way interaction of hemifield × electrode position × globality (F(1, 9)= 6.034, p<0.04). The P2 amplitudes were higher at the ipsilateral than at the contralateral electrodes (F(1, 9)=11.30, p<0.008). The P2 amplitudes were higher at the ipsilateral frontal electrodes, but lower at the contralateral frontal electrodes in the local condition than in the global condition (F(1, 9)=5.03, p<0.05).

Table III shows latencies and amplitudes of the anterior N2 elicited by standard stimuli. The anterior N2 showed shorter latencies at the contralateral than at the ipsilateral side (F(1, 9)=6.60, p<0.03). The latencies of this N2 component were longer when the global and local levels were inconsistent than when they were consistent (F(1, 9)=20.7, p<0.002). The N2 amplitudes were larger (more negative) at the contralateral than at the ipsilateral sides (F(1, 9)=19.5, p<0.002). The N2 also showed larger amplitudes in the local than global conditions (F(1, 9)=6.02, p<0.035). The difference in amplitudes of the anterior N2 between global and local conditions were more pronounced at the contralateral than at the ipsilateral sites (F(1, 9)=6.68, p<0.03). The significant interaction of globality × consistency (F(1, 9)=5.37, p<0.04) reflected the fact that the incongruency between global and local levels increased the amplitudes to local stimuli

Table III. Latencies and amplitudes of the anterior N2 elicited by standard stimuli (n=10).

Stimulus position	left visual field		right visual field	
Electrode	left	right	left	right
Latencies (ms)				
GC	314	312	290	311
GI	314	313	318	316
LC	315	309	307	316
LI	318	317	319	322
Amplitudes (μV)				
GC	1.23	1.24	1.02	1.50
GI	1.29	1.41	1.30	1.56
LC	0.96	0.02	0.55	1.16
LI	0.40	-0.57	-0.17	0.93

note: GC = global consistent; GI = global inconsistent; LC = local consistent; LI = local inconsistent

whereas reduced the amplitudes to global stimuli.

Table IV shows the mean peak latencies and amplitudes of the P3 component elicited by targets. There was no significant difference in the P3 amplitudes between global and local conditions. However, the P3 latencies elicited by global targets were shorter than those elicited by local targets ($F(1, 9)=42.2$, $p<0.0005$). There was a marginally reliable interaction of globality × hemifield ($F(1, 9)=4.64$, $p<0.058$), the global P3 latency advantage was larger for stimuli in the LVF than that in the RVF.

Topographic and Tomographic Analysis

Figures 5 and 6 illustrate topographic maps of voltage for consistent stimuli presented in the LVF. For both consistent and inconsistent stimuli in global and local conditions, the P1 component emerged first over the contralateral occipital region, its focus then shifted to the ipsilateral hemisphere. The N1 component was focused over the contralateral occipital-temporal sites. The frontal P2 in the local condition was focused over the ipsilateral side whereas the P2 in the global condition was focused over the midline of the skull. In the local condition the posterior N2 focused over the left occipital region regardless of the hemifield of presentation. In the global condition, however, this posterior N2 was not prominent; the topographic maps of voltage showed a focus over the left occipital region only for the stimuli presented in the RVF during the correspondent time course.

Table IV. Latencies and amplitudes of the P3 elicited by targets (n=10)

Target level	global	local
Latencies (ms)		
right visual field	439	503
left visual field	419	522
Amplitudes (μV)		
right visual field	10.6	11.3
left visual field	10.3	10.5

The distribution of differences in the posterior N2 (270-310 ms) between global and local conditions is shown with topographic maps in figure 7. For the consistent stimuli presented in the RVF, the differences focused over the left occipital site, whereas there was an additional focus over the left temporal site for the inconsistent stimuli. For both consistent and inconsistent stimuli presented in the LVF the differences focused over the left occipital site, and the left and right parietal sites. The right parietal focus located more anteriorly relative to the left one.

Tomographic maps of current source density are shown in top-view horizontal slices through the brain at 9 different depths with inter-slice distance of 1.0 cm. The deepest slice (z=0.0 cm) corresponds to the XY plane. Figures 8 and 9 show the LORETA images for the consistent stimuli in global and local conditions presented in the LVF and the RVF at 4 different depths showing strong activities. The LORETA computation displayed similar

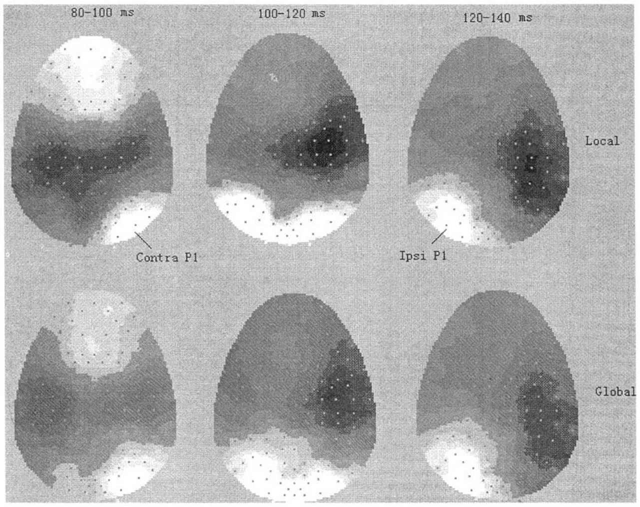

Figure 5. Voltage topographic maps related to the P1 components evoked by standard consistent stimuli in the LVF. Each column reflects the topography of the mean amplitude over the indicated latency range. The dots on the schematic heads represent the electrode positions. The grey level from black to white indicates a change from -1 to 1 uV for 80-120 ms, from -2 to 2 uV for 120-140 ms.

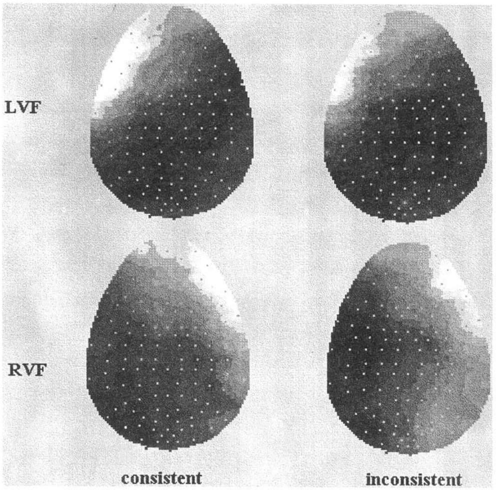

Figure 7. Topography of the difference in posterior N2 amplitudes between global and local processing conditions. The grey level from black to white indicates a change from -1.5 to 1.5 μV for the consistent stimuli in the LVF, from -1.2 to 1.2 μV for the consistent stimuli in the RVF, from -1.9 to 1.9 μV for the inconsistent stimuli in the LVF, from -1.6 to 1.6 μV for the inconsistent stimuli in the RVF.

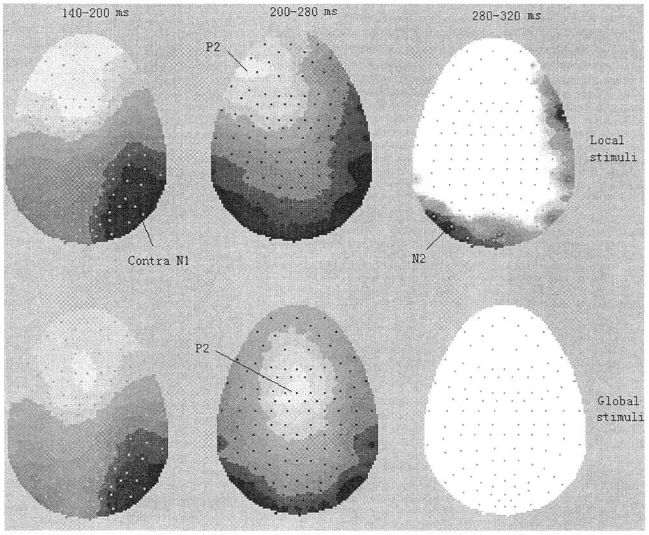

Figure 6. Voltage topographic maps related to the posterior N1, N2 and the anterior P2 components evoked by standard consistent stimuli in the LVF. The grey level from black to white indicates a change from -3 to 3 uV for 140-200 ms, from 0 to 5 uV for 200-280 ms, and from -0.6 to 0.6 uV for 280-320 ms.

results for all types of stimuli between 80-230 ms after the sensory stimulation. Over the P1 temporal range (80-130ms) the LORETA images showed first a dominant current focus over the occipital site contralateral to the stimulated hemifield, and then an ipsilateral focus over the occipital site enhanced while the contralateral focus decreased. At about 140 ms, a current focus over the contralateral occipital-temporal sites emerged and lasted for about 50 ms, which contributed to the posterior N1. At about 190 ms, an ipsilateral focus occurred while the contralateral one became weak. These two activities could be seen simultaneously at about 200 ms, and then merged to one focus. In the global condition this occipital activity shifted slightly to the ipsilateral parietal lobes and then disappeared at about 360 ms for the stimuli presented in the LVF and the RVF. In the local condition, this occipital focus shifted to the left parietal region and disappeared at about 240 ms for the stimuli presented in the LVF. For the stimuli presented in the RVF, this occipital focus also shifted to the left parietal region and disappeared at about 320 ms. Another occipital activity emerged over the right occipital-parietal sites at about 330 ms, and faded at about 360 ms.

The differences in current source activities associated with global and local processing took place at about 230 ms over the frontal region . In the local condition, when the consistent or inconsistent stimuli were presented in the

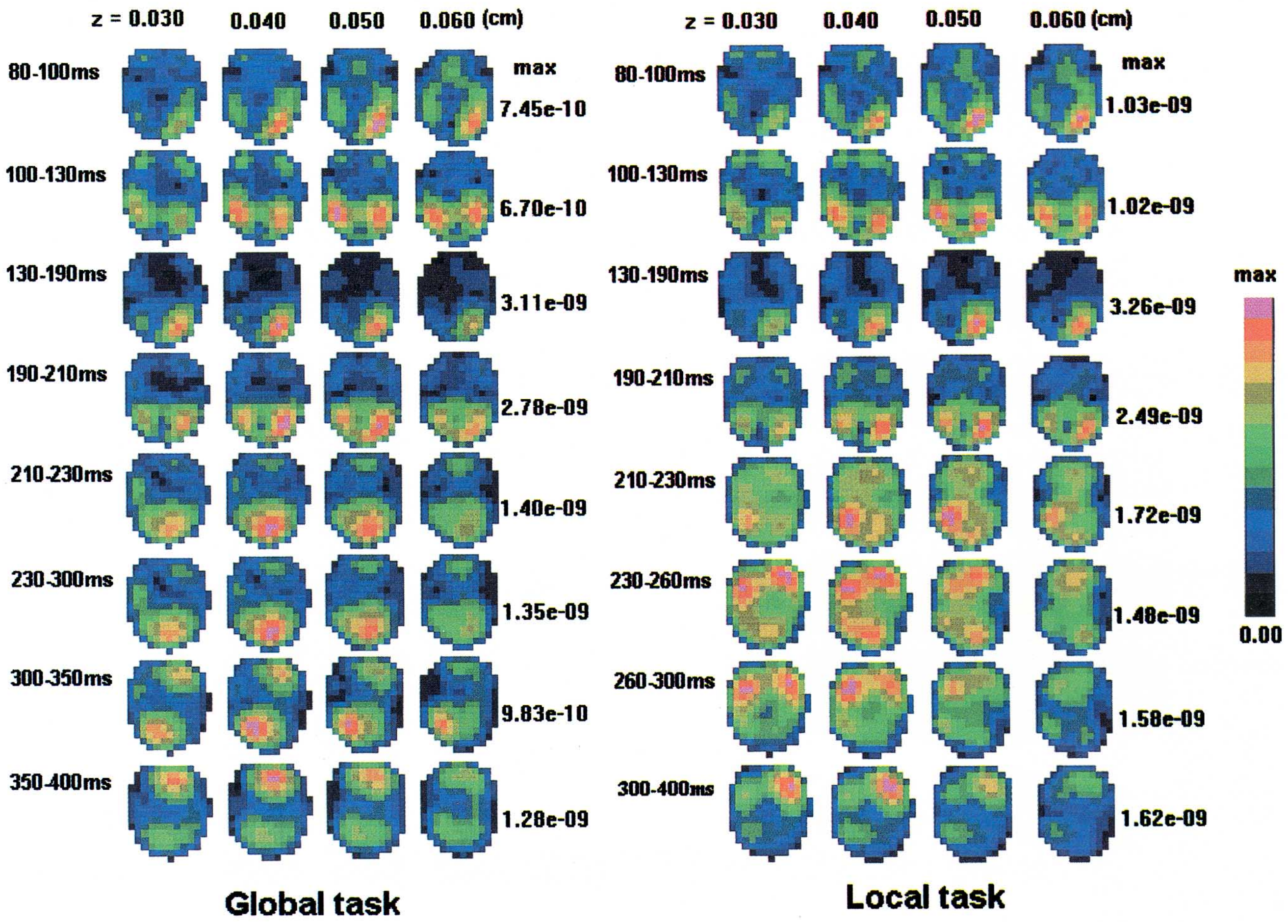

Figure 8. Tomographic maps showing distributions of current source density in relation to consistent stimuli presented in the LVF in global and local conditoins. The pictures shown include images in four slices in which strong activities are clear (i.e., z=0.03, 0.04, 0.05, 0.06 m).

LVF, two frontal foci at the left and right hemispheres appeared simultaneously at about 230 ms. The ipsilateral one decreased and disappeared at about 340 ms. The contralateral one also declined from 230 ms, but began to enhance at about 300 ms, and lasted over 400 ms. When stimuli were presented in the RVF, an ipsilateral frontal focus emerged at about 250 ms, decreased, and disappeared at about 340 ms. At about 300 ms a contralateral frontal focus became visible and lasted over 400 ms. The ipsilateral focus located slightly posteriorly relative to the contralateral one. In the global condition, however, there was only one contralateral focus, which emerged at about 330 ms and lasted over 400 ms for both consistent and inconsistent stimuli presented in the LVF or the RVF.

Discussion

This study investigated how hierarchical attention modulates brain potentials by recording high-density ERPs and computing 3-D distribution of current density in association with global or local processing of hierarchical stimuli. The pattern of behavioural data, similar to Navon's (1977) results, showed a global precedence effect. In line with the findings of the previous studies (Martin 1979; Sergent 1982), the present experiment also observed an asymmetry of the global RT advantage, being stronger for stimuli presented in the LVF than for those presented in the RVF.

The ERP data corroborated Han et al.'s (1997) findings that the amplitude of the occipital P1 was enhanced during local processing in comparison with that during global processing. Together with the previous research, the present study demonstrated that the attentional modulation of the P1 component in hierarchical processing is independent of the types of compound stimuli (linguistic or non-linguistic) and the stimulus positions (in the central or peripheral visual fields). As research has disclosed that the occipital P1 evoked by visual stimuli is

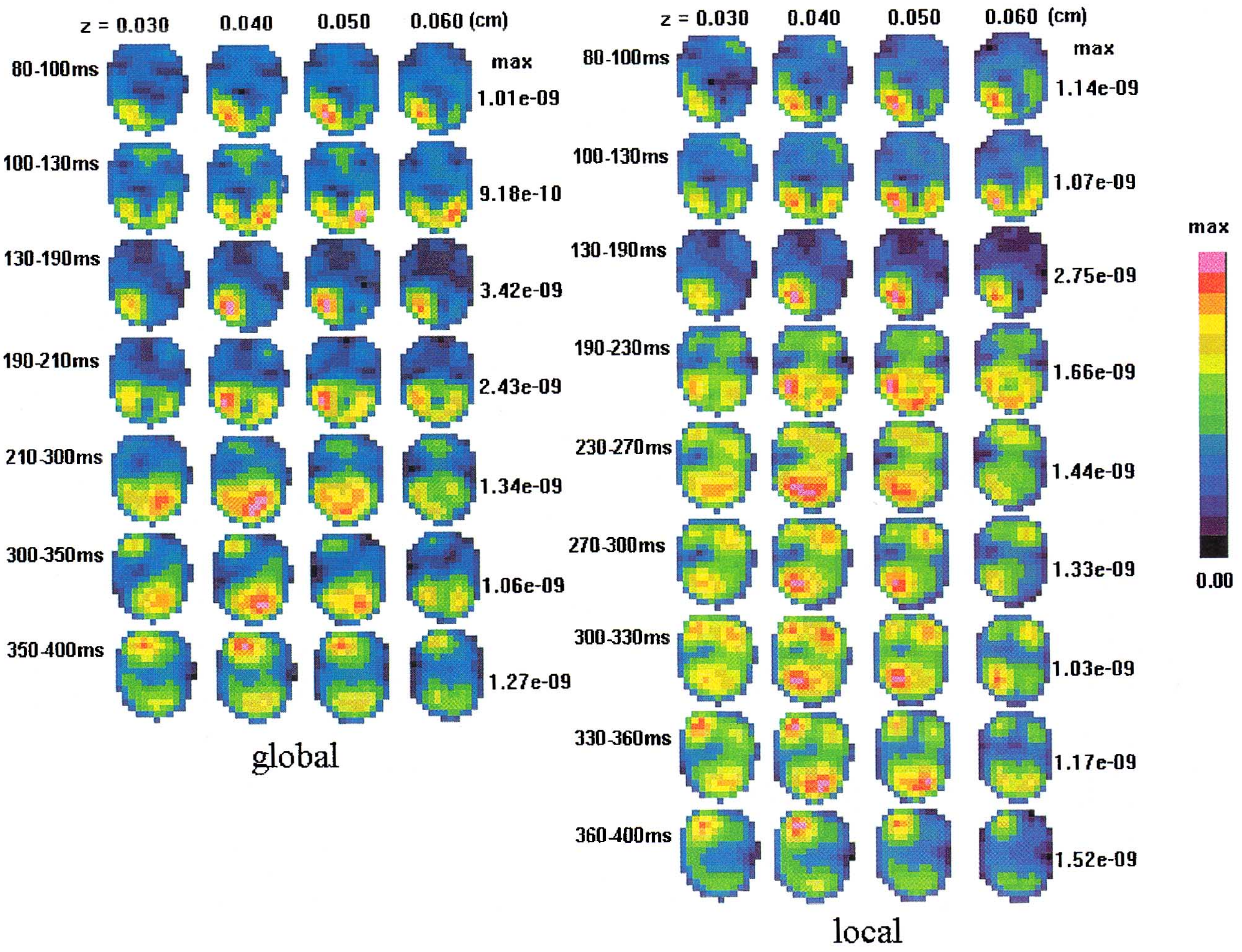

Figure 9. Tomographic maps showing distributions of current source density in relation to consistent stimuli presented in the RVF in global and local conditions. The pictures shown include images in four slices in which strong activities are clear (i.e., z=0.03, 0.04, 0.05, 0.06 m).

generated in the extrastriate cortex (Gomez et al. 1994; Heinze and Mangun et al. 1994; Hillyard et al. 1997; Mangun et al. 1993), the P1 effect observed in this study indicates that selective attention to specific levels of hierarchical patterns can modulate neural activities in the early stage of visual processing in the occipital cortex. Consistent with the results of PET study (Fink et al. 1996), these ERP results strongly suggest that the differences in behavioural performance between global and local conditions is mediated, at least partially, by neural substrates at the level of sensory processing. Previous research has shown that, when other non-spatial features (such as color, shape, motion or spatial frequency) are attended to, the typical response to attended stimuli includes a broad selection negativity which usually peaks between 150 to 300 ms post-stimulus (Anllo-Vento and Hillyard 1996; Eimer 1997; Harter et al. 1982; Kenemans et al. 1993; Previc and Harter 1982; Wijers et al. 1989). In comparison with these non-spatial attentional ERP effects, the current findings indicate that, similar to spatial selective attention, hierarchical attention can modulate neural activities at a stage earlier than that at which other non-spatial attentions operate.

The asymmetrical activities of the two hemispheres during hierarchical processing appeared at about 270 ms after sensory stimulation, indexed by the posterior N2. The N2 enhancement in the local condition relative to the global condition was larger over the left than over the right occipital-temporal regions. This is consistent with the results of other ERP studies employing the divided attention paradigm (Heinze et al. 1994; Johannes et al. 1996). The present study demonstrated further that the asymmetry of the N2 effect is independent of stimulus positions, being similar for stimuli presented in both the LVF and the RVF. The topographic maps showed additional asymmetrical activities over the parietal and temporal regions during the N2 time course. These results provide further evidence for the proposal that independent subsystems in the left and right hemispheres dominate local and global processing respectively (Rafal and Robertson 1995; Robertson and Lamb 1991) and that the temporal cortex may be engaged in encoding the relationship between global structure and local parts (Lamb et al. 1989). It is possible that the posterior N2 reflects the neural substrate for the asymmetrical global RT advantage observed here and in other behavioural studies (Martin 1979; Sergent 1982).

The effect of hierarchical attention on the anterior N2 was different from that on the posterior N2. The incongruency between global and local levels prolonged the anterior N2 peak latencies, and increased its amplitudes in the local condition whereas reduced its amplitudes in the global condition. One of the important issues about hierarchical processing is whether the same mechanism underlies the RT advantage and the interference effect (Lamb and Robertson 1989; May et al. 1995). The present ERP data showed that the interference effect does not necessarily occur on an ERP component which is modulated by attention to global or local level of hierarchical stimuli. The amplitudes of both the posterior N2 and the anterior N2 was enhanced by attention to the local level, but the incongruency between global and local levels only affected the anterior N2. These ERP data imply that the interference effect may be mediated by relatively anterior regions whereas the modulation of ERP amplitudes by hierarchical attention occurs at relatively broad regions of the brain.

The modulation of the P2 component by hierarchical attention observed here has not been reported in other studies (Han et al. 1997; Heinze and Münte 1993; Heinze et al. 1994). A key difference between the present study and the previous work is stimulus position. When stimuli were presented in the centre of the visual field (Han et al. 1997; Heinze and Münte 1993; Heinze et al. 1994), the frontal P2 recorded in left and right hemispheres were equally strong and occurred simultaneously for the global and local processing. In the present study where stimuli were presented in the LVF or RVF, the relative strength of the frontal activities in the global and local conditions varied as a function of stimulus and electrode positions. The P2 amplitudes related to local processing were enhanced at the ipsilateral frontal sites but decreased at the contralateral frontal sites relative to global processing. This may possibly stem from the additional frontal current focus elicited by local processing (see discussion below).

The P3 latencies were akin to the reaction times, showing a global advantage which was larger for targets presented in the LVF than for targets presented in the RVF. However, the P3 latencies to the consistent stimuli did not differ from those to the inconsistent stimuli. In comparison with Han et al.'s (1997) work, which showed interference effects on the P3 latencies and amplitudes for stimuli presented in the centre of the visual field, the results of the P3 component observed here suggest that, when stimuli were presented in the periphery of the visual fields, representation of the relationship between global and local levels of hierarchical stimuli were eliminated at the stages of target evaluation (represented by P3, Donchin 1977; Duncan-Johnson and Kopell 1981).

Tomographic maps of current density of the present study showed similar distributions of the posterior activities related to global and local processing within a time window of 80-230 ms after sensory stimulation, thus suggesting that brain activities in the global and local conditions differ only in magnitudes in the early stage of hierarchical processing. The tomographic maps showed further that the hierarchical stimuli activated not only the posterior regions but also the frontal brain. The contralateral frontal activity that occurred at about 300 ms and lasted over 400 ms was found in both global and local conditions. As the stimuli were presented in the LVF or the RVF and subjects were required to fixate the central fixation point, they had to inhibit their intention to move their eyes to the positions where the stimuli were displayed. Single cell recording (Goldberg and Segraves 1989) and lesion studies (Henik et al. 1994) have indicated that the frontal cortex is essential for both endogenously generating voluntary saccades and inhibiting reflexive saccades summoned by exogenous signal in the contralateral fields. Since the contralateral frontal activities observed here were related to stimulus positions but independent of the task requirement (detecting global or local targets), they may reflect the neural activities in association with inhibiting saccades to the stimulus positions.

In contrast, the ipsilateral frontal foci, which occurred as early as 230 ms after stimulus onset, existed strikingly only for the local task. This additional ipsilateral activity in the local condition was observed regardless of stimulus positions and the relationship between global and local levels of hierarchical stimuli. It may be responsible for the P2 enhancement related to local processing at the ipsilateral frontal sites considering overlapping of the time courses of the P2 and the ipsilateral frontal current focus. A key difference between global and local tasks is that there is only one global target in the field in the global task whereas more than one potential local target exist in the field in the local task. Thus it is possible that, although local items are identical to each other, it is still necessary to select an individual local element for further analysis of its task-related features in the local task (Han et al. in press). As research has shown that frontal activities increase with the number of targets in a set of stimuli (Posner et al. 1988) and the frontal cortex plays an important role in selection of targets from competing inputs (Posner and Dehaene 1994), we suggest that the ipsilateral frontal activity observed in the local condition may reflect the additional selection activity specially engaged in the local task.

In sum, the findings reported in this paper suggest that, in addition to occipital, parietal and temporal cortex, frontal regions may also be engaged in hierarchical processing, possibly carrying out a 'top-down' modulation of selection of individual local elements from hierarchical patterns, and thus is an important component of the cortical network for the processing of local parts of a global structure. Lesion studies did not show any effect of frontal lesions on responses to global and local levels of hierarchical patterns (Robertson et al. 1991). This divergence may be due to that paradigms of behavioural studies are not sensitive enough to disclose the role of frontal cortex in hierarchical processing.

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