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# Neural mechanisms of perceptual grouping in human visual cortex

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Abstract **The current work examined neural substrates of perceptual grouping in human visual cortex using event-related potential (ERP) recording. Stimulus arrays consisted of local elements that were either evenly spaced (uniform stimuli) or grouped into columns or rows by proximity or color similarity (grouping stimuli). High-density ERPs were recorded while subjects identified orientations of perceptual groups in stimulus arrays that were presented randomly in one of the four quadrants of the visual field. Both uniform and grouping stimulus arrays elicited an early**

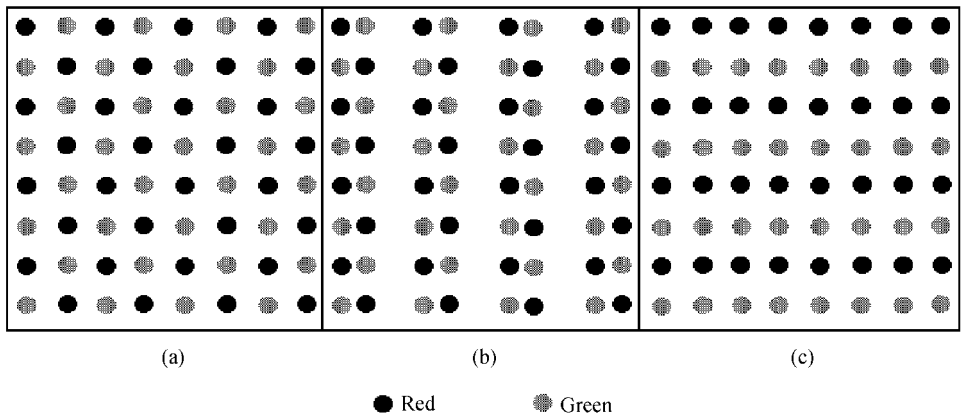


Fig. 1. Illustrations of the stimuli used in the present study. (a) The uniform stimulus; (b) the proximity-grouping stimulus in which local elements group into columns; (c) the similarity-grouping stimulus in which local elements group into rows.

1000 and 1400 ms. While keeping fixated at the fixation cross, subjects discriminated column versus row organizations of the grouping displays by button press with thumbs while ignoring the uniform stimuli. After 100 practice trials, subjects were presented with 2000 to 2600 trials in ten to thirteen blocks depending upon the amount of artifacts. The uniform, proximity-grouping, and similarity-grouping stimuli were presented randomly on 28%, 36% and 36% of the trials, respectively.

(ⅱ) Electrophysiological data recording and analysis. The electroencephalogram (EEG) was recorded from 120 scalp electrodes using an EEG/ERP system from NeuroScan Inc. The skin resistance of each electrode was made less than 5 kΩ. The recording from an electrode at the right mastoid was used as reference. Eye blinks and vertical eye movement were monitored with electrodes located below the left eye. The horizontal electro-oculogram was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG was amplified (band pass 0.1—70 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 1000 ms. Trials contaminated by eye blinks, eye movements, or muscle potentials exceeding 100 μV (peak-to-peak amplitude) at any electrode were excluded from the average.

Peak latencies were measured relative to stimulus onset. Statistical analysis was conducted at each pair of electrodes over the parietal and occipito-temporal regions and electrodes along the midline of the skull. The mean ERP amplitudes were subjected to repeated measure analysis of variance (ANOVAs) with factors being Grouping (proximity or similarity vs. uniform stimuli), Hemifield (left vs. right), Elevation (upper vs. lower), Hemisphere (left vs. right). The ANOVAs of behavioral data and ERP data at electrodes along the midline of the skull were conducted with Grouping, Hemifield, and Elevation as independent variables. Dipole modeling was used to localize the source of ERP components. Electrode positions were measured from each individual subject with a probe for sensing the 3-dimensional position of the probe tip with respect to a magnetic field source in the head support. Magnetic resonance (MR) images were obtained from 5 subjects for constructing realistic-head boundary-element models. The digitized fiducial landmarks corresponding to the electrode coordinates were coregistered with fiducial landmarks identified on whole-head MR scan so that the locations of estimated dipoles could be related to individual brain-skull anatomy. Dipoles were mapped onto the MR images of individual subjects to estimate source locations with respect to brain anatomy. The 3-dimensional coordinates of each dipole were transformed to the coordinates of Talairach and Tournoux[11] atlas by marking the anterior and posterior commissures on each subject's MR scan.

## 2 Results

(ⅰ) Behavioral data. Response accuracies were high (91.1% for proximity and 92.3% for similarity stimuli). RTs were slightly faster to proximity-than similarity-grouping stimuli (505±33.2 vs. 512±34.6 ms, $F(1,15) = 5.26$, $P < 0.04$). RTs were faster to the stimuli in the right than left visual fields (505±34.8 vs. 511±33.4 ms, $F(1,15) = 12.9$, $P < 0.003$) and to the stimusu

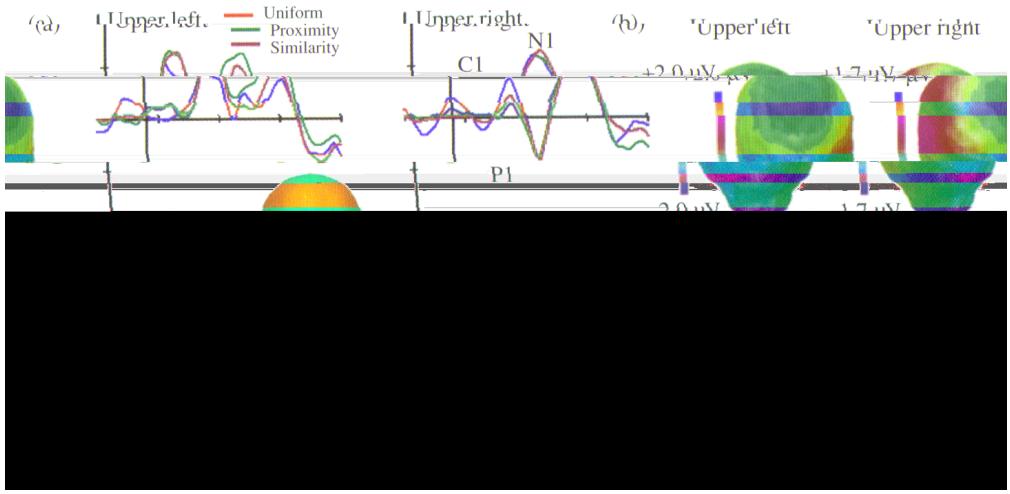


Fig. 2. (a) Grand average ERPs elicited by uniform and grouping stimuli recorded at parieto-occipital electrode (POz). (b) Voltage topographies calculated based on grand average ERPs to uniform stimuli at 60—80 ms. The foci of the positive C1 elicited by the stimuli in the lower VF are distributed slightly contralateral to the stimulated hemifields whereas this laterality effect is weaker for the negative C1 elicited by the stimuli in the upper VF.


Fig. 3. (a) Grand average ERPs elicited by uniform and grouping stimuli recorded at left lateral occipital electrode (P7). (b) Voltage topographies calculated based on grand average ERPs to uniform stimuli between 80 and 100 ms after stimulus onset. The P1 wave showed maximum amplitudes at lateral occipital areas contralateral to the stimulated hemifields.

Fig. 4. Dipole models showing the source that generated the C1 component. The best-fit dipolar source for the C1 at 60—80 ms is located to the calcarine cortex and shown in the MR images of a representative subject. The dipole orientations varied systematically as a function of stimulus positions. The positive pole of the dipole pointed inside the brain for the upper VF stimuli but outside the brain for the lower VF stimuli.

main effect of Grouping at parieto-occipital electrodes between 60 and 80 ms for the proximity-grouping condition ($F(1,15) = 5.59$, $P < 0.03$). The negative C1 was of smaller amplitude (less negative) to proximity-grouping than uniform stimuli in the upper visual field whereas the positive C1 was of larger amplitude (more positive) to proximity-grouping than uniform stimuli in the lower visual field. This C1 grouping effect was stronger for the upper than lower visual fields ($F(1,15) = 25.6$, $P < 0.001$). Moreover, the asymmetric elevation grouping effect was larger in the right than left visual fields ($F(1,15) = 32.9$, $P < 0.001$). No significant grouping effect was found in the P1 and the N1 time window. However, the P1 and N1 amplitudes were larger at electrodes contralateral than ipsilateral to the stimulated hemifields ($F(1,15) = 35.1$, $P < 0.001$). The effect of grouping was not significant in the C1 time window for similarity grouping condition ($F(1,15) = 3.05$, $P > 0.09$). However, the grouping effect at 60—80 ms was stronger when stimuli were presented in the upper than lower visual fields as indicated by the significant interaction of Grouping×Elevation ($F(1,15) = 25.5$, $P < 0.001$).

Voltage topography showed that the C1 elicited by the stimuli in the upper visual field showed negative foci over the parieto-occipital area whereas the C1 to the stimuli in the lower visual field had positive foci at the parieto-occipital region. The P1 component showed positive maximum amplitudes over the occipito-temporal regions contralateral to the stimulated hemifield regardless of stimulated elevations. The neural sources of C1 were estimated by dipole modeling based on realistic-head boundary-element models at 68—80 ms. The principle component analysis suggest that a single dipole provided the best solution for all stimulated locations during this interval. The best-fit C1 dipoles were localized to the calcarine fissure with Talairach coordinates of $x, y, z = -11, -76, -0.3$ (upper-right); 7, −72, 14 (upper-left); 23, −78, −6 (lower-left); and 7, −71, −6 (lower-right) (see Fig. 4). The goodness of fit of these dipole solutions (proportion of scalp variance accounted for) was 94% (upper-right), 86% (upper-left), 85% (lower-left), and 86% (lower-right), respectively.

## 3 Discussion

The present study showed that ERPs to either uniform or grouping stimuli were characterized by an early component at 60—90 ms post-stimulus. This component had maximum amplitudes over the parieto-occipital areas and was negative for stimuli in the upper visual field but positive for those in the lower visual field. This ERP component is identical to the C1 observed in the previous studies[9]. Our dipole modeling localized the C1 at 60—80 ms to the cortex close to the calcarine fissure, indicating that this early ERP wave possibly originates from the primary visual cortex. However, the dipole locations observed here are not exactly the same as the prediction of the cruciform model of the primary visual cortex[12], which states that stimuli presented to the upper and lower visual fields are represented by the cortex on the lower and upper banks of the contralateral calcarine fissure, respectively. The dipoles corresponding to the lower visual field stimuli were inferior to those associated with the upper visual field stimuli. It is possible that the low signal-to-noise ratio limited the precision of the dipole modeling used here. Alternatively, the incongruency between our results and the cruciform model may result from the overlap of the C1 with the early phase of the P1 in the lower visual field. As the P1 component had generators that were inferior to the C1 source (see the P1 voltage topographies), the dipoles calculated at 60—80 ms might reflect contributions of both the C1 and the early phase of the P1. The summation of the two components resulted in dipole solutions that are inferior to the area where the C1 sources are actually located.

Interestingly, the C1 was of smaller (less negative) amplitude to proximity-grouping than uniform stimuli in the upper visual field and of larger (more positive) amplitude in the lower visual field. Thus the proximity grouping generated a positive activity regardless of stimulus elevations rather than simply increased the C1 amplitude for stimuli in both the upper and lower visual fields. This is consistent with the previous ERP reports[6,7]. The current work complements the previous work by identifying the neural source of the grouping effect and provided ERP evidence that proximity grouping modulates activities of the primary visual cortex. The finding that perceptual grouping in humans has neural substrates as early as in the primary visual cortex is in agreement with the results of monkey studies that responses of neurons in V1 are modulated by grouping of stimuli inside and outside receptive fields[3]. Therefore it may be suggested that grouping operation is a common function of the primary visual cortex for both humans and monkeys. However, the significant grouping effect on the C1 was evident for proximity-grouping stimuli but not for similarity-grouping stimuli, suggesting that, relative to similarity, proximity is a factor that produces stronger grouping operations in the early visual cortex, which may contribute to the faster behavioral responses to proximity than similarity stimuli[4,5].

In addition, we found that the C1 grouping effect was stronger in the upper than lower visual fields. It has been hypothesized that processing in the lower visual field is more global and related to manipulations performed in peripersonal space whereas the upper visual field is primarily local and related to visual search and recognition mechanisms directed toward extrapersonal space[13]. If perceptual grouping reflects processing of global aspects of stimulus arrays, our observation is contrary to the

above hypothesis. However, the ecological significance of our results is still unclear.

Unlike the C1 component, the P1 with maximum amplitudes over lateral occipital areas was not influenced by grouping of local elements, nor was the following N1 component. Thus the C1 effect reflects grouping operation that is specific to the visual cortex close to the calcarine fissure. The lateral extrastriate cortex, where the P1 is generated[9,10], may not play an important role in the process of perceptual grouping.

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