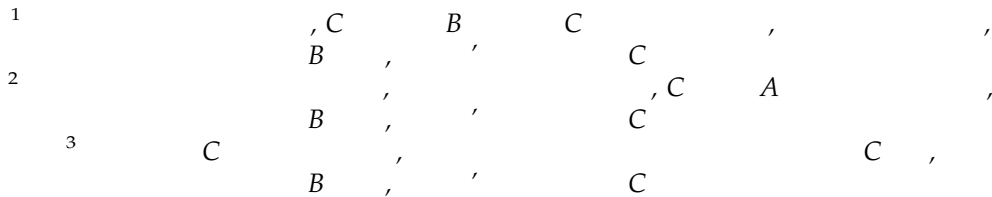


Modulation of Neural Activities by Enhanced Local Selection in the Processing of Compound Stimuli

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Abstract: The global precedence effect refers to the findings that responses are faster to a global structure than to its local parts and local responses are slowed by incongruent global information. We recorded high-density event-related potentials (ERPs) to study the role of enhanced local selection in the global precedence effect. Hierarchical stimuli were compound letters in which the local letters were either identical (homogeneous stimuli) or the central local letter was brighter than (bright stimuli) or different in color from the others (red stimuli). Subjects were asked to attend to the pop-out local letter of the red and bright stimuli during the local task whereas there was no such instruction for the homogeneous stimuli. Top-down attention to the pop-out local item weakened the global reaction time advantage and the interference effect. The enhanced local selection decreased the amplitude of an occipito-temporal negativity between 240–360 msec but increased the amplitude of a frontal-central negativity between 260–320 msec related to local processing. The incongruency between global and local letters enlarged the posterior N2 in the local condition and this effect was eliminated by enhanced local selection. These effects were evident regardless of whether the pop-out local letter was defined by color or luminance difference. The results support the proposal that distinct neural mechanisms over the posterior and anterior areas are engaged in the selection process that contributes to local processing of compound stimuli. *J. Neurosci.* 2003; 23:273–281. © 2003 Wiley-Liss, Inc.

Key words: event-related potential; global precedence effect; local selection; occipito-temporal cortex

INTRODUCTION

Human observers are often confronted with hierarchically organized scenes in which a global structure is composed of spatially separate local parts. Navon [1977] used compound letters (Fig. 1) to study how the visual system perceives global and local properties of hierarchical patterns. He found that reaction times (RTs) to identify global shapes are faster than those to the composing local parts (global RT advantage). In addition, local RTs are slowed by incongruent global information (global-to-local interference), but not vice

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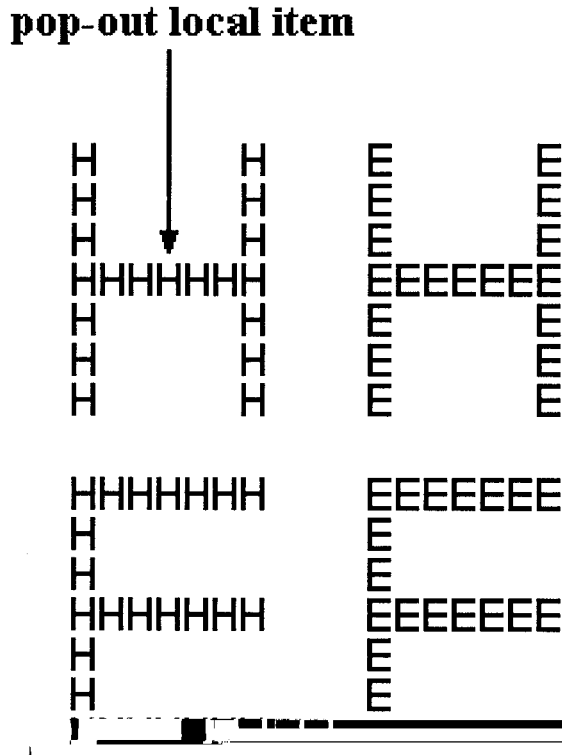


Figure 1.

Compound letters used. All local letters are white on a black background for the homogenous stimuli. The pop-out local item is either red or brighter than the others for the pop-out stimuli.

versa. On the ground of these findings, Navon suggests that the perceptual processing is temporarily organized so that global structures are perceived earlier than the composing local parts.

It has been proposed that global and local information of compound stimuli is mediated by low and high spatial frequency (SF) channels, respectively [Shulman et al., 1986; Shulman and Wilson, 1987]. The global precedence effect reflects per se the faster transmission speed of the low relative to high SF channels [Badcock et al., 1990; Hughes et al., 1996; Lamb and Yund, 1993, 1996]. However, removing low SFs from compound stimuli usually slows global RTs and eliminates global RT advantage, but does not influence the global-to-local interference [Lamb and Yund, 1993, 1996]. In particular, observers are still able to perceive the global structure of a compound pattern from which low SFs are removed. Thus, the sensory mechanism proposed by the researchers seems not sufficient to account for the differential processing of global and local aspects of compound stimuli.

Han et al. [1999b] and Han and Humphreys [1999] suggest that, on the one hand, perceptual grouping between local parts contributes to global perception and is critical to the global precedence effect. On the other hand, selection of an individual local item from the global structure is important for local perception. To test the latter hypothesis, Han and Humphreys [2002] used two sets of compound shapes (global arrows made up of local arrows) in which either all local items were identical (homogeneous stimuli) or a local item close to fixation was disparate in color (pop-out stimuli). They asked subjects to identify the unique local item of the pop-out stimuli in the local task whereas there was no such instruction for the homogeneous stimuli. Han and Humphreys found that top-down attention to the pop-out local item speeded local responses and reduced global-to-local interference.

Han et al. [2001] further investigated neural substrates underlying local selection by recording event-related potentials (ERPs) to the identification of global or local shapes (i.e., large arrows made up of small arrows). A typical ERP component that differentiates global/local processing is a negative wave over the occipito-temporal cortex peaking between 200 and 300 msec after stimulus onset (the posterior N2) [Han et al., 1997, 1999a, 2000; Heinze and Münte, 1993]. The posterior N2 is usually larger in the local relative to global conditions for the homogeneous stimuli. Han et al. [2001] found that instructions to attend to the pop-out item in the local task weakened the posterior N2 enhancement in the local relative to global conditions whereas enhanced a frontal-central negative wave (the anterior N2). They suggest that the anterior N2 and posterior N2 serve two distinctive aspects of attentional selection of an individual local item. The posterior N2 reflects a bottom-up filtering process to isolate one local item from the others for the identification of local shapes whereas the enhanced anterior N2 indexes top-down attention to a specific local item.

Most of the previous studies of the global precedence effect employed compound letters [Kinchla and Wolfe, 1979; Lagasse, 1993; Lamb and Robertson, 1988; Martin, 1979; Navon, 1983] whereas Han et al. [2001] used compound shapes in their ERP experiment. Thus, it is unclear to what degree the proposed neural mechanisms based on Han et al.'s [2001] ERP results can be applied to other studies using compound letters. In addition, because subjects were asked to attend to the red local item, one may argue that the results of the Han et al. [2001] study may result from selection of color rather than selection of specific local element. The current experiment addressed these issues by re-

TABLE I. Luminance levels and CIE coordinates of each stimulus pattern*

	Global shape H		Global Shape E	
	Local shape H	Local shape E	Local shape H	Local shape E
Homogeneous				
Luminance(cd/m ²)	0.380	0.780	0.530	0.820
CIE (X)	0.245	0.287	0.245	0.302
CIE (Y)	0.320	0.279	0.299	0.267
Red				
Luminance(cd/m ²)	0.340	0.540	0.320	0.630
CIE (X)	0.264	0.295	0.330	0.296
CIE (Y)	0.337	0.302	0.306	0.291
Bright				
Luminance(cd/m ²)	0.940	1.350	1.170	1.420
CIE (X)	0.250	0.254	0.250	0.267
CIE (Y)	0.266	0.310	0.295	0.272

* The background had a luminance of 0.02 cd/m².

Recording high-density ERPs to the processing of global or local levels of compound letters. We used the same paradigm as that in the Han et al. [2001] study but defined the pop-out local letter by either color (red stimuli) or luminance (bright stimuli) difference. If similar ERP effects of top-down attention to the pop-out item of compound letters were observed for the red and bright stimuli, they should reflect mechanisms specifically underlying selection of a local item from the global structure rather than selection of particular features (such as color). 120-channel ERPs were recorded to evaluate the generators of the effects of enhanced local selection in the brain.

MATERIALS AND METHODS

Ten healthy undergraduate students (2 females; all right-handed; aged between 21 to 36 years, mean age 26) participated in this experiment as paid volunteers and gave informed consent. All subjects had normal or corrected-to-normal vision and reported no color blindness. Each stimulus (Fig. 1) consisted of a global letter ("E" or "H") made up of local letters ("E" or "H") in a 7 × 7 matrix. The global and local letters subtended an angle of 3.3 × 5.6° and 0.4 × 0.6° at a viewing distance of 57 cm, respectively. Three sets of stimuli were used. The homogeneous stimuli were made up of identical white local letters. The local letter at the centre of each stimulus was red for the red stimuli and brighter than the others for the bright stimuli. The luminance level and CIE coordinates of each stimulus are shown in Table I.

Trials began with a centrally located white cross as fixation, which was replaced by the stimulus display for a duration of 400 msec. The interstimulus interval varied randomly between 600–1,200 msec. Subjects were requested to discriminate global or local letters in separate blocks of trials by pressing one of two keys with the right or the left thumb. For each set of stimuli, after 50 practice trials, a total of 600 trials in 6 blocks were presented respectively in the global and local conditions. The global and local letters were consistent in 300 trials and inconsistent in the remaining 300 trials. For the red and bright stimuli, subjects were asked to discriminate the red or the brighter local letter in the local task whereas there was no such instruction for the homogeneous stimuli.

The electroencephalographic (EEG) activity was recorded with a 128-channel EEG/ERP equipment. 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 skin resistance of each electrode was made less than 5 kohms. The position of each electrode was measured with a probe for sensing the 3D 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 eye. The horizontal electro-oculogram was recorded from electrodes placed about 1.5 cm lateral to the left and right external canthi. EEG was amplified with a half-amplitude band pass of 0.1–40 Hz and continuously digitized on-line at a sampling rate of

TABLE II. Reaction times for each stimulus condition*

	Global		Local	
	Consistent stimulu	Inconsistent stimulu	Consistent stimulu	Inconsistent stimulu
RTs (msec)				
Homogeneous	427 ± 25.3	446 ± 27.5	477 ± 22.8	510 ± 27.2
Red	425 ± 20.6	439 ± 24.1	449 ± 17.1	461 ± 17.7
Bright	410 ± 16.7	415 ± 16.5	431 ± 12.5	437 ± 12.9
Accuracy (%)				
Homogeneous	96.7 ± 0.737	93.9 ± 1.28	96.0 ± 1.02	90.2 ± 1.83
Red	95.6 ± 0.740	93.6 ± 0.937	94.4 ± 1.18	92.4 ± 1.21
Bright	95.6 ± 0.453	94.2 ± 1.00	95.9 ± 0.395	93.6 ± 0.936

* Values are expressed as mean RT ± SE or mean accuracy ± SE.

256 Hz. The ERPs were averaged using epochs of 200 msec before stimulus onset and continuing for 800 msec from the stimulus onset. Trials contaminated by artifacts exceeding $\pm 75 \mu\text{V}$ at any electrode or incorrect behavioral responses were excluded from the averages. Mean voltage of ERPs were obtained (1) at 20-msec intervals starting at 60 msec after stimulus onset and continuing until 300 msec post-stimulus, and (2) at 40-msec intervals from 300 to 560 msec poststimulus. The posterior P1, N1, and N2 were measured and analyzed at seven pairs of occipito-temporal electrodes; the frontal P2 and anterior N2 were measured at three pairs of frontal-central electrodes. The baseline for these measures was the mean voltage of a 200-msec pre-stimulus interval and the latency was measured relative to the stimulus onset. Voltage topographies of difference waves were plotted on a realistic head model of a randomly selected participant with averaged electrode coordinates from all the participants.

RTs and response accuracies were subjected to a repeated measure analysis of variance (ANOVA) with Stimulus Set (homogeneous, red, and bright stimuli), Globality (discrimination of global or local letters), and Consistency (global and local letters were consistent or inconsistent) as independent variables. The peak latencies and mean amplitudes of ERP components were subjected to ANOVAs with Stimulus Set, Globality, Consistency, and Hemisphere (electrodes over the left or right hemisphere) as independent variables.

RESULTS

RTs to the bright stimuli (see Table II) were faster than those to the red stimuli ($F(1,9) = 6.55, < 0.03$),

which in turn were shorter than those to the homogeneous stimuli ($F(1,9) = 5.08, < 0.05$). Global RTs were faster than local RTs ($F(1,9) = 16.03, < 0.003$). RTs were slower when global and local letters were inconsistent than when they were consistent ($F(1,9) = 39.98, < 0.001$). This interference effect was larger for the homogeneous than for the red and bright stimuli ($F(1,9) = 5.04, 16.74$, respectively, < 0.05). The global RT advantage was smaller for the bright than homogeneous stimuli ($F(1,9) = 5.60, < 0.03$). The accuracy was higher for the discrimination of global than local letters ($F(1,9) = 6.29, < 0.03$) and was reduced by the incongruency between global and local letters ($F(1,9) = 27.01, < 0.001$). The interference effect was larger for the homogeneous than for the red and bright stimuli ($F(2,18) = 9.32, < 0.002$).

The grand average ERPs recorded at occipito-temporal and frontal-central sites elicited by the homogeneous, red, and bright stimuli are illustrated in Figure 2a–c, respectively. ERPs to the identification of global and local levels of compound letters were characterized by sequences of peaks that varied in morphology according to scalp location. There was a positive deflection that peaked between 80 and 140 msec (P1) over bilateral occipital, temporal, and parietal sites. The P1 was followed by a negativity over the lateral occipital and temporal sites between 140 to 200 msec (N1). There were also long-latency negativities between 240 and 360 msec over the occipital and temporal (the posterior N2) and frontal and central (the anterior N2) sites.

The P1 peaked slightly earlier in the global than local conditions ($F(1,9) = 9.16, < 0.02$, e.g., 112 vs. 118 msec at occipito-temporal electrodes). The early phase of the P1 component (80–100 msec) showed larger amplitudes in the global than local conditions

($F(1,9) = 6.62, < 0.03$). At the later phase of the P1 (120–140 msec), however, discrimination of local letters elicited larger amplitudes ($F(1,9) = 6.40, < 0.03$). The occipito-temporal N1 was of larger amplitudes between 140 and 200 msec in the local relative to global conditions ($F(1,9) = 5.60, < 0.04$). The N1 amplitudes were also enlarged when global and local letters were consistent than when they were inconsistent ($F(1,9) = 6.39, < 0.03$). This interference effect was more salient for the homogeneous than for the bright stimuli ($F(1,9) = 5.06, < 0.05$) and was stronger in the local than in the global condition for the bright stimuli ($F(1,9) = 6.53, < 0.03$).

The bright stimuli elicited smaller posterior N2 over the occipito-temporal areas relative to the homogeneous and red stimuli ($F(1,9) = 7.60, 5.85$, respectively, < 0.04). Separate analysis for each stimulus set showed that, for the homogeneous stimuli, the posterior N2 was larger (more negative) in the local relative to global conditions between 240 and 360 msec ($F(1,9) = 6.15, < 0.03$) whereas a reverse pattern was evident for the red and bright stimuli ($F(1,9) = 4.95, 8.07$,

respectively, < 0.05). In addition, modulation of the posterior N2 by enhanced local selection was more salient over the left than the right hemisphere ($F(2,18) = 3.66, < 0.05$). For the homogeneous stimuli, the incongruency between global and local letters enhanced the posterior N2 in the local condition whereas had little effect in the global condition ($F(1,9) = 18.56, < 0.001$). For the red and bright stimuli, however, no significant interference effect was observed on the posterior N2. The anterior N2 amplitudes over the frontal-central electrodes did not differ between the global and local conditions for the homogeneous stimuli (> 0.05). However, the anterior N2 amplitudes between 260 and 320 msec were larger in the local than global conditions for the red and bright stimuli ($F(1,9) = 9.61, 18.72$, respectively, < 0.002).

To localize the effects of enhanced attention to the pop-out local item, voltage topographies were calculated based on the difference waves obtained by subtracting ERPs in the global condition from those in the local condition. As can be seen in Figure 3, for the homogeneous stimuli, enhanced negativities between 260 and 320 msec were evident over the occipito-temporal areas. For the red and bright stimuli, however, enhanced negativities in the same time window showed a maximum over the frontal-central region. Moreover, positivities were obtained in the difference waves over bilateral occipito-temporal areas, reflecting the fact that the posterior N2 component was more negative in the global than local conditions.

DISCUSSION

The current study aimed to examine the neural correlates of enhanced selection of an individual local element in perception of hierarchical patterns. ERPs to the homogeneous or pop-out compound stimuli were recorded while subjects identified global or local letters. The key manipulation was to ask subjects to attend to the pop-out (red or brighter) local letter in the local task for the pop-out stimuli whereas there was no such instruction for the homogeneous stimuli. The ERP results appeared to be consistent with our previous work that used compound shapes [Han et al., 2001].

that guiding subjects' attention to the pop-out local item facilitates local processing. The global-to-local interference was weakened by enhanced local selection, consistent with our previous findings [Han and Humphreys, 2002; Han et al., 2001]. However, the local-to-global interference was also smaller for the pop-out than homogenous stimuli, possibly because representation of the pop-out local letter as an independent object made local information isolated from global processing.¹

The early ERP components (P1 and N1) were modulated by attention to the global or local levels of compound letters, consistent with the previous reports [Han and Chen, 1996; Han et al., 1997, 1999a]. The ERP correlates of enhanced local selection were evident over occipito-temporal and frontal-central areas. For the homogeneous stimuli, the posterior N2 was of larger amplitudes in the local relative to global conditions. Similar results were found in the previous studies [Han et al., 1997, 1999a, 2000; Heinze and Münte, 1993; Heinze et al., 1998]. Moreover, when subjects were asked to attend to the pop-out local item, however, the posterior N2 was decreased remarkably. This led to smaller amplitudes of the posterior N2 in the local relative to global conditions. Importantly, this effect was evident for both the bright and red stimuli. Modulations of the anterior N2 by enhanced local selection showed a contrast pattern.

The anterior N2 did not differ between global and local conditions when local letters in compound stimuli were identical. Guiding subjects' attention to the pop-out local item, however, enlarged the anterior N2 related to local processing over the frontal-central region. Again this effect was evident regardless of whether the pop-out local item was defined by color or brightness difference.

Unlike our previous work [Han et al., 2001] that used between-subject comparison, both the anterior and posterior N2 effects were obtained in the current experiment using within-subject comparison. Thus, it is unlikely that these effects result from the difference between two particular groups of subjects. Furthermore, even though compound letters were used in the present study, modulations of the anterior and posterior N2 showed a similar pattern as in the previous work that used compound shapes [Han et al., 2001], suggesting that the effects were independent of stimulus properties (letters or shapes) at the global and local levels of compound stimuli. In addition, modulation of the posterior N2 by top-down attention to the pop-out local item could not result from enhanced attention to color or brightness because Hillyard and colleagues [Hillyard and Münte, 1984; Anllo-Vento and Hillyard, 1996] have shown that attention to specific visual features (such as color and orientation) was indexed by enhanced rather than decreased posterior negativities.

¹RT results of our previous work showed that the pop-out local item increased local-to-global interference relative to the homogenous stimuli [Han et al., 2001]. However, the current work found that the pop-out local item decreased local-to-global interference relative to the homogenous stimuli. We thank a reviewer for noting this point. The inconsistent results made us rethink the nature of the interference between global and local processing and came to the following analysis. The interference effect reflects per se the interaction between global and local processing at specific stages of perceptual and cognitive processing and motor responses. The interference effect also reflects the relative advantage of the global and local processing of compound stimuli (e.g., large global-to-local interference reflects an advantage of global relative to local processing). On the one hand, if global and local processing can be isolated to a certain degree to reduce the interaction between them under some conditions, the interference would be reduced. Relative to the homogenous stimuli, the pop-out stimuli could be represented as a large letter and a small red letter instead of a large letter and small letters composing the large one. Thus, the processing of global and local shapes at the level of object representation may be more isolated for the pop-out than homogenous stimuli. The isolation of the global and local object representations consequently reduced both global-to-local and local-to-global interferences. On the other hand, top-down attention to the unique local letter enhances local processing so that local information produces interference on global processing. This would result in increased local-to-global interference. The above framework may help to reconcile the inconsistent

RT results. Note that RTs to the homogenous stimuli in our previous work [Han et al., 2001] did not show any local-to-global interference, suggesting isolation of local information from global processing. Under this circumstance, the main effect of the unique local item was reflected in the enhanced local processing and increased local-to-global interference. In the current work, however, RTs to the homogenous stimuli showed local-to-global interference possibly because of unique stimulus parameters such as visual angles and local element density (these stimulus factors have been shown to influence relative to advantage of global and local processing) [see Kinchla and Wolfe, 1979; Martin, 1979]. Therefore, the unique local letter first generated isolation of local information from global processing and decreased local-to-global interference. On the other hand, enhanced top-down attention to the unique local letter also facilitated local processing and tended to increase local-to-global interference. If the former effect was stronger than the latter one, the net result was that local-to-global interference was reduced. and local element density (these stimulus factors have been shown to influence relative to advantage of global and local processing) [see Kinchla and Wolfe, 1979; Martin, 1979]. Therefore, the unique local letter first generated isolation of local information from global processing and decreased local-to-global interference. On the other hand, enhanced top-down attention to the unique local letter also facilitated local processing and tended to increase local-to-global interference. If the former effect was stronger than the latter one, the net result was that local-to-global interference was reduced.

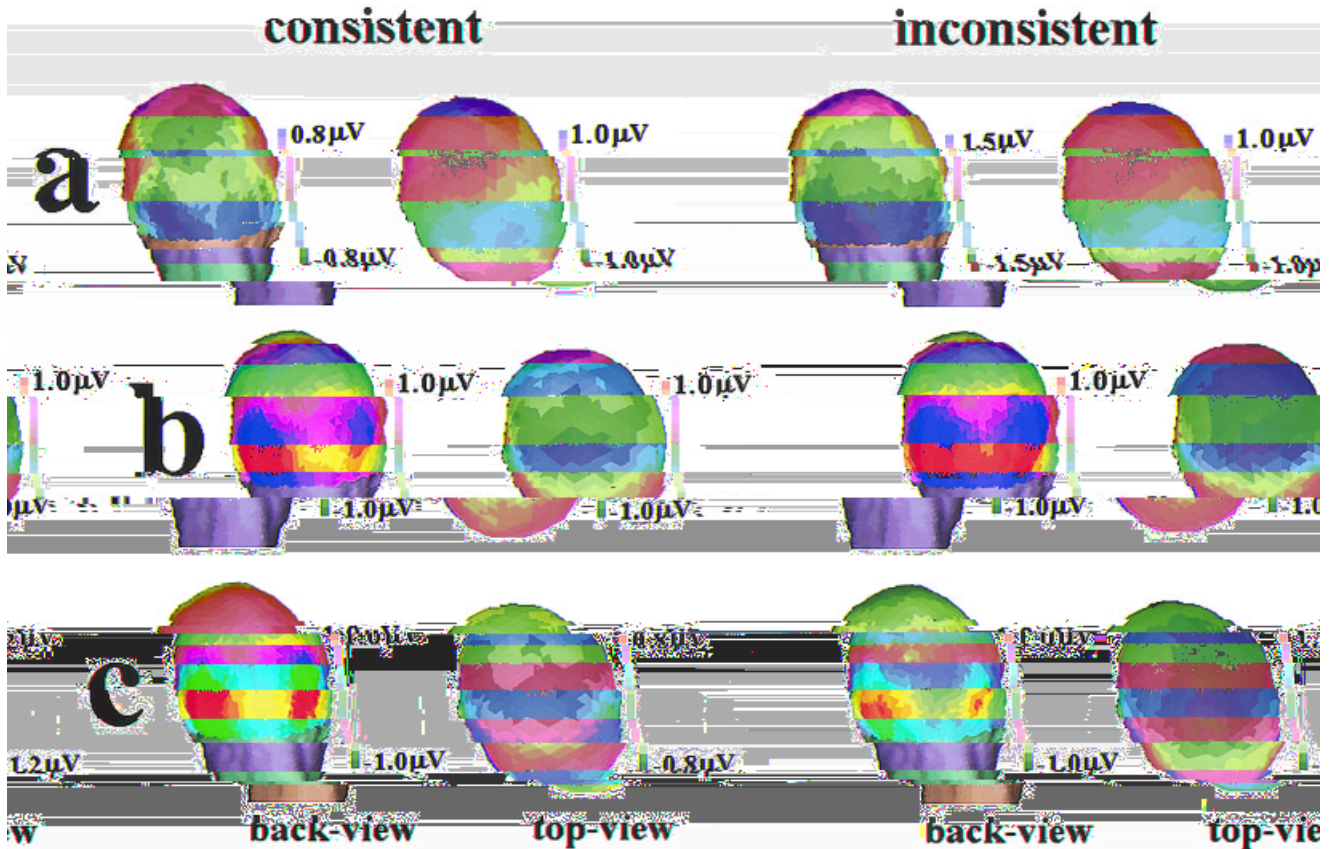


Figure 3.

Voltage topographies of the difference waves that were obtained by subtracting ERPs in the global condition from those in the local condition. The left two columns show the results when global and local letters were consistent and the right two columns show the results when global and local letters were inconsistent. **a:** homogeneous stimuli; **b:** bright stimuli; **c:** red stimuli.

Although a number of ERP studies have found enhanced posterior N2 in the local relative to global conditions [Evans et al., 2000; Han et al., 1997, 1999a, 2000; Heinze and Münte, 1993], the mechanism that the enhanced posterior N2 underlies is still unclear. Heinze and Münte [1993] suggested that the posterior N2 is an index of early global/local target perception. However, the enhanced posterior N2 in the local condition was observed for both target and nontarget stimuli [Han et al., 2003]. The enhanced posterior N2 in the local condition may not be the neural substrates of differential global/local processing based on low spatial frequencies because it could not be eliminated by low-pass filtering [Han et al., 2003].

According to Han et al. [1999b], even though all local items of the homogeneous stimuli are task relevant, an individual local item has to be selected and input into the stage of shape analysis while

other unselected local items are filtered from further processing. This selection process is not required for the global task because there is only one task-relevant object (i.e., the global letter) in each compound stimulus. It is possible that both bottom-up and top-down processes may help the selection of an individual local element. For example, subjects may try to focus on one of the local letters in the local task for the homogeneous stimuli even though the target of this top-down selection may change across trials because all local items are identical and any one of the few local letters around the fixation may serve as targets of the top-down selection. Nevertheless, the pop-out stimuli provided a target at a fixed location and subjects were instructed to attend to the pop-out item. Therefore the top-down selection may be stronger for the pop-out than homogeneous stimuli. On the other hand, for the pop-out

stimuli, the distinctive physical features (color or brightness) defining the pop-out local item provide an additional cue for isolation of the pop-out item from the others. This bottom-up process is more difficult or slower for the homogenous than pop-out stimuli because all local letters are identical in the homogenous stimuli.

The contrast patterns of the modulations of the posterior N2 and the anterior N2 by enhanced attention to the pop-out local letter are consistent with the above analysis. Han et al. [2001] proposed that the enhanced posterior N2 in the local relative to global conditions reflects the bottom-up filtering process involved in the local task to isolate one local item from the others. When a local item differs from its neighbors in one feature dimension (i.e., color or brightness) and pops out from the global structure, the filtering process is weakened and results in elimination of the posterior N2 enhancement in the local relative to global conditions. We show here that the effects of enhanced local selection were similar for red and bright stimuli, indicating that the bottom-up mechanism underpinning local selection is independent of the features defining the pop-out local item.

The anterior N2 enhancement observed in the

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