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Neural mechanisms of perceptual grouping in humans as revealed by high density event related potentials

Shihui Han[a,*], Yulong Ding[b], Yan Song[b]

[a]Department of Psychology, Center for Brain and Cognitive Sciences, Peking University, 5 Yiheyuan Road, Beijing 100871, People's Republic of China

[b]Beijing Lab of Cognitive Science, University of Science and Technology of China, 19A Yuquan Road, Beijing 100039, People's Republic of China

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Abstract

Behavioral studies suggest that perceptual grouping by proximity occurs earlier than grouping by similarity. This notion is supported by recent electrophysiological evidence that proximity grouping generates earlier occipital activation relative to grouping by shape similarity. The current work further investigated neural substrates that differentiate grouping by proximity and grouping by colour similarity by recording high density event related potentials. Subjects discriminated perceptual groups defined by either proximity or colour similarity. Proximity grouping resulted in short-latency modulations of medial occipital activity followed by longer latency modulations in the occipito-parietal cortex. Grouping by colour similarity, however, produced only long-latency occipito-temporal modulations. The results support the proposal that grouping by proximity and grouping by similarity have neural substrates over distinct time courses and cortical areas. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

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Perceptual grouping refers to the function of the human perceptual system to organize discrete entities in the visual field into chunks or perceptual objects for higher-order processing. Gestalt psychologists first identified laws that guide grouping of object constituents into perceptual wholes [7]. For example, the principle of proximity states that spatially close objects tend to be grouped together. The principle of similarity claims that elements with similar features in the field tend to be grouped together. Grouping processes have been assumed to take place at an early stage in the visual processing stream [2,6].

One of the important issues regarding perceptual grouping is whether or not the same neural substrate underpins the grouping processes based on different Gestalt laws. Behavioural research [1,3,4] found that subjects responded faster to the discrimination of perceptual groups defined by proximity than by similarity of shape, suggesting that proximity grouping takes place earlier and/or faster than grouping by similarity. A recent study evaluated grouping related neural substrates by recording event related brain potentials (ERPs) to discriminations of perceptual groups defined by proximity or shape similarity [5]. It was found that proximity grouping induced a positive activity between 100 and 120 ms after stimulus onset over the medial occipital cortex. This early positivity was followed by an occipito-parietal negativity with an onset of 180 ms and larger amplitudes over the right than the left hemisphere. However, grouping by shape similarity was reflected only in a long-latency occipito-temporal negativity with an onset of 260 ms and larger amplitudes over the left than right hemispheres. The ERP results suggest that the grouping processes defined by different Gestalt laws may have distinct neural substrates.

Behavioral research has shown that similarity of colour is a powerful principle to guide grouping [10]. The current work compared ERP correlates to grouping by proximity with those to grouping by colour similarity to examine whether these grouping processes share similar neural substrates. We recorded high density ERPs from human subjects who discriminated displays in which local elements were either evenly spaced, grouped based on proximity, or grouped based colour similarity. Difference waves were obtained by subtracting ERPs to the uniform stimuli from ERPs to the grouping stimuli to elucidate substrates of the

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* Corresponding author. Tel.: +86-10-6275-7179; fax: +86-10-6275-1830.

E-mail address: shan@pku.edu.cn (S. Han).

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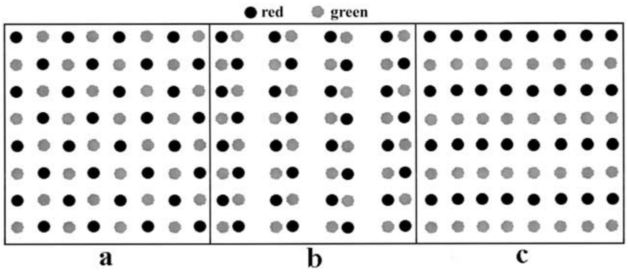

Fig. 1. Illustrations of the stimuli used in the present study. (a) The uniform stimulus; (b), the proximity-grouping stimulus in which local elements group into columns; (c), the similarity-grouping stimulus in which local elements group into rows.

grouping processes. Voltage topographies of ERPs were calculated to estimate the generators of grouping related difference waves.

ERPs were recorded from 16 healthy volunteers (12 men, four women; aged 20–26 years). All subjects were right handed, had normal or corrected-to-normal vision and reported no colour blindness. The stimuli consisted of a square lattice of elements (red or green disks) in an 8×8 array (Fig. 1). The uniform stimulus consisted of alternate red and green disks distributed evenly across the lattice. The proximity-grouping stimuli consisted of alternate red and green disks arranged in arrays to form rows or columns by adjusting the distances between two adjacent rows or columns so that the distances between two near or remote rows (or columns) were 0.14 and 1.1°, respectively. The similarity-grouping stimulus was made by moving the red and green disks in the uniform stimulus to form rows or columns with elements of identical colour. Each local shape and global stimulus array subtended an angle of $0.47^\circ \times 0.47^\circ$ and $7.8^\circ \times 7.8^\circ$, respectively. The horizontal or vertical distance between two adjacent local shapes was 0.57° for the uniform and similarity-grouping stimuli. A white fixation cross of $0.3^\circ \times 0.2^\circ$ was continuously visible in the centre of a black background which had a luminance of 0.02 cd/m^2. The stimulus patterns had a luminance of 0.88 cd/m^2. The red and green disks had Commission Internationale de L'Eclairage (CIE) coordinates of 0.541/0.320 and 0.289/0.603, respectively. The stimulus duration was 200 ms. The interstimulus interval varied randomly between 800 and 1200 ms. Subjects discriminated column versus row

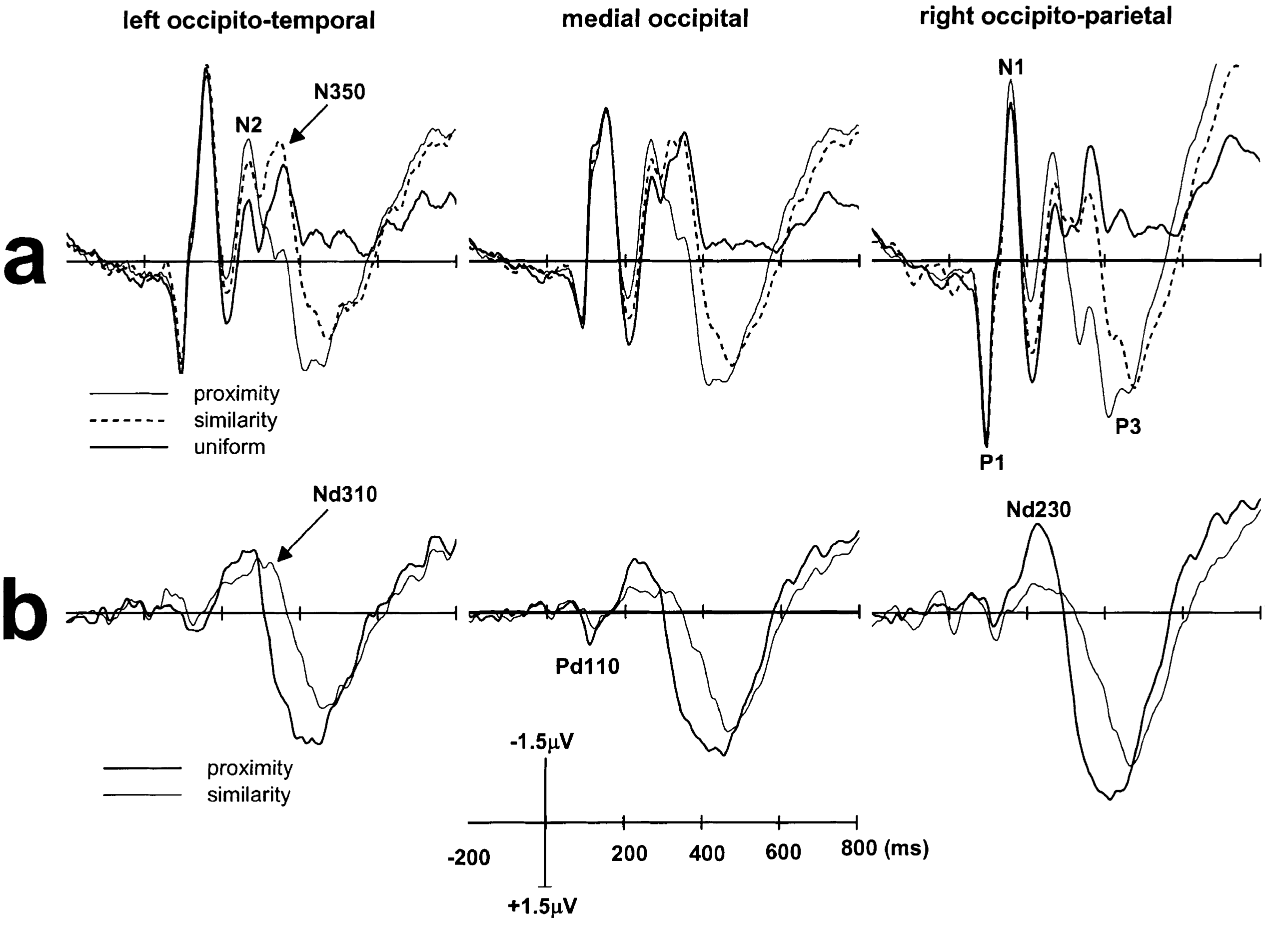

Fig. 2. The effect of grouping by proximity and by colour similarity. (a) Grand averaged ERPs elicited by the uniform and grouping stimuli at three electrodes over different brain areas; (b), difference waves related to proximity and similarity grouping.

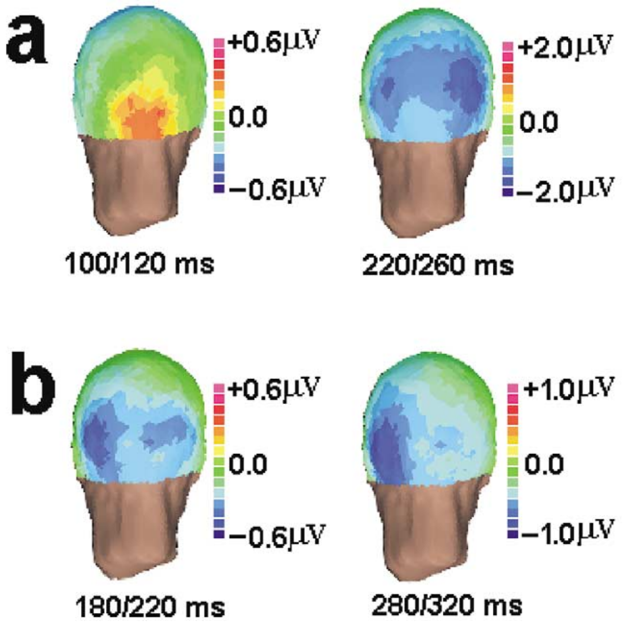

Fig. 3. Scalp voltage maps of difference waves related to: (a), grouping by proximity: the Pd110 focused over the medial occipital cortex and the Nd230 focused over the right occipito-parietal areas; and (b), grouping by similarity of colour: the Nd310 focused over the left occipito-temporal areas.

organizations of the grouping displays by pressing one of the two buttons. After 100 practice trials, subjects were presented with 1000 trials in ten blocks. The uniform, proximity-grouping, and similarity-grouping stimuli were presented randomly on 32, 34 and 34% of the trials, respectively.

The electroencephalogram was recorded as in our previous work [5]. The ERPs in each stimulus condition were averaged separately off-line, with averaging epochs beginning 200 ms before stimulus onset and continuing for 1000 ms. Trials contaminated by eye blinks or muscle potentials exceeding ±75 μV at any electrode or response errors were excluded from the average. The baseline for ERP measures was the mean voltage of the 200-ms prestimulus interval. The mean voltage of ERPs and difference waves were obtained at 20-ms intervals starting at 60 ms and continuing until 500 ms post-stimulus at occipital, parietal and temporal electrodes. The mean peak amplitudes of difference waves were subjected to analyses of variance with Grouping (proximity or similarity versus uniform stimuli) and Hemisphere (electrodes on the left versus right hemisphere) as independent variables over the occipital, temporal and parietal electrodes. To determine the effects in a conservative way, only the smallest F value that showed significant effect was reported.

Reaction times (RT) were faster to proximity- than similarity-grouping stimuli (514 versus 534 ms; $t = 4.736$, $P < 0.001$), consistent with previous reports [1,3]. There was no significant difference in error rate between the two conditions (4.6 versus 4.3%; $t = 0.708$, $P > 0.5$).

Grand averaged ERPs and grouping related difference waves are shown in Fig. 2. Proximity grouping was first indexed by a positive wave that peaked between 100 and 120 ms over the medial occipital cortex (Pd110) indicated by the main effect of grouping ($F_{(1,15)} = 4.82$, $P < 0.04$). This positivity was followed by an occipito-parietal negativity between 180 and 260 ms (Nd230; $F_{(1,15)} = 4.62$, $P < 0.04$), which had a larger amplitude over the right than the left hemisphere suggested by a significant interaction of Grouping × Hemisphere ($F_{(1,15)} = 4.57$, $P < 0.05$). Scalp topographies were drawn on a subject's head model to visualize the foci of the effects of proximity and similarity grouping (Fig. 3). Although the similarity-grouping related difference wave showed a small positivity over the medial occipital cortex, this effect was not significant. The effect of grouping by colour similarity was only reflected in a broad negativity between 180 and 380 ms over the occipito-temporal region (Nd310) indicated by the main effect of Grouping ($F_{(1,15)} = 4.49$, $P < 0.05$). The late phase of the Nd310 (260–380 ms) showed a larger amplitude over the left than the right hemisphere as indicated by a significant interaction of Grouping × Hemisphere ($F_{(1,15)} = 4.58$, $P < 0.05$).

Although the local elements were defined by different colours in the current study, proximity grouping induced similar medial occipital modulations at 110 ms as in our previous work [5], suggesting that proximity grouping largely depends on representation of a spatial relationship between local elements and is independent of visual features (such as shape and colour) that define local items. It is unlikely that the Pd110 reflects a response of orientation discrimination that particularly engaged in the grouping stimuli because the earliest ERP component related to visual discrimination is a negative wave that peaks at about 165 ms (N1) [12]. In addition, the Pd110 was evident for the proximity-grouping condition but not for the similarity-grouping condition despite the fact that visual discrimination was required under both conditions. The Pd110 corroborates evidence from other studies [8,11] in reinforcing that the striate or prestriate cortex is involved in early perceptual processing such as figure-ground segregation and grouping. The Pd110 may reflect local circuitry activity in the early visual areas. Alternatively, re-entrant feedback from higher visual areas may induce stronger responses to the grouping stimuli in the early visual areas and produce the Pd110. These need to be distinguished in further studies.

The Nd310 elicited by similarity grouping peaked even later than the late component (Nd230) related to proximity grouping. The onset delay of similarity-grouping difference waves provide a neurophysiological basis for the slower behavioural responses to similarity- than proximity-stimuli. Note that subjects had to select the grouping stimuli first and then discriminate columns versus rows of the displays. Thus, the latency difference between the Nd310 and the Nd230 may reflect the delay of similarity-grouping processing at the stage of selection, discrimination, or other postperceptual analysis. Topographies of these negativities indicate that the occipito-parietal areas are engaged in proximity grouping whereas the occipito-temporal areas are involved in similarity grouping, suggesting that distinct brain areas are involved in different grouping operations. Different hemispheric lateralization in proximity and similarity grouping may result from the dominance of the two hemispheres in low versus high spatial frequency analysis (see Ref. [5] for more discussion).

The effect of grouping by shape similarity was also characterized by an occipito-temporal negativity with a left hemisphere dominance [5]. The similar morphology, scalp distribution, and hemisphere dominance of the difference waves in the two studies suggest that grouping based on shape or colour may be mediated by a similar mechanism over the occipito-temporal cortex. However, it is possible that, relative to shape, colour is a more salient object feature, and thus generated earlier onset of grouping operations (indexed by the earlier onset of difference wave and shorter RTs in the current than in our previous work) and perceptual dominance in grouping discrete items [10]. Our findings provide a neurophysiological basis for understanding the results of recent psychophysical studies [9], which showed that luminance difference facilitated orientation-based texture segregation whereas additional colour information had no effect. Local elements with different orientations are segregated into different groups possibly via occipito-temporal substrates. The early medial occipital mechanism might be engaged in segregation when an additional luminance cue was introduced to separate the local elements along opposite texture boundaries by providing spatial distance information. The additional colour cue, however, failed to enhance orientation-based segregation because similar neural substrates underlie both grouping by colour similarity and grouping by orientation similarity.

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