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*Chinese Science Bulletin* 2006 Vol. 51 No. 3 298–303

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(Received May 25, 2005; accepted July 4, 2005)

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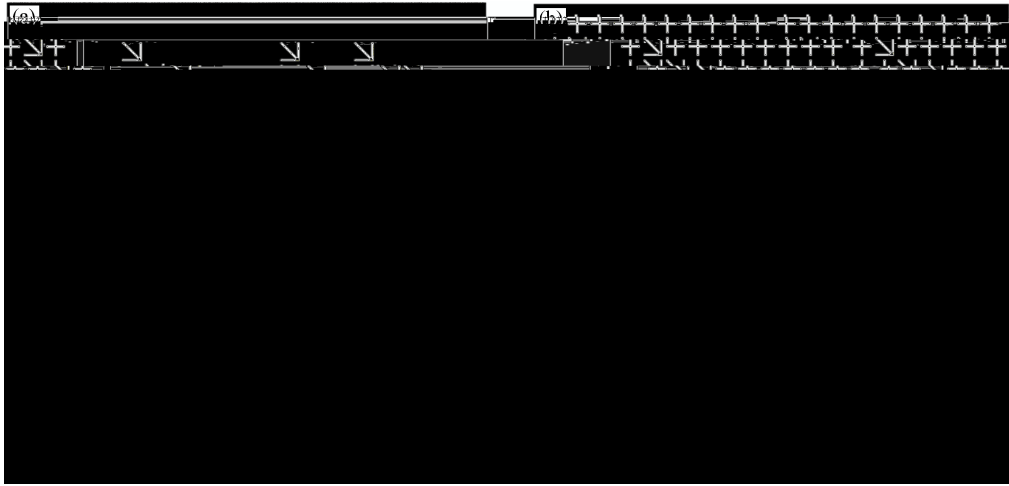


Fig. 1. Illustration of compound stimuli used in the current study. (a) Compound shapes presented on a black background; (b) Compound shapes presented on a background of crosses.

scan consisted of 2 epochs of 28 trials, alternating between global and local attention conditions. Data from the first four seconds of each scan were excluded from data analysis to get a stable baseline. Thus there were 30 s for each epoch. Each epoch began with the presentation of a word (“Global” or “Local” in Chinese) which served as a cue to indicate target level (global or local) and stayed on screen for 2 s. Subjects were asked to remain fixated on the fixation cross and discriminate shapes at the global or local level of compound stimuli (arrow vs. triangle) by pressing two buttons with the left and right index fingers, respectively. The order of global and local tasks was counter-balanced across subjects. Instructions emphasized both response speed and accuracy.

### 1.3 fMRI Image acquisition and analysis

Brain imaging was performed using a 1.5-T GE Signa MR scanner with a custom head coil at Beijing Chaoyang Hospital. Fifteen axial slices of functional images that covered the whole cerebral cortex were acquired using echo-planar imaging (64×64×15 matrix with 3.75×3.75×7-mm spatial resolution, TR = 2000 ms, TE = 40 ms, FOV=240 mm, flip angle = 90°). Anatomical images were obtained with a standard 3D T1-weighted sequence (resulting in a 256×256×84 matrix with 0.938×0.938×2.0-mm spatial resolution, TR = 585 ms, TE = minimum). Subjects’ heads were immobilized during the scanning sessions using pieces of foam.

SPM99 (the Wellcome Department of Cognitive Neurology, UK) was used for data processing and

analysis. Following correction for differences in the timing of slice acquisition within a volume, the functional images were realigned to the first scan to correct for the head movement between scans. The structural image was coregistered with the mean functional image produced during the process of realignment. All images were normalized to a 2×2×2 mm<sup>3</sup> Montreal Neurological Institute (MNI) template in Talairach space using bilinear interpolation. Functional images were spatially smoothed using a Gaussian filter with a full-width at half maximum (FWHM) parameter set to 8 mm. The image data were modeled using a box-car function. Contrasts were used to compare the effect of global/local processing in both experiments. Regions preferentially engaged in global processing were defined as areas more activated in the global than local discrimination conditions. A reverse contrast was used to define regions preferentially engaged in local processing. Random effect analyses were then conducted across the group of subjects based on statistical parameter maps from each individual subject to allow population inference. Areas of significant activation were identified at the cluster level for values exceeding an uncorrected P value of 0.001 for each individual subject and an uncorrected P value of 0.005 for the group analysis. Clusters of voxels smaller than 30 voxels were not displayed. The SPM coordinates for standard brain from Montreal Neurological Institute (MNI) were converted to Talairach coordinates using a non-linear transform method (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html>).

vs. 533 ms,  $F_{(1,13)} = 58.1$ ,  $p < 0.001$ ), consistent with the results of our previous behavioral studies<sup>[10]</sup>.

## 2.1 Behavioral results

Subjects correctly responded to 91% of the compound stimuli in both Experiments 1 and 2. Repeated measure analysis of variance (ANOVA) was conducted on response accuracy and reaction times with Grouping (Experiment 1 vs. Experiment 2) and Level of Attention (global vs. local) as independent variables. There was a significant main effect of grouping on reaction times ( $F_{(1,13)} = 11.5$ ,  $p < 0.005$ ), suggesting faster responses in Experiment 1 than in Experiment 2. The interaction of Grouping x Level of Attention was also significant ( $F_{(1,13)} = 49.0$ ,  $p < 0.001$ ). Post-hoc analyses confirmed that global responses were faster than local responses in Experiment 1 (501 vs. 529 ms,  $F_{(1,13)} = 5.5$ ,  $p < 0.03$ ) but were slower than local responses in Experiment 2 (588

## 2.2 fMRI results

Brain areas involved in global and local processing in each stimulus condition are summarized in Table 1 and illustrated in Fig. 2. In Experiment 1 the discrimination of the local shapes resulted in activation in the left precentral gyrus and right superior temporal gyri, whereas the discrimination of the global shapes induced activation in the medial occipital cortex. In Experiment 2 the discrimination of the global shapes was associated with activation in the inferior temporal gyrus, inferior frontal gyrus, and superior parietal gyrus of the right hemisphere, and the inferior parietal gyrus of the left hemisphere. The discrimination of the local shapes produced significant activation in the left posterior inferior parietal gyrus.

Table 1 Brain areas involved in global and local processing in each condition shown in the group analysis<sup>a)</sup>

Condition/region	Voxels, no.	BA	X	Y	Z	Z value
Experiment 1						
Global processing						
Medial occipital gyrus	53	18	4	-75	24	2.73*
Local processing						
Left precentral gyrus	124	4	-40	-9	52	3.15**
Right superior temporal gyri	309	22	55	2	-5	3.13**
Experiment 2						
Global processing						
Right inferior temporal gyrus	104	37	55	-53	-7	3.54**
Right inferior frontal gyrus	2571	44	46	9	18	3.14**
Right superior parietal gyrus	263	40	44	-38	48	3.12**
Left inferior parietal gyrus	108	40	-65	-24	26	3.11**
Local processing						
Left posterior inferior parietal gyrus	252	39	-44	-59	32	3.27**

a) \*\*,  $p < 0.001$  (uncorrected); \*,  $p < 0.005$  (uncorrected); Voxels, no. = number of voxels in a cluster.



Fig. 2. Activation increases associated with global/local processing. (a) Illustration of brain areas involved in global and l

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The behavior data replicated our previous findings<sup>[10]</sup>. A global precedence effect was observed when local elements were grouped into global shapes by proximity, whereas a local precedence effect was evident when local elements were grouped into global shapes by shape similarity. The results are consistent with the proposition that local element grouping is critical in determining the relative advantage of global and local processing of compound stimuli<sup>[10]</sup>.

Interestingly, our fMRI data showed that neural substrates underlying global and local processing of compound shapes were modulated by the way the local elements were grouped into global structures. We first showed that, when local elements were grouped into global arrows or triangles based on proximity (Experiment 1), processing of the global shapes induced activation in the medial occipital cortex. This is consistent with the results of previous neuroimaging studies<sup>[6,11]</sup> and in support of the view point that a large attentional window is set up to include more local elements in the global condition relative to the local condition and thus induce stronger visual activities. We showed further that the discrimination of the local shapes resulted in activation in the left precentral gyrus and right superior temporal gyrus when local elements were grouped together by proximity. This is different from the previous findings that the processing of the local level of compound letters activates the left inferior occipital cortex<sup>[5,6]</sup>. Given that subjects discriminated closed vs. open forms in the current experiment but other visual features such as orientation in the prior neuroimaging studies<sup>[5,6]</sup>, it may be proposed that visual features required for discrimination may influence neural substrates for local processing. Our fMRI results suggest that the processing of closure at the local level of compound stimuli may not be distinguished from the processing of global shapes at the early stage of the visual pathway. Instead, higher-level brain structures in both the dorsal (the left precentral gyrus) and ventral (the right superior temporal gyrus) visual pathway were involved in the local processing of compound shapes.

Experiment 2 further examined the neural substrates of global/local processing when shape similarity dominated local element grouping. We found that, when local elements were grouped into global structures by shape similarity, the global processing of compound

stimuli did not activate the occipital cortex. Instead, the right inferior temporal, frontal, and parietal cortices, and the left inferior parietal cortex showed stronger activation in the global than in local conditions. The local processing, however, produced significant activation only in the left posterior inferior parietal cortex. The patterns of activation in association with global and local processing of compound shapes in Experiment 2 were different from those in Experiment 1. It appears that higher-level brain structures such as temporal, parietal, and frontal cortices were engaged in the global processing of compound stimuli when the global shapes were formed by a principle of perceptual grouping (i.e. shape similarity) that occurs later than proximity<sup>[12]</sup>. The stimuli used in Experiment 2 were different from those used in Experiment 1 in that global shapes were surrounded by crosses which might induce additional high-spatial frequency components. However, the physical features of our stimuli contributed little to the fMRI results because the contrast was defined to compare the differential neural activity between global and local tasks that employed identical stimuli. Thus the neural mechanisms underlying global/local processing revealed here were stimulus-independent.

The fMRI results observed here extend previous research by showing that the neural mechanisms mediating global/local processing are modulated not only by stimulus location<sup>[6,7]</sup> and stimulus category<sup>[9]</sup> but by perceptual grouping of local elements as well. Unlike previous work which showed that stimulus location and stimulus category modulated hemispheric asymmetry in global/local processing, our fMRI results indicate that perceptual grouping of local elements is critical for the involvement of higher-level brain structures in global/local processing. In particular, global perception was dissociated from local processing in the visual cortex when local elements were grouped by proximity whereas temporal, parietal, and frontal cortices were involved in global perception of compound stimuli when global structures were formed by local element grouping by shape similarity.

These neuroimaging results can explain the variation of behavioral performance in discrimination of global and local shapes when the principle determining local element grouping is changed from proximity to similarity of shape. The perceptual salience of global shapes is higher when local elements are grouped by proximity

than by similarity of shape<sup>[10]</sup> and thus activation of the visual cortex is possibly enough for accomplishing the global perception of compound stimuli. This in turn results in faster behavioral responses to the global than local level of compound stimuli. However, the perceptual salience of global shapes is reduced when global shapes are formed by similarity grouping<sup>[10]</sup>. As a consequence, the perception of global shapes cannot be accomplished in the visual cortex and higher-level brain structures such as parietal and frontal lobes have to be involved. The engagement of additional neural resources in the global processing of compound stimuli led to longer reaction times for the identification of global shapes. Embedding the compound shapes in a background consisting of crosses might increase the difficulty in selecting local items<sup>[13]</sup> and thus the local processing induced activation of the parietal cortex which had been demonstrated to play a critical role of selective attention<sup>[14,15]</sup>.

In the current study the global and local shapes were consistent in half of the trials and inconsistent in the other half of the trials. The consistent and inconsistent stimuli were also presented randomly in the same blocks of trials. The box-car design used in the current work made it difficult to isolate neural mechanisms for global/local processing of consistent and inconsistent stimuli. However, the consistency between global and local shapes might contribute little to the differential fMRI results between Experiments 1 and 2 because the percentage of the consistent and inconsistent trials was identical for both experiments.

We have shown neuroimaging evidence for modulation of neural substrates of global processing of compound stimuli by perceptual grouping of local elements. Particularly, higher-level brain structures were involved in global perception when perceptual salience of global shapes was reduced by weakening local element grouping. The results suggest that global perception of compound stimuli is mediated by different brain areas depending upon how local elements are grouped into global structures.

This work was supported by National Natural Science Foundation of China (Grant Nos. 30225026 & 30328016), the Ministry of Science and Technology of China (Grant No. 2002CCA01000), and the Beijing Key Laboratory.

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(Received October 9, 2005; accepted December 2, 2005)