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Neural substrates for visual perceptual grouping in humans

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Abstract

Two experiments investigated the neural mechanisms of Gestalt grouping by recording high-density event-related brain potentials (ERPs) during discrimination tasks. In Experiment 1, stimulus arrays contained luminance-defined local elements that were either evenly spaced or grouped into columns or rows based on either proximity or similarity of shape. Proximity grouping was indexed by a short-latency positivity (110–120 ms) over the medial occipital cortex and a subsequent right occipitoparietal negativity. Grouping by similarity was reflected only in a long-latency occipitotemporal negativity. In Experiment 2, proximity grouping was examined when local elements were defined by motion cues, and was again associated with a medial occipital positivity. However, the subsequent long-latency negativity was now enhanced over the left posterior areas. The implications of these results to the neural substrates subserving different grouping processes are discussed.

Descriptors: Cortex, Event-related potentials, Gestalt, Grouping, Proximity, Similarity

Human viewers can rapidly extract global configuration information from complex visual scenes containing multiple separate or overlapping objects. It has been widely accepted that perceptual grouping is fundamental to this process and occurs at an early stage of visual analysis. For example, computational theories of vision postulate an early stage of representation that encodes visual elements into clusters to form plausible objects for further processing (Marr, 1982). Similarly, theories of visual attention hypothesize that perceptual grouping takes place preattentively to form perceptual units that become the substrates of subsequent higher order attentional processing (Duncan, 1984; Duncan & Humphreys, 1989; Kahneman & Henik, 1981; Moore & Egeth, 1997; Neisser, 1967).

The process of grouping object constituents into perceptual wholes is usually guided by Gestalt principles (Koffka, 1923; Wertheimer, 1923). Two of the most fundamental grouping principles are proximity and similarity. The principle of proximity states that nearby objects tend to be perceived as belonging to a common group. The principle of similarity states that elements that are similar to one another tend to be grouped together.

Several studies suggest that proximity is a more salient cue than similarity in guiding perceptual grouping. For example, Quinlan and Wilton (1998) presented subjects with displays comprising a row of seven colored shapes. Subjects were asked to rate the degree to which the central target shape grouped with either the left or the right flanking shapes. Quinlan and Wilton found that subjects showed stronger tendency to group local elements by proximity than by similarity of shape. Other researchers measured reaction times (RTs) to discriminations of perceptual groups defined by Gestalt laws. For instance, Ben-Av and Sagi (1995) had subjects report horizontal or vertical organization of stimulus arrays that were made up of local elements. They found that subjects responded faster to orientations of perceptual groups formed by proximity than by similarity of shape. Han et al. (Han & Humphreys, 1999; Han, Humphreys & Chen, 1999a, 1999b) asked subjects to discriminate global shapes made up of local elements that were grouped by either proximity or similarity of shape. They also found faster RTs to proximity relative to similarity stimuli. Taken together, the findings indicate that proximity grouping is perceived faster and/or earlier than grouping by similarity of shape in visual perception.

Despite the findings of behavioral studies, however, there has been little neurophysiological evidence that different cortical processes subserve different Gestalt grouping operations. Indeed, the lack of neurophysiological evidence of grouping has led to the suggestion that the grouping processes defined by different Gestalt laws reflect a common neural mechanism (Leeuwenberg & Boselie, 1988).

Recent studies of neurons in the primary visual cortex (V1) of monkeys reveal processing similar to Gestalt grouping. For example, Kapadia, Ito, Gilbert, and Westheimer (1995) found that responses of 40% of complex cells in V1 were increased when a second nearby, collinear, iso-oriented line was placed outside the

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excitatory core of the receptive field. Sugita (1999) found cells in V1 that responded to two line segments as if they were one continuous long line when an intervening stimulus patch was positioned in space to block the view of the discontinuity. Other studies showed that responses of cells in V1 and the posteromedial lateral suprasylvian area were synchronized when visual stimuli in receptive fields of cells in the two brain areas moved at the same speed in the same direction (Engel, Kreiter, König, & Singer, 1991), suggesting that temporal coding of neural responses may be a possible mechanism of the grouping process.

Although these neurophysiological findings suggest that grouping may involve modulation of processing in early visual areas, there is no evidence that such modulation occurs in humans with the complex displays used to study grouping. The current work investigated neural mechanisms of grouping by proximity and similarity of shape by recording event-related brain potential (ERP) from human subjects viewing such complex displays. We compared ERPs elicited by proximity- and similarity-grouping stimuli to identify the chronometry of the two grouping processes, and used voltage topographies of 120 channel ERPs to estimate the intracerebral sources of grouping-related modulations. The experimental design was similar to that used in previous behavioral studies of perceptual grouping (Ben-Av & Sagi, 1995; Han et al., 1999a). Participants were asked to discriminate orientations of groups composed of local elements. To examine the generality of the findings, local figures were defined by luminance contrast in Experiment 1, and by motion contrast in Experiment 2.

EXPERIMENT 1

In Experiment 1, participants were presented with stimulus arrays made up of local filled bright squares and circles on a dark background (Figure 1). The local elements were either (1) evenly spaced (uniform stimuli); (2) grouped into columns or rows by adjusting the distances between adjacent local elements (grouping by proximity); or (3) grouped by forming columns or rows of squares and circles (grouping by similarity of shape). ERPs were obtained separately for the uniform and grouping stimuli. Difference waves were obtained by subtracting ERPs to the uniform stimuli from ERPs to the grouping stimuli to estimate the ERP correlates of the grouping processes.

Methods

Participants

Fourteen graduate students (2 female, 12 male, aged between 18 and 35 years) participated in this experiment as paid volunteers. All had normal or corrected-to-normal vision. All participants were right-handed, without neurological disorders, and gave informed consent according to the guidelines of the University of Science and Technology of China.

Stimuli

White stimulus elements were presented on a black background presented on a 15-in. color monitor at a viewing distance of 57 cm. A white fixation cross of $0.3° \times 0.2°$ was continuously visible in the center of the monitor. The stimuli consisted of a square lattice of elements (either filled circles or squares) in an 8×8 array, as shown in Figure 1. The uniform stimulus consisted of alternate circles and squares distributed evenly across the lattice. This arrangement prevented the local elements from grouping into rows or columns. The proximity-grouping stimuli consisted of alternate

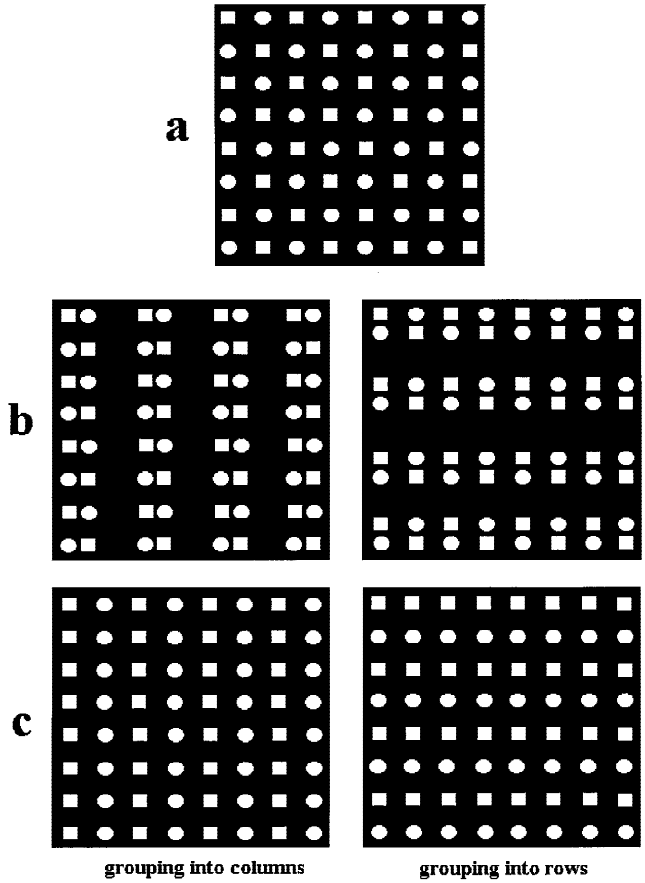

Figure 1. Illustration of the stimuli used in Experiment 1. (a) The uniform stimulus; (b) proximity-grouping stimuli; (c) similarity-grouping stimuli.

circles and squares arranged in arrays to form separate perceptual groups (i.e., rows or columns) by adjusting the distances between two adjacent rows or columns of local elements so that the distances between two near or remote rows (or columns) were 0.14° and 1.1°, respectively. The similarity-grouping stimuli were made by moving the circles and squares in the uniform stimulus to form rows or columns of elements with the same shape. The distance between two adjacent columns or rows was 0.57° for the uniform and similarity-grouping stimuli. Each local shape subtended an angle of $0.47° \times 0.47°$ and global stimulus pattern subtended an angle of $7.8° \times 7.8°$. The background had a luminance of 0.02 cd/m^2. The stimulus patterns had a luminance of 3.46 cd/m^2. The stimulus displays were presented for 200 ms. Interstimulus intervals were randomized between 800–1,200 ms.

Procedure

Participants were asked to indicate the presence of row- or column-grouped stimuli (regardless of whether proximity or similarity cues produced grouping) by pressing one of two keys with either the left or the right thumb. Uniform stimuli required no response. Each participant completed 100 practice trials, followed by 1,000 trials in ten 100-trial blocks. The uniform stimuli, proximity-grouping stimuli, and similarity-grouping stimuli were presented randomly on 32%, 34%, and 34% of the trials, respectively. Half of the participants responded to rows with the left hand and to columns with the right hand. This arrangement was reversed for the remain-

ing participants. Participants were instructed to maintain fixation on the central cross throughout the task.

ERP Data Recording and Analysis

The electroencephalogram (EEG) was recorded from 120 scalp electrodes (Figure 2). The position of each electrode was measured with a 3D probe relative to fiducial marks on the skull. The average of the recordings from electrodes at the left and right earlobes was used as reference. Eye blinks and vertical eye movement were monitored with electrodes located below the left and right eyes. The horizontal electro-oculogram was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG was amplified (bandpass 0.1–40 Hz) and digitized at a sampling rate of 250 Hz. The ERPs in each stimulus condition were averaged separately off-line with averaging epochs beginning 200 ms before stimulus onset and continuing for 1,200 ms. Only trials with correct responses were analyzed. Trials contaminated by eye blinks, eye movements, or muscle potentials exceeding 150 μv (peak-to-peak amplitude) at any electrode were excluded from the average. ERPs and difference waves were measured with respect to the mean voltage during the 200-ms prestimulus interval. Peak latencies were measured relative to stimulus onset. Mean voltages of ERPs and difference waves were obtained at successive 20-ms intervals starting at 60 ms after stimulus onset and continuing until 600 ms poststimulus.

As the preliminary analyses did not show significant differences in behavioral and ERP data between vertical and horizontal grouping stimuli, the data in the two conditions were combined for further analyses. The mean amplitudes of ERPs to the grouping stimuli and grouping-related difference waves were measured over cortical areas where the components showed maximal amplitudes, and then subjected to a repeated measure analysis of variance (ANOVA) with grouping (grouping by proximity vs. similarity of shape) and hemisphere (electrodes on the left vs. right hemisphere) as independent variables. Components were quantified at sites of maximal amplitude, using symmetrical electrodes over the two hemispheres. ERP waves elicited by uniform and grouping stimuli include a positive wave (P85) between 70 and 100 ms over the lateral occipital sites, which was followed by a negative wave (N110) over the medial occipital sites between 100 to 120 ms. Two other negative waves peaking between 120 and 180 ms (N150) and between 220 and 280 ms (N260) were also observed over the occipitotemporal regions. An additional occipitotemporal negativity between 300 and 380 ms (N340) was evident only for the similarity-grouping stimuli. Both the proximity- and similarity-grouping stimuli elicited a frontal positivity between 190 and 250 ms (P220) and a P3 between 300 and 700 ms over the central-parietal areas.

The P85, N110, N150, and N260 ERP components were measured and analyzed at electrodes over the lateral occipital regions. The P3 was measured and analyzed at the parietal electrodes. In difference waves, the Pd110 was measured and analyzed at the lateral occipital electrodes. The Nd230 and Nd340 were measured and analyzed at the occipital, temporal, and parietal electrodes. Voltage topographies of grouping related difference waves were plotted on a realistic head model of a randomly selected participant. Averaged electrode coordinates from all the participants were used to locate the electrodes on the head model. Statistical comparisons of scalp distributions were performed on normalized amplitudes.

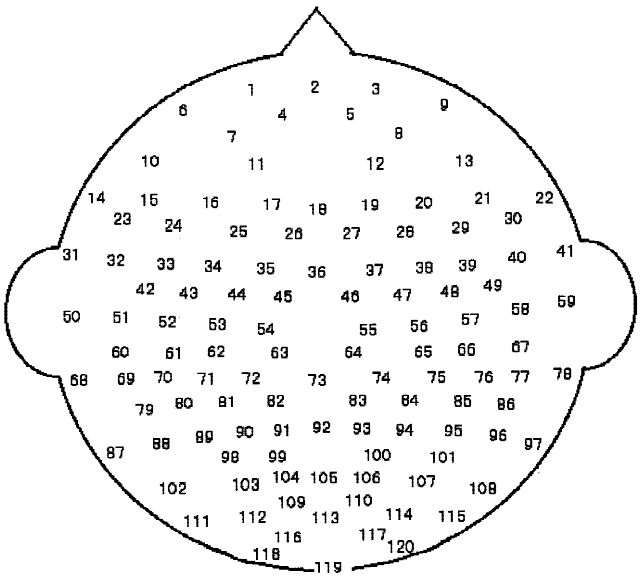

Figure 2. The diagram of 120-channel scalp montage used in the present study. Each electrode was named with a number from 1 to 120. Electrodes 2, 18, 36, 73, 92, 105, 113, and 119 were arranged along the midline of the skull. Other electrodes were located approximately symmetrically over the two hemispheres.

Results

Performance

RTs to the proximity-grouping stimuli were faster than those to the similarity-grouping stimuli (525 vs. 575 ms, $F(1,13) = 24.2$, $p < .001$). Response accuracy was also higher in proximity- than similarity-grouping conditions (95.9% vs. 93.3%, $F(1,13) = 11.5$, $p < .005$).

Electrophysiological Data

Figure 3 shows grand averaged ERPs to the uniform and grouping stimuli. The amplitude of the P85 was larger over the right than the left hemisphere, $F(1,13) = 7.34$, $p < .02$, but did not differ between proximity- and similarity-grouping conditions, $F < 1$. However, the N110 showed smaller amplitudes to proximity- than similarity-grouping stimuli, $F(1,13) = 8.97$, $p < .01$. In contrast, the N260 was of larger amplitude to proximity- than similarity-grouping stimuli, $F(1,13) = 16.89$, $p < .002$. The proximity-grouping stimuli elicited larger P3 amplitudes, $F(1,13) = 19.95$, $p < .001$, with shorter latencies, $F(1,13) = 22.57$, $p < .001$, relative to the similarity-grouping stimuli.

To visualize the effects of proximity and similarity grouping, grouping-related difference waves were obtained by subtracting ERPs to the uniform stimuli from ERPs to proximity- or similarity-grouping stimuli (Figure 4). Proximity grouping was first reflected in a positivity between 100 and 120 ms (Pd110), $F(1,13) = 4.81$, $p < .05$. Topographic analysis (Figure 5a) showed that the Pd110 had an amplitude maximum over medial occipital areas. The initial positivity was followed by a negativity between 180 and 280 ms (Nd230), $F(1,13) = 36.81$, $p < .001$, with maximum amplitude over the occipitoparietal areas. The Nd230 showed larger amplitudes over the right than the left hemisphere, $F(1,13) = 9.03$, $p < .01$. The distribution of the Nd230 is shown in Figure 5a.

Grouping by similarity of shape was indexed by a broad bilateral occipitotemporal negativity between 260 and 420 ms (Nd340),

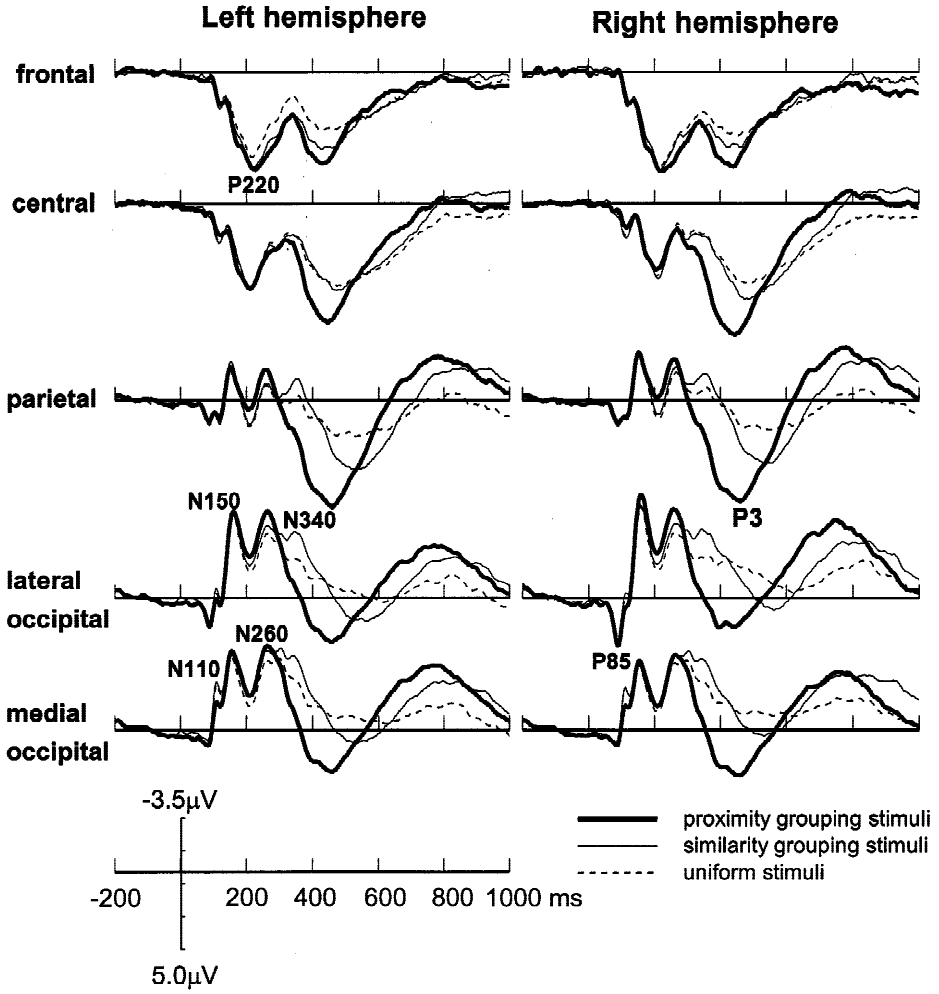

Figure 3. Grand average ERPs across the 14 participants elicited by the uniform and grouping stimuli in Experiment 1. The ERPs (plotted negative polarity upward) are shown for left and right frontal, central, parietal, lateral occipital, and medial occipital sites.

$F(1,13) = 6.68$, $p < .02$. The later phase of the Nd340 (380–420 ms) showed larger amplitudes over the left than the right hemisphere, $F(1,13) = 4.68$, $p < .05$. The distribution of the Nd340 is shown in Figure 5b. Difference waves also showed a late widely distributed positivity in proximity- and similarity-grouping conditions, which resulted from larger P3 to the grouping than the uniform stimuli.

Voltage topographies suggested that the long-latency negativities associated with proximity and similarity grouping originated from different regions of visual cortex (Figure 5). An ANOVA comparing the relative amplitudes of grouping-related negativities at parietal and temporal sites showed a significant interaction between grouping-type and location, $F(1,13) = 9.14$, $p < .01$, reflecting the fact that proximity grouping produced relatively larger parietal negativities whereas similarity grouping produced relatively larger temporal negativities.

Discussion

The behavioral data of Experiment 1 showed that participants responded faster with fewer errors to proximity- than similarity-grouping stimuli. This difference is consistent with the results of previous reports (Ben-Av & Sagi, 1995; Han & Humphreys, 1999; Han et al., 1999a, 1999b).

The neural mechanisms related to the grouping processes were revealed by the difference waves. Proximity grouping was associated with a short-latency enhanced positivity (Pd110) over the medial occipital cortex. Enhanced parietal negativities (Nd230) were also seen in the proximity-grouping condition, particularly over the right hemisphere. In contrast, grouping by similarity of shapes produced only longer-latency occipitotemporal negativities (Nd340), with an asymmetric left hemisphere focus. These findings suggest that neural mechanisms of the grouping process by proximity and similarity of shape may differ in both time course and neural origin.

The Pd110 related to proximity grouping may reflect an early representation of spatial parsing of local elements in visual cortex. This provides electrophysiological evidence for short-latency clustering of elements based on proximity. The early occipital positivity and earlier onset of occipitoparietal negativity in the proximity-grouping condition also provide electrophysiological correlates of the faster behavioral responses to proximity- than similarity-grouping targets (Ben-Av & Sagi, 1995; Han et al., 1999a, 1999b). Moreover, the Nd waves showed larger amplitudes over the oc-

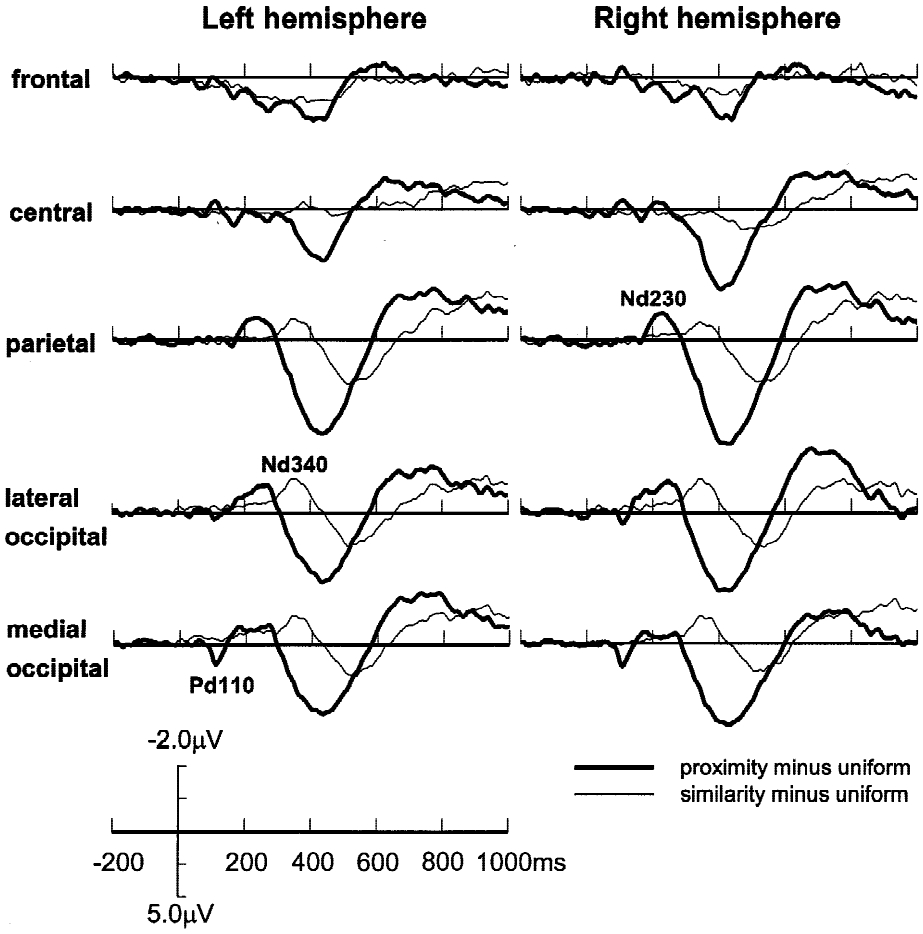

Figure 4. Difference waves reflecting proximity- and similarity-grouping processes and the difference between the two grouping conditions in Experiment 1.

cipitoparietal areas for the proximity-grouping process and over the occipitotemporal areas for the similarity-grouping process. This scalp-distribution difference suggests that the dorsal pathway may be preferentially involved in proximity grouping, whereas the ventral pathway may play a larger role in representing similarity of local elements based on their shapes. This proposal is consistent with previous studies that suggest that the dorsal occipitoparietal stream processes spatial features of stimuli whereas the ventral occipitotemporal stream processes object features (such as shape and color; Haxby et al., 1994; McIntosh et al., 1994; Ungerleider & Haxby, 1994).

In addition, our data showed that neural activities related to proximity- and similarity-grouping had different hemispheric distributions. The asymmetry of long-latency negativities suggests a greater role for the right hemisphere in proximity grouping and a greater role for the left hemisphere in similarity grouping. It has been suggested that perceptual grouping could be achieved by the application of lowpass filtering of visual images (Beck, Sutter, & Ivry, 1987; Ginsburg, 1986; Reed & Wechsler, 1990) and that the right and left hemispheres dominate the processing of low and high spatial frequencies (Kitterle, Christman, & Hellige, 1990), respectively. Because the double row (or column) of local elements in the proximity stimuli would introduce power at lower spatial frequencies not present in uniform and similarity stimuli, this relatively low spatial frequency information might be used in proximity grouping. In contrast, observers would have to use higher spatial frequency information to detect the shape cues needed for similarity grouping. Therefore, the stronger long-latency activities of the right and left hemispheres during proximity and similarity grouping may reflect asymmetries in the processing of low and high spatial frequencies in the image.

Finally, the ERP results suggest that late processing stages also differ between proximity- and similarity-grouping tasks. For example, the P3 component, which is associated with stimulus evaluation and categorization (McCarthy & Donchin, 1981; Mecklinger & Ullsperger, 1993; Mecklinger, Ullsperger, & Baldeweg, 1993), was significantly delayed in similarity- relative to proximity-grouping tasks. The P3 delay may be partially due to the longer latency of the similarity-grouping process as reflected by the Nd340 in the difference waves. The larger P3 amplitude in proximity relative to similarity conditions may reflect the difference in confidence with which perceptual decisions were made (Kerkhof & Uhlenbroek, 1981; Squires, Squired, & Hillyard, 1975).

EXPERIMENT 2

Experiment 1 showed that the proximity-grouping-related difference wave was characterized by an occipital positivity (Pd110). Because Experiment 1 used only stimuli that were defined by luminance contrast, it is unclear whether similar occipital activity

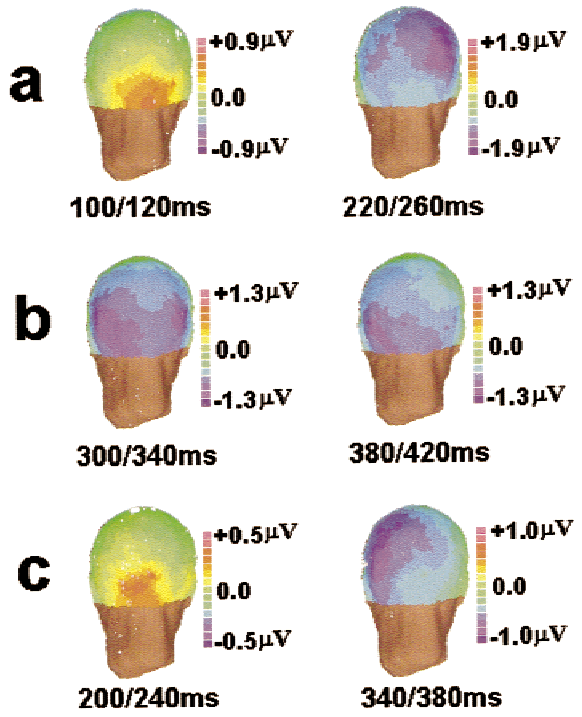

Figure 5. Scalp voltage maps (viewed from the back of the head) showing the distribution of grouping-related difference waves. (a) Proximity grouping in Experiment 1. The voltage maps reveal a medial occipital distribution of the Pd110 and a right occipito-parietal distribution of the Nd230. (b) Similarity grouping in Experiment 1. The voltage maps reveal a left occipito-temporal distribution of the Nd340. (c) Proximity grouping in Experiment 2. The voltage maps reveal a medial occipital distribution of the Pd230 and a left occipito-parietal distribution of the Nd380.

would occur for stimuli with local stimulus objects defined by a different stimulus feature. To test this possibility, Experiment 2 employed stimuli in which local elements were defined by motion contrast. The background was composed of randomly moving dots. Local circles and squares were made up of stationary random dots.

Experiment 2 also provided information on the importance of low spatial frequencies to the proximity-grouping process. In Experiment 1, proximity grouping could have been facilitated by the operation of channels tuned to low spatial frequencies (Ginsburg, 1986), although there is some evidence that perceptual grouping can also occur with highpass filtered images (Janez, 1984). In contrast, the stimuli in Experiment 2 gave the observer no steady-state spatial frequency cues in either low or high spatial frequencies to perform the task. Each frame of a stimulus display in Experiment 2 was a random-dot pattern, and in itself provided no information about the presence, absence, shape, or spacing of the motion-induced local circles and squares. It was only the integration of high-spatial-frequency information across frames that differentiated stationary from moving dots, and the movement contrast that defined the locations of the local shapes.

Methods

Participants

Sixteen graduate students (3 female, 13 male, aged between 20 and 26 years) participated as paid volunteers. All had normal or corrected-to-normal vision. All participants were right-handed, without neurological disorders, and gave informed consent according to the guidelines of the University of Science and Technology of China.

Stimuli and Procedure

These were the same as those in Experiment 1 except for the following. A large square of 11.9° × 11.9° made up of white randomly moving dots was continuously displayed in the center of a black background. The size of each random dot was 0.02° × 0.02°. Each pixel had 50% probability of being white. Local circles and squares were formed by stopping dot motion for 200 ms in circular and square areas that corresponded to the local shapes of Experiment 1. Only the uniform and proximity-grouping stimuli were used in Experiment 2 because the difference between the motion-induced circular and square shapes was insufficient to support similarity grouping under these conditions. The stimulus pattern had a luminance of 6.97 cd/m^2.

A green fixation cross of 0.3° × 0.2° was continuously visible in the center of the stimulus display. Participants responded to rows versus columns of the proximity-grouping stimuli by pressing one of two keys with the left or the right thumb while withholding responses to the uniform stimuli. Participants were presented with 792 trials in four blocks after 120 practice trials. To maintain the same proportion of horizontal–vertical grouping discrimination trials as in Experiment 1, uniform and proximity-grouping stimuli were presented randomly on 32% and 68% of the trials, respectively.

ERP Data Recording and Analysis

ERPs were quantified as in Experiment 1. The mean amplitudes of ERPs to the uniform and grouping stimuli were subjected to ANOVAs with grouping (uniform vs. grouping by proximity) and hemisphere (electrodes on the left vs. right hemisphere) as independent variables. The difference waves were obtained by subtracting ERPs to the uniform stimuli from ERPs to the grouping stimuli and were subjected to ANOVAs with hemisphere (electrodes on the left vs. right hemisphere) as independent variables.

Results

Performance

RTs for discrimination of rows versus columns of proximity-grouping stimuli were 611 ms with 92.8% response accuracy. RTs in Experiment 2 were significantly slower than those in Experiment 1, $F(1,28) = 13.1$, $p < .001$. Response accuracy was also lower in Experiment 2 than in Experiment 1, $F(1,28) = 4.2$, $p < .05$.

Electrophysiological Data

Grand averaged ERPs elicited by proximity-grouping and uniform stimuli are shown in Figure 6. ERPs to those stimuli were characterized by posterior occipital negativities between 220 and 300 ms (N260) and between 300 and 400 ms (N350). A positive component between 200 and 300 (P250) and a negative-going component between 380 and 460 ms (N420) were also observed over the frontal areas.

The N260 had larger amplitudes at the electrodes over the right than the left hemisphere, $F(1,15) = 14.49$, $p < .002$. This hemispheric asymmetry was more pronounced for the uniform stimuli than for the proximity-grouping stimuli, $F(1,15) = 9.48$, $p < .01$. The N350 amplitude was greater to the proximity-grouping stimuli relative to the uniform stimuli, $F(1,15) = 10.38$, $p < .006$. The

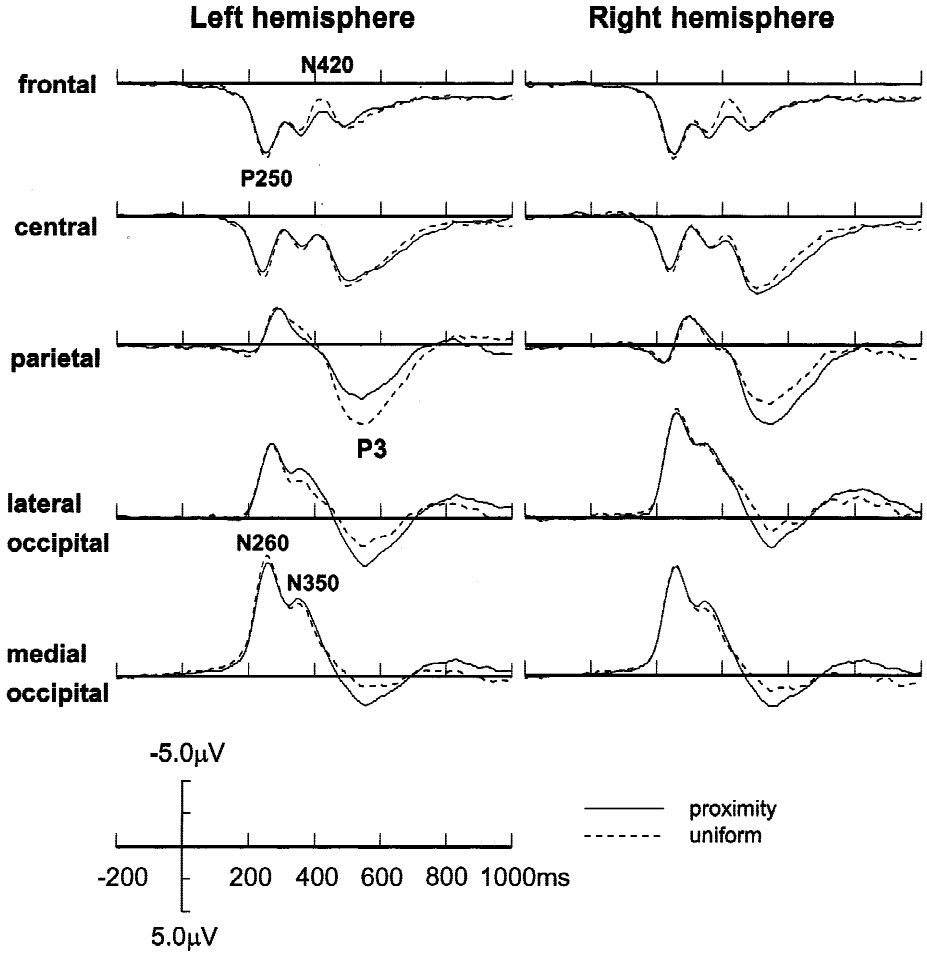

Figure 6. Grand average ERPs across the 16 participants elicited by the uniform and proximity-grouping stimuli in Experiment 2. The ERPs (plotted negative polarity upward) are shown for left and right frontal, central, parietal, lateral occipital, and medial occipital sites.

N350 also showed larger amplitudes over the right than the left hemisphere, $F(1,15) = 12.11$, $p < .004$, and this asymmetric effect was stronger for uniform than for proximity-grouping stimuli, $F(1,15) = 11.80$, $p < .004$. The frontal N420 was enlarged to uniform compared to proximity-grouping stimuli, $F(1,15) = 9.60$, $p < .007$.

Difference waves revealed a positivity between 180 and 260 ms (Pd230), $F(1,15) = 4.67$, $p < .05$ (Figure 7). The Pd230 had a distribution over the medial occipital areas, as illustrated in the voltage topographies (Figure 5). A longer-latency negativity was evident at 340–400 ms (Nd380), $F(1,15) = 9.29$, $p < .008$, with maximum amplitude over the left occipitoparietal areas, $F(1,15) = 4.96$; $p < .04$. A positivity peaking at about 400 ms was observed over the frontal electrodes (Pd400), $F(1,15) = 8.25$, $p < .01$. Similar to those in Experiment 1, difference waves also showed a late widely distributed positivity that resulted from the larger P3 elicited by the grouping stimuli. ANOVA showed that distributions of the shorter latency positivity in the difference waves did not differ between Experiments 1 and 2, $p > .1$. However, lateralization of the long-latency negativity in the difference wave was significantly different between the two experiments, $F(1,28) = 17.28$, $p < .005$.

Discussion

Though behavioral responses in Experiment 2 were slower and less accurate than those in Experiment 1, participants still performed the task with a high accuracy, indicating that motion contrasts can support proximity grouping and that steady-state low-spatial-frequency information is not essential for such grouping to occur. The ERPs to grouping and uniform stimuli differed from those in Experiment 1, but this was expected because of the difference between stimuli defined by motion versus luminance contrasts.

Nevertheless, the grouping-related difference wave in Experiment 2 was characterized by an initial occipital positivity (Pd230) with a scalp distribution that was similar to that of the Pd110 in Experiment 1. The fact that the early occipital activity observed in Experiment 2 showed a similar polarity and scalp distribution with the Pd110 observed in Experiment 1 suggests that the Pd230 may reflect a similar proximity-grouping process in the visual cortex as we discussed for the Pd110 in Experiment 1. Although the Pd110 may have represented the analysis of low-spatial-frequency information present only in the proximity-grouped stimuli, a similar explanation for the Pd230 is undermined by the lack of differen-

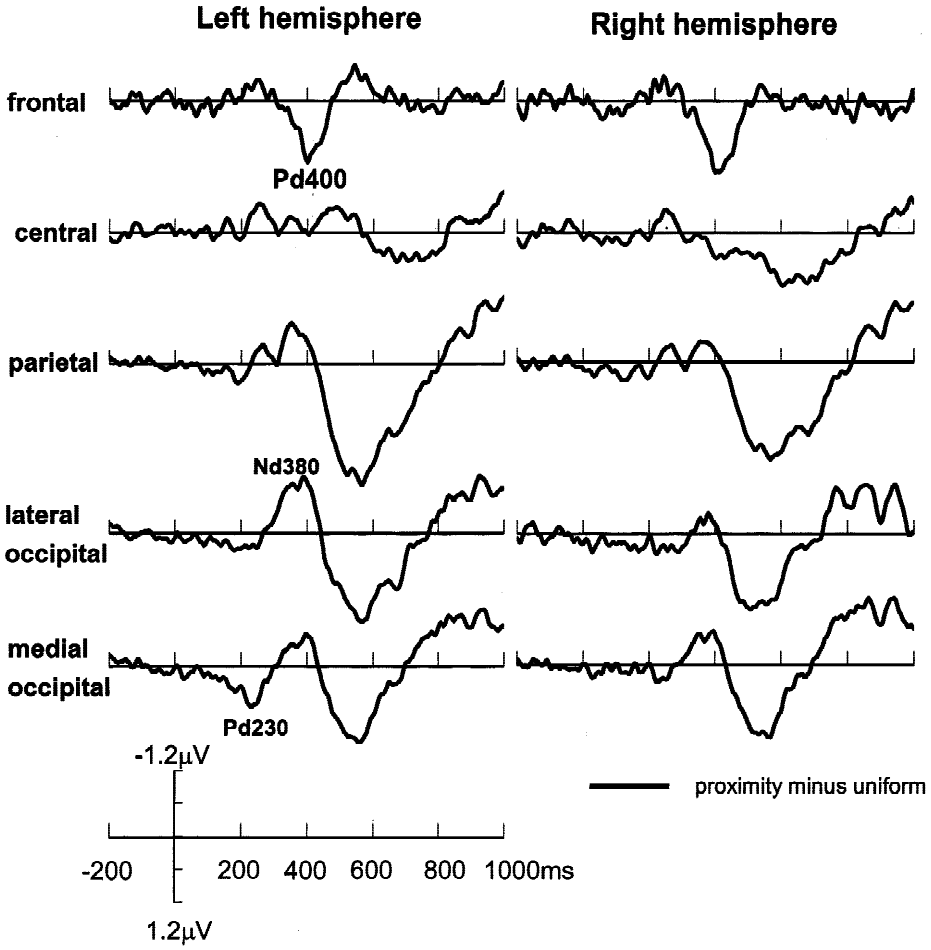

Figure 7. Difference waves reflecting proximity grouping in Experiment 2.

tially orientated low-frequency energy in the random-dot patterns. The longer latency of the occipital positivity in Experiment 2 relative to Experiment 1 is not surprising because multiple frames would be required to discriminate regions of stationary dots from the background of randomly moving dots. It is difficult to estimate the number of frames that might be required to define local-shape locations to detect the proximity grouping and discriminate its orientation, but the latency differences in the ERPs (N150 vs. N260, and N260 vs. N350), the difference waves (Pd110 vs. Pd230), and the RTs (525 vs. 611 ms) suggest a fairly consistent delay of five to seven frames. Some of this delay may come from the intrinsically slower responses and longer latency-integration time of high-spatial-frequency channels (Breitmeyer, 1975). Together, these two sources should easily accounts for the consistent five- to seven-frame delay that occurred throughout the physiological and behavioral responses.

The Pd230 was also followed by a longer latency negativity over the posterior areas, which was increased in amplitude over the left hemisphere. The different lateralization of the longer latency negativities in Experiments 1 and 2 is consistent with different relative contributions of the left and right hemispheres at a later stage of the proximity-grouping process, depending on the spatial frequency content of the stimulus arrays. When low spatial frequencies were available (Experiment 1), the right hemisphere contributed more to the grouping process. In contrast, when participants could group the stimuli only on the basis of higher spatial-frequency information, the left hemisphere became dominant. These results are consistent with the assertion that the right and left hemispheres contribute relatively more to the processing of low and high spatial frequencies respectively (Ivry & Robertson, 1999; Kitterle et al., 1990; Sergent, 1987).

Another difference between Experiment 1 and 2 is the late frontal positivity observed in Experiment 2 but not in Experiment 1. Others have shown that increasing task demand (Chao & Knight, 1996, 1997) or categorization difficulty (Swick, 1998) generates enhanced frontal components. The late frontal positivity of Experiment 2 probably represents the same effect.

General Discussion

The present study recorded 120-channel ERPs to investigate neural substrates underlying perceptual grouping defined by proximity and similarity. Behavioral performance showed that grouping by proximity were perceived faster with fewer errors than grouping by similarity of shape, supporting a dominance of proximity over similarity of shape in grouping local elements into perceptual wholes (Ben-Av & Sagi, 1995; Han & Humphreys, 1999; Han et al., 1999a, 1999b).

The ERP data showed that grouping by proximity was first characterized by an enhanced positivity over the medial occipital

cortex, which occurred at shorter latencies in Experiment 1 where local elements were defined by luminance contrast, and at longer latencies in Experiment 2 where local elements were defined by motion contrast. The occipital activation did not depend on the existence of low-spatial-frequency information in stimulus displays or on the particular stimulus feature (luminance vs. motion contrast) upon which the grouping was based. In addition, this occipital activity was not evident in the similarity-grouping conditions, suggesting that it could not result from a non-proximity-specific aspect of the task.

Thus, the occipital activation observed here appears to reflect neural activities linked to proximity-grouping process. Although our ERP data did not demonstrate exactly where the proximity-related positivity was generated, the voltage topographies are consistent with an origin in striate or prestriate cortex. This finding suggests a broader role for human visual cortex than the analysis of local features, as suggested by previous animal studies (Hubel & Wiesel, 1962; Livingstone & Hubel, 1988). Such a broader role might include a representation of the relationship between local elements based on spatial distances. In this context, it is interesting that the grouping-related response of visual cortex does not depend on how local elements are defined (i.e., by luminance vs. motion difference). Although other studies indicate that the primary visual cortex is involved in the process of figure–ground segregation based on luminance, color, texture, and motion cues (Lamme, 1995; Reppas, Niogl, Dale, Sereno, & Tootell, 1997; Skiera, Petersen, Skaleg, & Fahle, 2000; Super, Spekreijse, & Lamme, 2001), the current work provides electrophysiological evidence that perceptual grouping of local elements defined by luminance or motion cues is also reflected in modulations of early visual areas.

Studies of single neurons in primate striate cortex have shown enhanced responses when nearby context stimuli share the same orientation as the stimuli in the receptive fields (Kapadia et al., 1995). This result may reflect short-range interactions between neurons that are based on both spatial distance and similar receptive field properties. The proximity-grouping-related occipital activity observed here, however, likely reflects longer range interactions between neurons rather than stimulus interactions between nearby receptive fields. Various types of interactions among neurons are consistent with the occipital activations observed here, including synchronization of neuronal responses in cells responding to similar stimulus components (Eckhorn, 1994; Gray, Engel, König, & Singer, 1989; Usher & Donnelly, 1999), and excitatory and/or inhibitory horizontal connections between cells (Gilbert, 1992; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998).

Long-latency activity related to proximity grouping showed a right hemisphere dominance when low spatial frequencies were available in stimulus displays (Experiment 1), consistent with the functional magnetic resonance imaging (fMRI) findings that the right extrastriate cortex is activated by the low-spatial-frequency grouping operations involved in illusory contour perception (Hirsch et al., 1995). However, the long-latency activity was larger over the left hemisphere when low spatial frequencies were eliminated (Experiment 2). The results suggest that either the right or the left hemispheres can dominate the later stages of grouping depending on whether the low- or high-spatial-frequency contents are available in stimulus displays.

Unlike proximity grouping, grouping by similarity of shape elicited only long-latency negativities over the occipitotemporal areas. The occipital activities possibly stemmed from contributions of relatively low-level factors, for example, the collinearity of the horizontal or vertical edges of the local squares in the similarity condition may aid the grouping process and lead to activities in the early visual cortex. The occipitotemporal scalp localization of the similarity-related negativity is consistent with the key role of temporal areas in representation of object features such as shape and color (Gross, 1994; Logothetis & Sheinberg, 1996; Tanaka, 1993). Similarity grouping, whether based on collinearity of component orientation or complete shape identification, depends on an analysis of higher spatial frequencies than does proximity grouping based on luminance contrasts. The corresponding higher amplitude negative difference wave over the left hemisphere is consistent with the hemispheric asymmetry in Experiment 2 where proximity grouping was also based on high spatial frequencies. The left hemisphere predominance observed for both similarity grouping (Experiment 1) and proximity grouping based on high spatial frequencies (Experiment 2) may reflect a more rapid and accurate processing of high spatial frequencies in the left hemisphere (Kitterle, Christman, & Conesa, 1993; Sergent, 1987; Watten, Magnussen, & Greenlee, 1998).

In conclusion, our findings suggest that grouping by proximity and grouping by similarity of shape may be mediated by neural mechanisms that are different in time course, spatial distributions, and hemispheric predominance. The occipital cortex was involved at the early stage of proximity grouping regardless of whether or not the grouping was based on low-spatial-frequency information. At longer latencies, proximity grouping showed a more dorsal scalp distribution, suggesting relatively greater activation of dorsal stream visual structures. Long-latency neural activities related to similarity grouping showed left hemisphere predominance, consistent with the high-spatial-frequency content of the stimuli, and occipitotemporal focus, suggesting relatively greater activation of ventral stream structures.

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