stimulus pattern subtended an angle of 6.0° × 6.0°. The target stimuli were the same as the nontargets except that they were only 62% of the size of nontarget stimuli. In Task 2 the stimuli were the same as those in Task 1 except for the following. The targets and nontargets were of the same size. Four dots (0.19° × 0.19°) at the corners of an imaginary square appeared along with the stimuli (illustrated in Fig. 2a). Each of the dots was 5.3° from fixation. The dots were white when accompanying nontargets but were red or green when accompanying targets. In Task 3 the stimuli were the same as in Task 1 except that the targets and nontargets were the same size and the fixation cross was either red or green in target displays (illustrated in Fig. 2b). In all tasks both the target and the nontarget displays were presented for 150 ms. The interstimulus intervals were randomized between 300–500 ms.

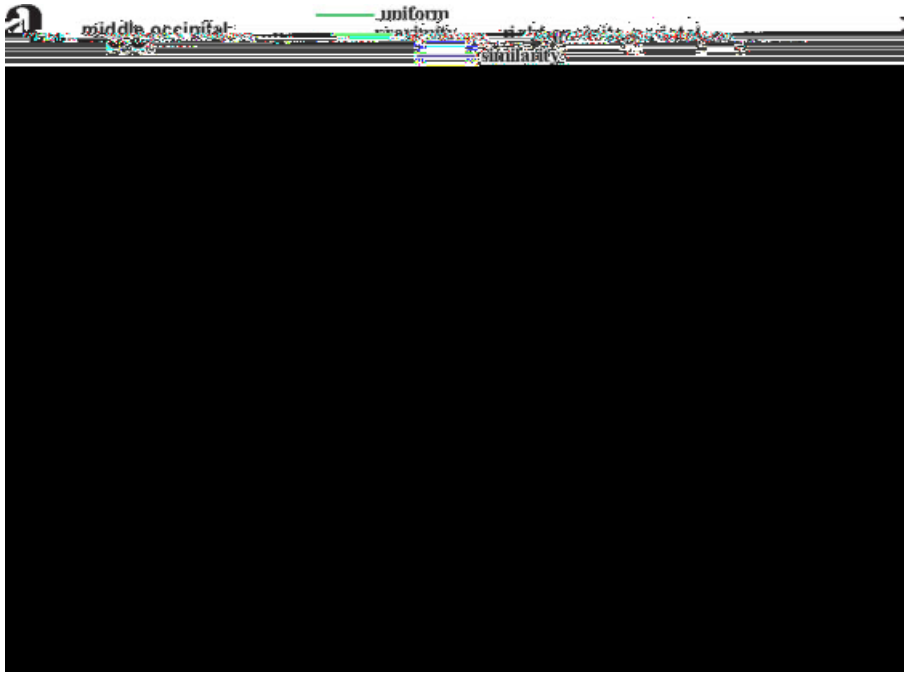
P cd ı

In Task 1 subjects were asked to indicate the presence of row- or column-grouped target stimuli (regardless of whether proximity or similarity cues produced grouping) by pressing one of two keys with either the left or the right index finger while ignoring the nontarget stimuli. In Tasks 2 and 3 subjects discriminated the color change of the four dots around the target stimuli or the color change of the fixation cross accompanying the target stimuli by pressing one of two keys. In each task each subject completed 100 trials for practice, followed by 960 trials in four 240-trial blocks. Targets appeared randomly on 20% of trials. The uniform stimulus, proximity-grouped stimuli, and similarity-grouped stimuli were each presented randomly on one-third of the nontarget trials. The procedure of randomization guaranteed that the sequence of the stimuli was different between any two blocks of trials for every subject. Participants were instructed to maintain fixation on the central cross throughout the task while responding to targets as quickly and accurately as possible. The order of the tasks and the assignment of responding hand with the two types of targets (column vs. row in Task 1; red vs. green in Tasks 2 and 3) were counterbalanced across participants.

ERP Da a R c d a d A a

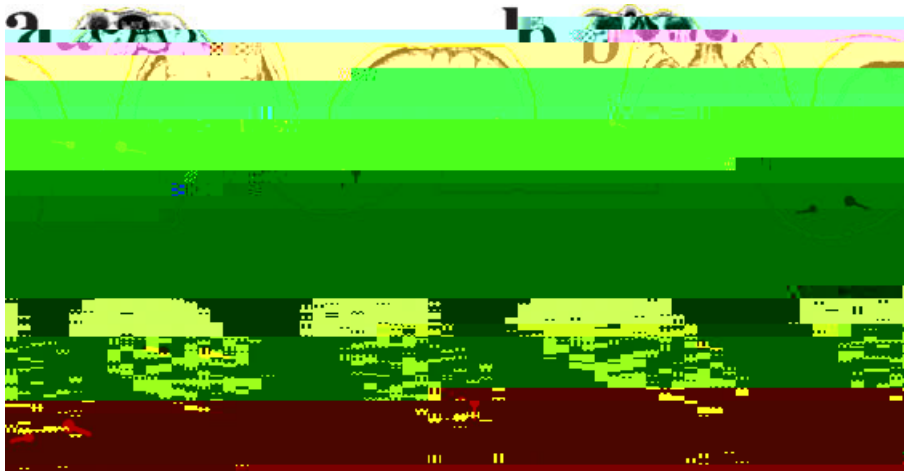
The electroencephalogram (EEG) was recorded using a 128-channel NeuroScan system from 120 scalp electrodes labeled with numbers 1–120. Electrodes 59–71 were arranged along the midline of the skull and the others were located approximately symmetrically at the two sides of the skull. The skin resistance of each electrode was made less than 5 k°. The recording from an electrode at the right

mastoid was used as reference. Eye blinks and vertical eye



F ı 3.

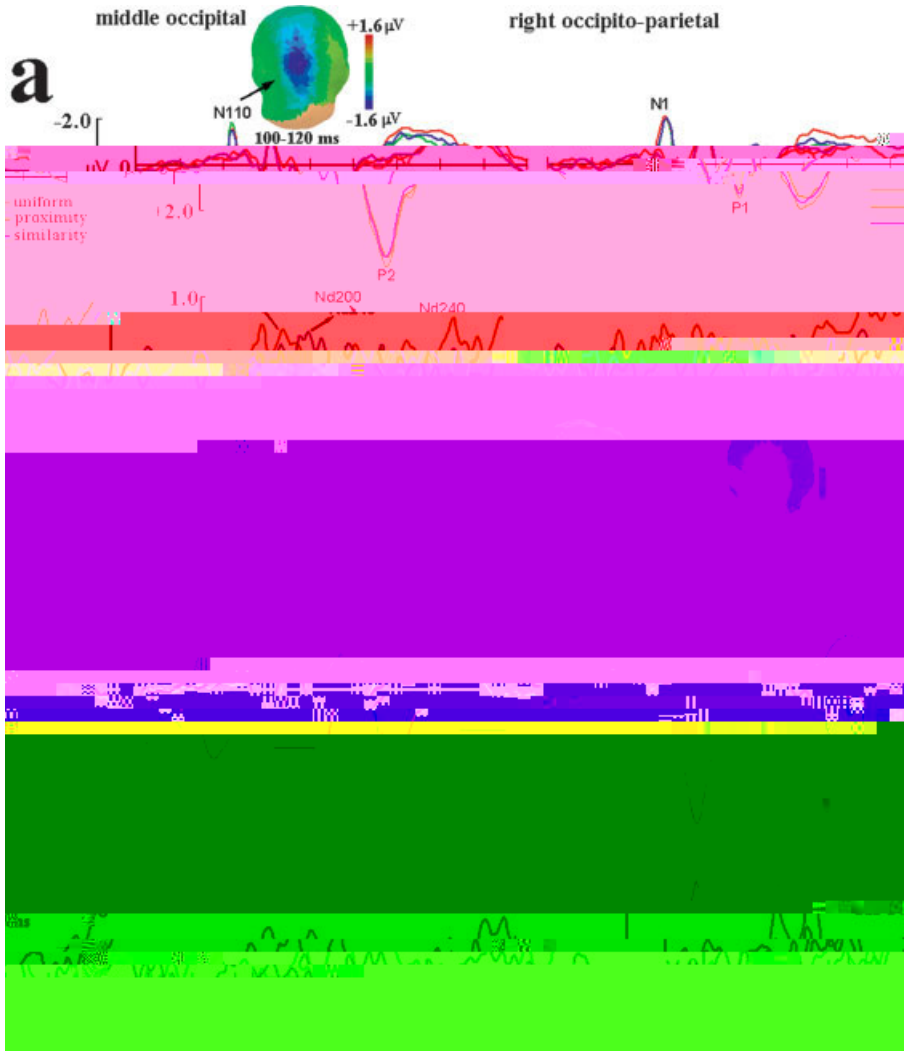
a: Grand average ERPs at posterior electrodes elicited by uniform and grouped nontargets in Task 1. The voltage topographies show maximum amplitudes over the medial occipital area for the P2 but over bilateral occipital areas for the P1. **b:** Grouping related difference waves in Task 1 obtained by subtracting ERPs to the uniform nontargets from those to proximity- or similarity-grouped nontargets. The voltage topography at 92–116 ms (Pd100) shows maximum amplitude over the medial occipital area. The long-latency component (Nd240) shows maximum amplitudes over occipito-parietal area for proximity grouping whereas over the occipito-temporal area for similarity grouping.



F ı 4.

a: The best-fit dipolar source for the Pd100 at 90–110 ms. The dipole was located in the calcarine cortex and is shown in the MR image (top row) and the realistic-head boundary-element model (bottom row) of a representative subject. **b:** The best-fit dipolar sources for the P1 at 90–110 ms. Two dipoles were located to bilateral extrastriate cortex and shown in the MR image (top row) and the realistic-head boundary-element model (bottom row) of a representative subject.

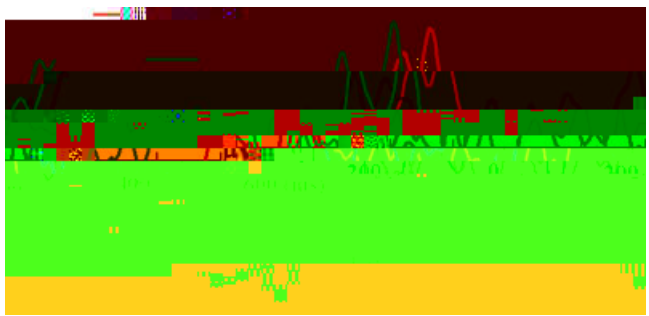
ital sites (Fig. 3b). The neural generators of the Pd100 were then estimated by fitting one dipole to its grand average voltage distribution between 90 and 110 ms based in a realistic-head boundary-element model. The best-fit dipole was situated in the calcarine cortex and slightly lateralized to the right hemisphere (Fig. 4a) with Talairach coordinates of x, y, z = 11.3, –72.3, 10.5. The dipole solution accounted for 92% of the variance of the topography of the Pd100 at 90–110 ms. The Pd100 was followed by a long latency negativity peaking at about 240 ms (Nd240) ($F(1,17) = 9.91$, < 0.01) with maximum amplitudes over bilateral occipito-parietal areas (see the voltage topography in Fig. 3b). Similarity grouping was indexed only by a long latency negativity (Nd240) ($F(1,17) = 5.06$, < 0.04), which showed maximum amplitude in the occipito-temporal areas (see the voltage topography in Fig. 3b).



F ı 5.

a: Grand average ERPs (top row) and grouping related difference waves at posterior electrodes in Task 2. The voltage topographies show maximum distribution of the N110 at 100–120 ms and the early grouping related positivity (Pd100) at 92–112 ms over the medial occipital area. **b:** Grand average ERPs (top row) and grouping related difference waves at posterior electrodes in Task 3. The grand average voltage topography shows maximum distribution of the long latency grouping related activities (Nd220) over the medial occipital area at 212–240 ms.

the presence of the Pd100 when the refractory effect was controlled for). Taken together, the ERP and fMRI results suggest that the proximity-defined larger-scale organization of discrete visual elements in the visual field may take place as early as 100 ms after sensory stimulation and has a neural generator in human calcarine cortex. In addition, both the ERP and fMRI results showed that the calcarne activity is specific to the proximity grouping. There is no evidence for grouping by similarity being associated with such early



F ı 6.

Grouping-related difference waves at middle occipital electrode in Tasks 1, 2, and 3. The Pd100 is labeled to illustrate the difference of the Pd100 amplitude across tasks.

We are grateful to one of the reviewers for indicating this possibility and suggesting running the control experiment reported in the Appendix.

neural activity in the calcarine cortex, even though subjects performed the same discrimination task in the two stimulus conditions. One may notice that the contextual effects in the primary visual cortex observed in single-unit recording studies [Kapadia et al., 1995; Marcus and Van Essen, 2002], which reflect integration between stimuli inside and outside receptive fields of neurons, occur much earlier (50–60 ms poststimulus) than the early grouping effect observed here (about 100 ms poststimulus). It is possible that the grouping-related Pd100 reported here arose from the synchronous activities of neuronal populations engaged in a large-scale grouping process and thus requires longer time to reach maximum amplitudes.

Our ERP results showed that the sensory responses indexed by the P1 component had generators in bilateral extrastriate cortex. This is consistent with previous reports [Clark and Hillyard, 1996; Heinze et al., 1994; Mangun et al., 1997; Martinez et al., 2001; Noesselt et al., 2002]. However, the proximity-grouping-related activity was located in the medial visual cortex and close to the calcarine fissure. Thus, it appears that, although the Pd100 partially overlapped the P1 component in time, they had neural sources in different locations in the visual cortex, suggesting that perceptual grouping operations are dissociated from at least some aspects of sensory processing in the visual cortex even though they may overlap in time.

Proximity grouping was also reflected in long latency activities (Nd240) with an occipito-parietal distribution. This is in line with the prior fMRI observations that proximity grouping also induced activations over bilateral inferior parietal cortices [Han et al., 2005]. Unlike proximity grouping, grouping by shape similarity was indexed only by a long-latency negativity (Nd240) with an occipito-temporal distribution. The electrophysiological correlates of similarity grouping may have generators in the right medial occipital cortex, given that our fMRI results showed stronger activation for similarity-grouped stimuli than for uniform stimuli in this area [Han et al., 2005]. Thus, our combined ERP and fMRI findings provide evidence that grouping operations defined by proximity and similarity of shape are dissociated in both the temporal and the spatial domain. The delayed neural activities for similarity grouping are possible neural substrates for the slower behavioral responses to similarity- rather than to proximity-defined stimuli [Han and Humphreys, 1999; Han et al., 1999a,b].

Moreover, our ERP results show that the early grouping operations are modulated by task relevance and by whether stimulus arrays of grouped stimuli fall within an attended spatial region. The proximity-grouping-related Pd100 occurred most strongly within the calcarine cortex when the task required participants to judge the orientations of spatial groups. This early proximity-grouping-related neural activity was weakened when the nontarget stimuli were of low (Task 2) relative to high (Task 1) task relevance (see Fig. 6). In addition, the Pd100 was eliminated when the nontargets were of low task relevance and fell outside the attended area (Task 3). The contrast between the results of Tasks 1 and 3 is in agreement with our previous fMRI observations which showed fMRI activations in the calcarine cortex associated with proximity grouping in Task 1 but not in Task 3 [Han et al., 2005]. The combined ERP and fMRI results indicate that the early grouping operations in the visual cortex are influenced by the allocation of attentional resources, i.e., being salient only when stimulus arrays of grouped stimuli fall in an attended area of space. The early grouping process is reduced when visual elements fall outside an attentional window. However, the contrast between the results of Tasks 1 and 2 is different from our previous fMRI observations, where the calcarine activation associated with proximity grouping did not differ between in Tasks 1 and 2 [Han et al., 2005]. One possible account of the discrepancy between the ERP and fMRI results is that, relative to the ERPs, the fMRI signals recorded from the calcarine cortex included stronger effects of feedback from high brain structures because of the fMRI signal's longer response latency. The electrophysiological signals are thus more sensitive than the hemodynamic responses in disclosing the differential neural activities in the visual cortex in association with the early grouping operation. The ERP results indicate that attentional resources influence grouping in nontarget stimuli, but this occurs most strongly when the grouping cues present are used for the behavioral task with other items (i.e., the target stimuli).

The lateralized long-latency ERP correlates of proximity grouping, occurring between 180 and 280 ms (i.e., Nd240), were also decreased when nontargets were of low task relevance (Task 2 and 3 relative to Task 1). However, a long-latency activity was evident over the medial occipital cortex when the stimuli fell outside the attentional window (i.e., the Nd220 in Task 3). This indicates a further distinction between the late and early grouping processes. It is possible that feedback from higher visual areas facilitates the late component of perceptual grouping even when early grouping is impaired by a lack of attentional resources. This effect was specific to proximity-grouping here, since the long-latency ERP correlates of similarity grouping (Nd240) were decreased by low task relevance and eliminated by the shrinking of the attentional window. This may reflect the generally weaker effects of similarity grouping on performance, which remain more dependent on spatial attention than proximity-grouping.

Our ERP findings conflict with the core idea of contemporary theories of visual perception that grouping operations at early stages of visual perception are independent of allocation of visual attention [Humphreys, 1998; Mattingly et al., 1997; Ward et al., 1984] and attention only performs on perceptual objects formed at a preattentive stage by grouping operations [Duncan, 1984; Duncan and Humphreys, 1989; Kahneman and Henik, 1982; Marr, 1982; Treisman, 1986]. The modulation of early grouping-related activity by task relevance and size of attended area (e.g., the Pd100) cannot be explained by the fading of grouping information in memory [Moore and Egeth, 1997]. Together with our prior fMRI findings, the current ERP results support the

proposal that attention is engaged even in the early process of grouping operations [Ben-Av et al., 1992; Mack et al., 1992]. The process of grouping operations that form perceptual units is facilitated by spatial attention. Therefore, it may be proposed that attention may be involved in both the early and late stages of visual perception to facilitate the formation of perceptual units and selection of perceptual objects, respectively.

The current ERP results also showed neural modulations linked to sensory processing. For instance, the P1 component, which was localized to the bilateral extrastriate cortex, was of larger amplitude in Task 1 than in Tasks 2 and 3. The pattern of the P1 modulation by task relevance was similar to that of the early grouping-related activity (Pd100). Previot.krevi-

ing. Both column and row proximity-grouped target stimuli were used in each block of trials. However, there were only uniform and column proximity-grouped nontarget stimuli in two blocks of trials, whereas only uniform and row proximity-grouped nontarget stimuli in the other two blocks. Each subject completed 160 trials for practice, followed by 640 trials in four 160-trial blocks. The interstimulus intervals were randomized between 800 and 1200 ms. EEG was re-