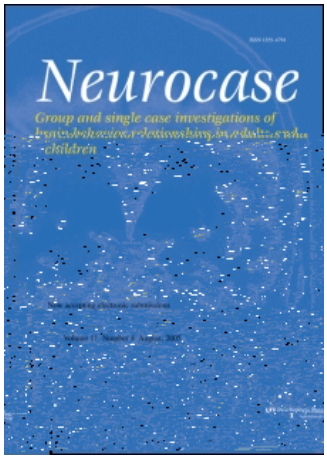

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The Fronto-Parietal Network and Top-Down Modulation of Perceptual Grouping

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The Fronto-Parietal Network and Top-Down Modulation of Perceptual Grouping

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We examined the role of the fronto-parietal cortex in top-down modulation of perceptual grouping by proximity, collinearity, and similarity, by recording event related brain potentials from two patients with fronto-parietal lesions and eight controls. We found that grouping by proximity and collinearity in the controls was indexed by short-latency activities over the medial occipital cortex and long-latency activities over the occipito-parietal areas. For the patients, however, both the short- and long-latency activities were eliminated or weakened. The results suggest that the fronto-parietal network is involved in facilitation of both the early and late grouping processes in the human brain.

Keywords: ERP; Perceptual grouping; Proximity; Collinearity; Fronto-Parietal lesion

Introduction

A basic function of human perceptual system is to organize discrete entities in the visual field into chunks or perceptual units for higher-order processing. Such processes of grouping, that underlying perceptual organization, occur during early stages of vision (Lamy & Tsal, 2001; Vecera & Behrmann, 2001). This proposal is supported by data on where grouping takes place in the brain. For example, animal studies show that neural activity in the primary visual cortex is influenced by collinearity (Kapadia, Ito, Gilbert, & Westheimer, 1995) or common fate (Sugita, 1999) based on information falling both inside and outside the receptive fields of the cells. Human neuroimaging studies also show evidence that the human primary visual cortex is involved in perceptual grouping. For instance, event-related brain potential (ERP) studies of humans have demonstrated that, relative to stimulus arrays in which local elements were distributed evenly in space, stimulus arrays with elements grouped by proximity generated positive-going neural activity at 100 ms after sensory stimulation (Pd100) over the medial occipital cortex (Han, Song, Ding, Yund, & Woods, 2001, 2002). The Pd100 was further localized to the calcarine cortex using dipole modeling in realistic head models and functional magnetic resonance imaging (fMRI) (Han, Jiang, Mao, Humphreys, & Qin, 2005a, 2005b). Similarly, fMRI studies have identified activation in the striate and extrastriate cortices linked to perceptual grouping by collinearity (Altmann, Bülthoff, & Kourtzi, 2003; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003). Relevant neuropsychological work too shows that grouping by collinearity can be intact when lesions spare the primary visual cortex, but disrupt higher visual areas (Giersch, Humphreys, Boucart, & Kovacs, 2000). Consistent with the localization within the first stage of neural processing, ERP studies demonstrate that the neural activity associated with collinear grouping can occur between 40 and 80 ms after stimulus onset (Khoe, Freeman, Woldorff, & Mangun, 2004; Han, Li, Casco, & Campana, 2007).

Many researchers also assume that, in addition to occurring at early stages of processing, perceptual grouping can operate pre-attentively. Thus there is evidence for grouping by collinearity in the case of patients showing visual extinction, who can be unaware of a stimulus in their contralesional visual fields unless it groups with an ipsilesional partner (Humphreys, 1998; Mattingly, Davis, & Driver, 1997). This fits with the idea that attention selects for higher-order analysis between perceptual objects formed at a pre-attentive stage by grouping operations (Duncan & Humphreys, 1989; Kahneman & Henik,

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1981; Treisman, 1986), rather than attention facilitating grouping operations to form perceptual units. Nevertheless, there has been evidence that perceptual grouping can be affected by top-down attention. For example, the ability to identify perceptual groups defined by proximity or similarity can be impaired when attention is engaged in a secondary concurrent task (Ben-Av, Sagi, & Braun, 1992; Mack, Tang, Tuma, & Kahn, 1992). Facilitation of the detection of a central Gabor patch (a Gabor patch consists of a sinusoidal contrast modulation convolved with a Gaussian function) by collinear flankers also requires the flankers to be attended (Freeman, Sagi, & Driver, 2001, 2004). Recent neuroimaging studies provide further evidence that interactions between attention and perceptual grouping can take place as early as in human primary visual cortex. For instance, we have recently found that an attentional effect on the integration of collinear Gabor patches can occur as early as 50 ms after stimulus delivery over the occipital area (Wu, Chen, & Han, 2005). Stimulus arrays of Gabor patches elicited a negativity over the posterior occipital cortex at 48–72 ms which was enhanced when attention was allocated along the collinear patches in the stimulus arrays than when attention was directed to the orientation orthogonal to the collinear patches. Having participants attend to the color of a central fixation cross, rather than to more global stimulus patterns, also weakened the early ERP component normally responsive to grouping by collinearity (Han et al., 2007). We have also demonstrated similar modulation of grouping related activities in human primary visual cortex using fMRI, when grouped stimuli are of low relative to high task relevance (Han et al., 2005a, 2005b). These data indicate that grouping operations in the visual cortex are influenced, at least to some degree, by top-down modulation from higher brain structures that control visual attention.

There is now considerable evidence that visual attention is controlled by a fronto-parietal network that provides top-down modulation of activities in early visual areas (Corbetta, 1989). fMRI studies have frequently observed activation of this network in tasks involving orienting of spatial attention (Gitelman et al., 1999; Kim et al., 1999; Nobre et al., 1997; Yantis et al., 2002). Attentional orienting can in turn result in enhanced activity in the visual cortex associated with stimuli presented at attended relative to unattended locations (Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Hopfinger, Buonocore, & Mangun, 2000; Mangun & Hillyard, 1991; Martinez et al., 2001; Luck, Chelazzi, Hillyard, & Desimone, 1997). In addition, damage to the fronto-parietal network can lead to impaired spatial orienting to the contralesional field (Posner, Walker, Friedrich, & Rafal, 1984; see Mesulam, 1999 for review) and result in absence of attentional modulation of the visual activities (Han et al., 2004, Han & Jiang, 2004). These findings strongly suggest that the fronto-parietal network plays a major role in modulating perceptual processing in the visual cortex.

In the present paper we tested the role of the fronto-parietal network in the top-down attentional modulation of grouping in the visual cortex, for a range of different Gestalt laws. ERPs were recorded using high-density electrodes from two patients with fronto-parietal lesions. Similar to our previous ERP studies (Han et al., 2005a, 2005b), participants were presented with stimulus arrays in which local elements were either evenly distributed or grouped into rows or columns, (i) by the proximity or the similarity of the shapes (Experiment 1) or (ii) by the collinearity or similarity of orientation

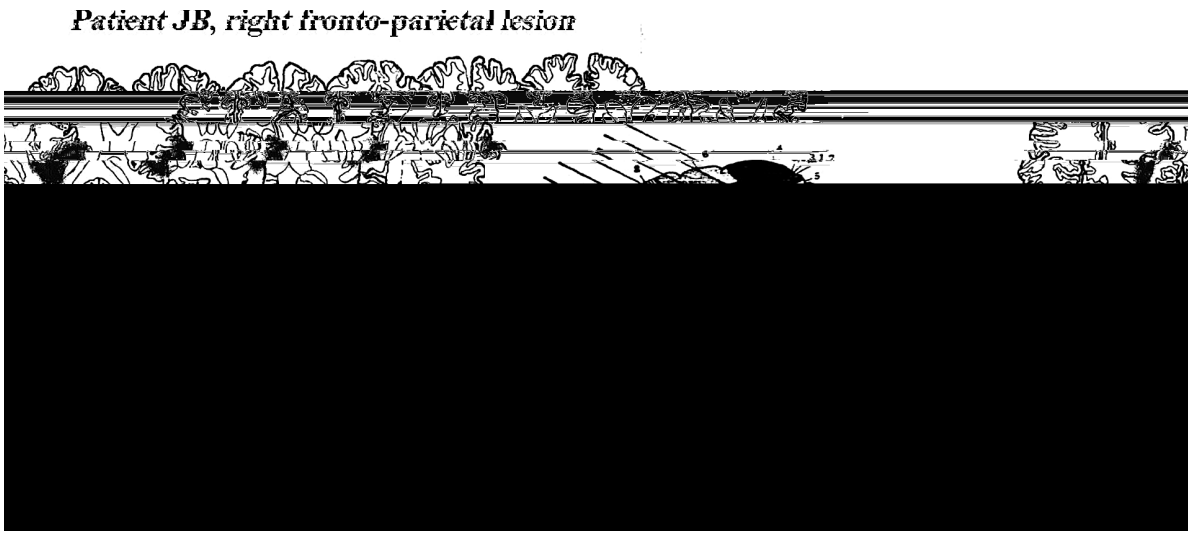

Fig. 1. Illustration of the brain damages of the two patients. MRI scans show JB's lesions in the right fronto-parietal areas and MH's lesions in the left parietal cortex.

Stimuli and procedures

Experiment 1

White stimulus elements were presented on a black background on a 17-inch color monitor at a viewing distance of 100 cm. A white fixation cross of 0.28 × 0.28° (width and height) was continuously visible in the center of the monitor. Nontarget stimuli consisted of a square lattice of grey elements (either filled circles or squares) in an 8 × 8 array, as shown in Figure 2. The luminance of the grey elements was 43.2 cd/m^2. The uniform stimulus consisted of alternate circles and squares distributed evenly across the lattice. This

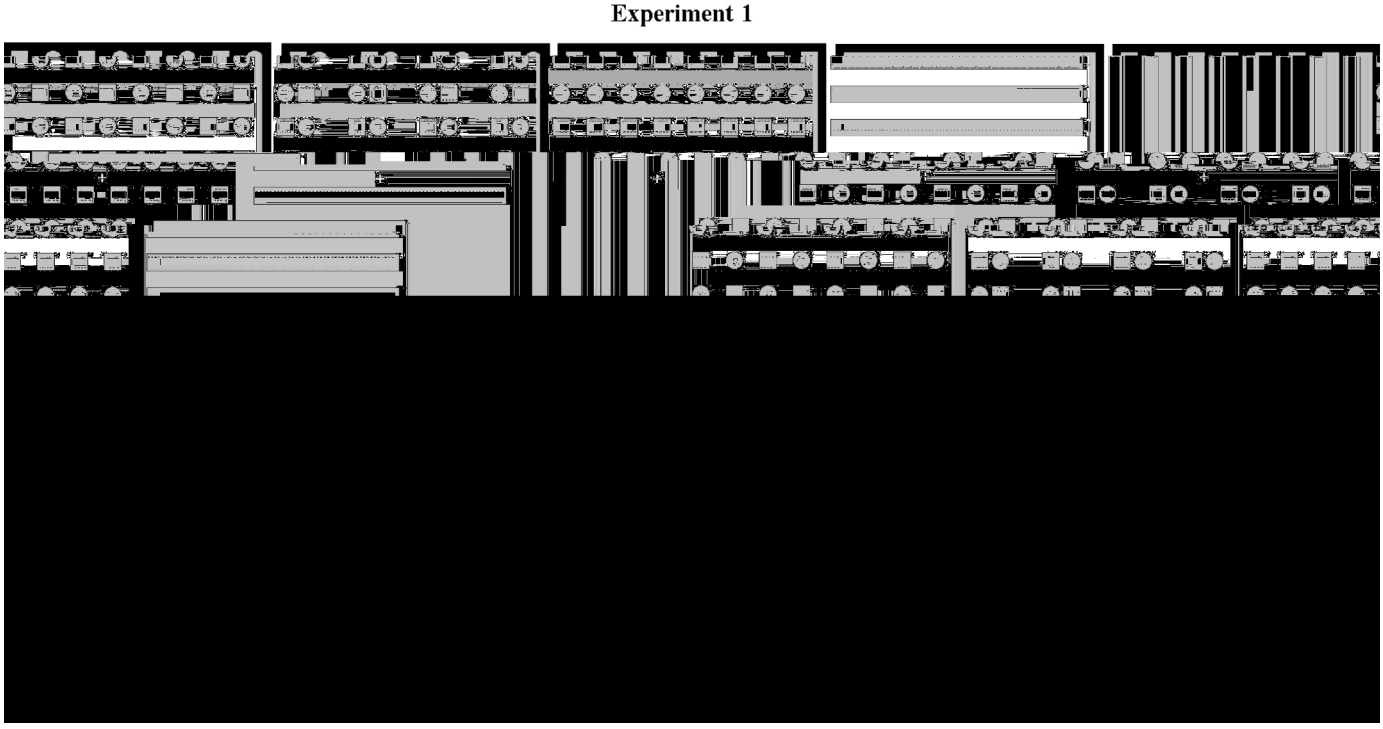

Fig. 2. Illustration of the stimulus arrays in Experiments 1 and 2. In Experiment 1 local circles and squares were white on a black background and grouped into columns or rows based on proximity or shape similarity in the grouped stimuli, whereas the elements were evenly spaced in the uniform stimulus. In Experiment 2 local Gabor patches were presented on a grey background and grouped into columns or rows based on collinearity or similarity of orientation in the grouped stimuli, whereas the elements were evenly spaced in the uniform stimulus. Subjects identified the orientations (vertical vs. horizontal) of the grating in both experiments.

arrangement prevented the local elements from grouping into rows or columns. The proximity-grouped stimuli consisted of alternate 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 spaces between two near or remote rows (or columns) were 0.12° and 0.85°, respectively. The similarity-grouped stimuli were made by placing 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 0.40° for the uniform and similarity-grouped stimuli. Each local shape subtended an angle of $0.51° \times 0.51°$ and the global stimulus pattern subtended an angle of $6.9° \times 6.9°$. Target stimuli were horizontal and vertical square wave gratings of $0.51° \times 6.9°$ (width and length). The luminance of the gratings was the same as that of the grey elements in nontarget stimuli. Both the target and the nontarget displays were presented for 150 ms. The interstimulus intervals were randomized between 300 and 700 ms. While maintaining fixation, participants were asked to discriminate orientations of target grating (vertical or horizontal) by pressing one of two keys on a respond pad with index and middle fingers of the left or right hand while ignoring the non-target stimuli. Each subject completed 132 trials for practice, followed by 1320 trials in ten blocks. There were 120 nontarget stimuli and 12 target stimuli in each block of trials.

Experiment 2

The stimuli and procedure in Experiment 2 were the same as those in Experiment 1 except the following. The background luminance was 15.9 cd/m^2. Nontarget stimuli consisted of a square lattice of Gabor patches arranged in an 8×8 array (Figure 2). The Gabor patches were orientated either 0, 45, 90, or 135° relative to the horizontal meridian of the visual field. Each Gabor patch had a wavelength (λ) and Gaussian distribution equal to 0.20° of visual angle (spatial frequency, 5.0 cycles per degree), with centre-to-centre separation of 4λ (0.80°) between two neighbouring Gabor paches. Neighbouring Gabor patches in the vertical or horizontal dimension did not share the same orientation in the uniform stimulus. The collinear grouped stimuli were made by placing vertical Gabor patches into the same column or by placing horizontal Gabor patches into the same row. The similarity-grouped stimuli were made by placing vertical Gabor patches into the same row or by placing horizontal Gabor patches into the same column.

Data acquisition and analysis

The electroencephalogram (EEG) was recorded with Ag/AgCl electrodes from 128 scalp electrodes relative to the vertex reference. Electrodes were applied to the scalp using carefully positioned nylon cap in accordance with the 10–5 extension of the International 10–20 electrode system (Oostenveld & Praamstra, 2001). Eye blinks and eye movements were monitored by bipolar horizontal and vertical electro-oculogram (EOG) derivations. EEG signals were amplified by BioSemi Active-One amplifiers with a band pass at 0.16–128 Hz at the sampling rate of 512 Hz. EEG recordings were tex refer9,c(reco..0174 0 TD0.0004 Tc06231 Tv

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Table 1. Behavioral data for the patients and controls in Experiments 1 and 2

	Experiment 1		Experiment 2	
	Patients	Controls	Patients	Controls
Reaction times (ms)	1008	854	988	854
Hit (%)	88.3	91.7	95.0	95.0
False alarm (%)	4.2	5.4	4.0	5.2

shorter than those of the patients, reaction times, hits, and false alarms did not differ significantly between the patients and controls in both experiments ($p > .05$), possibly because of the small number of subjects. The behavioral task in the current study was designed to make subjects pay attention to the visual stimuli. The behavioral data recorded were not relevant to the main purpose of this study and thus are not discussed further.

ERPs to nontarget uniform and grouped stimuli in both experiments were characterized for short-latency components with maximum amplitudes over the posterior areas. Figure 3 illustrates the grand averaged ERPs and the difference waves related to grouping recorded at the posterior electrodes from the controls in Experiment 1, where local elements in grouped arrays were integrated into columns or rows by proximity or shape similarity. The ERPs to both uniform and grouped stimuli showed first a positive wave peaking at 90 ms (P1) after stimulus onset, with maximum amplitudes over the occipital regions bilaterally (Figure 3a). The P1 was followed by a negativity peaking at 110 ms (N110) with maximum amplitudes over the medial occipital area, which in turn was followed by a negative component peaking at 180 ms (N180) over bilateral occipital areas. There was also a long-latency positive component peaking at 230 ms (P2) with maximum amplitudes over the parietal area.

To examine the neural activity specifically related to the process of proximity grouping, we calculated difference waves by subtracting ERPs to the uniform stimulus from those to the proximity-grouped stimuli, which revealed two components. There was first a positivity at 100–120 ms (Pd100) after stimulus onset ($F(1, 7)=20.9$, $p < .005$) with maximum amplitudes over the posterior medial occipital area. This Pd100 has been reported in our previous ERP studies of young adults and was localized to the calcarine cortex (Han et al., 2001, 2002, 2005a). The Pd100 was followed by two consecutive negativities, the Nd160 between 140 and 180 ms ($F(1, 7)=5.68$, $p < .05$) over the occipital area and the Nd230 between 220 and 280 ms ($F(1, 7)=7.95$, $p < .05$) over the parietal area. Both the Nd160 and Nd230 showed larger amplitudes over the right than the left hemisphere ($F(1, 7)=5.74$ and 23.3, respectively, both $p < .05$). The voltage topographies of the difference waves related to proximity grouping are shown in Figure 3b.

Similarly, we calculated difference waves by subtracting ERPs to uniform stimuli from those to similarity-grouped stimuli to examine the neural activities related to similarity grouping. Unlike the difference waves related to proximity grouping, the difference wave related for similarity grouping was indexed only by a long-latency negativity between 230 and 320 ms (Nd280, $F(1, 7)=10.7$, $p < .01$), as shown in Figure 3c. The Nd280 was also of larger amplitude over the right than left hemispheres ($F(1, 7)=6.45$, $p < .05$). The voltage topographies of the Nd280 showed that the right hemisphere dominance was evident only in the early phase of the Nd280 (Figure 3d).

To investigate whether fronto-parietal lesions influenced the grouping processes observed in healthy subjects, we conducted similar analysis of the ERPs recorded from the patients. Figure 4 illustrates the grand averaged ERPs and the difference waves recorded at the posterior electrodes from the patients in Experiment 1. Unlike the results of the controls, the ERPs from the patients did not show P1 or N180 waves at the occipital electrodes (e.g., OZ and O2, Figure 4). The P1 wave was present at the right parietal electrodes, but was of smaller amplitude relative to that recorded from the controls. The effect of parietal lesions on the P1 amplitude was significant at the occipital electrodes ($F(1, 8)=7.33$, $p < .05$) and marginally significant at the parieto-occipital electrodes ($F(1, 8)=3.77$, $p < .08$). Nevertheless, the N110, which showed its largest amplitude over the medial occipital area, was enlarged compared with those recorded from the controls ($F(1, 8)=5.43$, $p < .05$). The later P2 component showed a similar pattern but did not reach significance. Interestingly, the difference wave related to proximity grouping for the patients showed only a negativity peaking between 180 and 220 ms (Nd190, $F(1, 1)=352.8$, $p < .05$). This negativity had an occipital focus, larger in the right hemisphere, as illustrated in the voltage topography of the Nd190 (Figure 4a). The difference wave for similarity grouping was also indexed by a negativity peaking at about 240 ms over bilateral occipital areas (Nd240, $F(1, 1)=617.7$, $p < .05$). Relative to the results of the controls, parietal damage eliminated the early proximity effect over the medial occipital cortex.

To examine the grouping processes determined by collinearity or by similarity of orientation, grand averaged ERPs and the difference waves were calculated from the controls in Experiment 2, as illustrated in Figure 5. The ERPs to both uniform and grouped stimuli showed a positivity peaking at 100 ms (P1) after stimulus onset, with maximum amplitudes over the occipital areas bilaterally (Figure 5a). The P1 wave was followed by a negativity peaking at 130 ms (N130) with maximum amplitudes over the medial occipital area, which in turn was followed by a long-latency positive component peaking at 230 ms (P2), with maximum amplitudes over the posterior occipital area. We also calculated difference waves by subtracting ERPs to uniform stimuli from those to collinearity-grouped stimuli to examine the neural activities related to collinearity grouping. The difference waves specific to collinearity grouping were characterized by two consecutive negativities between 130 and 150 ms (Nd130, $F(1, 7)$

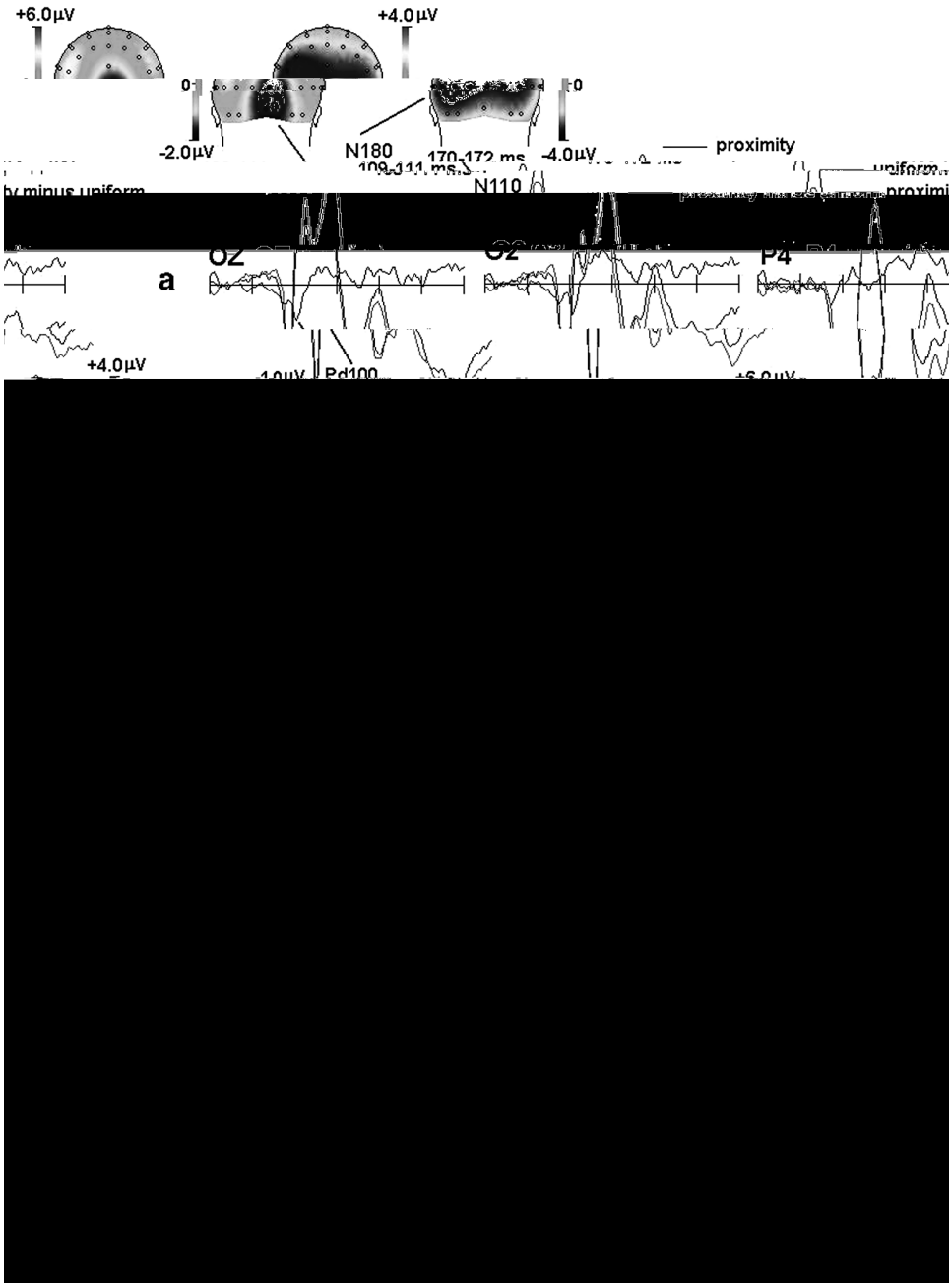

Fig. 3. ERP results of the controls in Experiment 1. (a) Illustration of ERPs, voltage topographies of each ERP component to the uniform stimulus, and the difference waves related to proximity grouping; (b) voltage topographies of the difference waves related to proximity grouping; (c) illustration of ERPs and the difference waves related to similarity grouping; (b) voltage topographies of the difference waves related to similarity grouping.

=9.41, $p < .05$) and between 220 and 280 (Nd240, $F(1, 7)$ =9.99, $p < .01$), respectively. The Nd130 showed maximum amplitudes over the medial occipito-parietal area, whereas the Nd240 showed maximum amplitudes over bilateral occipital areas. The difference waves related to similarity grouping in Experiment 2 also showed a negative deflection; however, this effect did not reach significance ($p > .05$).

To investigate whether fronto-parietal lesions influenced the grouping processes determined by collinearity, we conducted similar analysis of the ERPs recorded from the patients in Experiment 2. Figure 6 illustrates the grand averaged ERPs and the difference waves recorded at the posterior electrodes from the patients in Experiment 2. The ERPs recorded from the patients did not show the P1wave at the occipital electrodes (e.g., OZ and O2). The P1 was present at the right parietal electrodes, but was of smaller amplitude relative to that recorded from the controls. The effect of parietal damage on the P1 component was significant at occipital

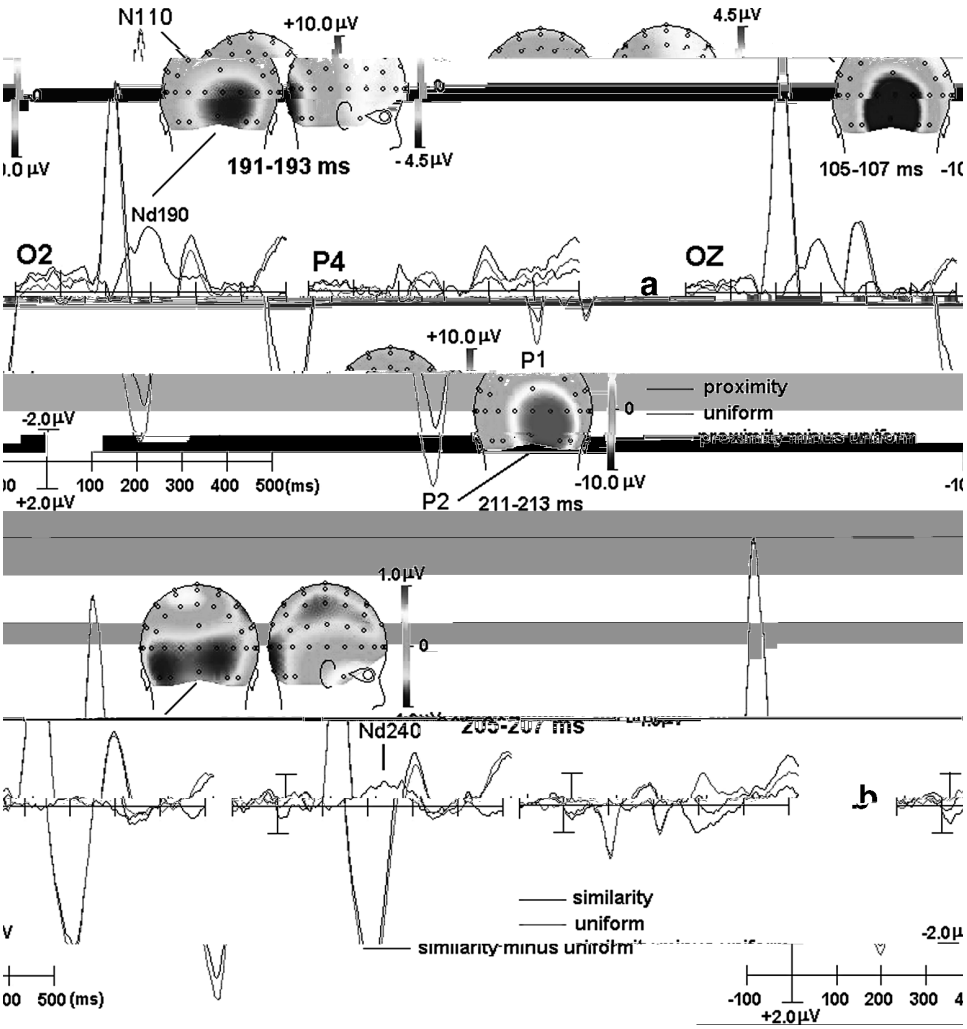

Fig. 4. ERP results of the patients in Experiment 1. (a) Illustration of ERPs, voltage topographies of each ERP component to the uniform stimulus, and the difference waves related to proximity grouping; (b) illustration of ERPs, the difference waves related to similarity grouping, and voltage topographies of the difference waves related to similarity grouping.

electrodes ($F(1, 8)=5.14$, $p < .05$). The N130 and the following P2 showed larger amplitudes relative to those recorded from the controls. However, these effects did not reach significance ($p > .05$). Noticeably, there were no significant grouping effects in the ERP results for either collinearity or similarity grouping ($p > .05$). This indicates that the fronto-parietal damage in these patients seriously reduced the early grouping effects in the occipital areas that were undamaged in the patients. MH had not damage to occipital cortex. JB had minor left occipital damage but failed to show attention-enhanced grouping effects even in her spared right occipital regions.

Discussion

The fronto-parietal network is involved in a variety of visual selective attention tasks, including attention to spatial location (Gitelman et al., 1999; Kim et al., 1999; Nobre et al., 1997) and to objects (Fink, Dolan, Halligan, Marshall, & Frith, 1997). There is also evidence for the engagement of this network in attentional modulation of neural activities in the visual cortex. While the visual activity was enhanced to stimuli at attended than unattended locations in healthy subjects, these attentional effects were reduced in patients with parietal lesions (Han et al., 2004; Han & Jiang, 2004). The current work studied the effects of fronto-parietal lesions on perceptual grouping in the visual cortex, using high-density ERPs to examine early grouping effects in controls and two patients with primarily fronto-parietal and parietal damage, respectively. Similar to our previous ERP studies (Han et al., 2001, 2002, 2005a, 2005b), grouping processed were indexed by difference waves obtained by subtracting ERPs to grouped arrays vs. those to evenly distributed elements.

In Experiment 1, proximity grouping in controls was first indexed by a positivity over the medial occipital cortex

Pd100 is modulated by top-down attention (Han et al., 2005a). The Pd100 is significantly reduced when the features making up the perceptual groups were of low rather than of high task relevance. In addition, the Pd100 was also influenced by the size of spatial attentional window, being present when grouped stimulus arrays fell inside the attended area but eradicated when grouped stimulus arrays fell outside the attended area. Here the comparison of ERPs between the patients with fronto-parietal lesions and the

elements into larger 'chunks' whereas the late grouping operations function to process the features of the perceptual groups (e.g., orientation in this study) in other brain areas. The functional roles of the early and late grouping processes require different feedback from the parietal cortex, which facilitates mainly the initial segmentation operation.

Similar effects of fronto-parietal lesions on grouping by collinearity were observed in Experiment 2. The collinear grouping effects in the controls were indexed by an early Nd130 over the medial occipital area and a late Nd250 over the occipital cortex bilaterally. However, non-collinear Gabor patches that were similar in orientation did not generate significant ERP grouping effect, suggesting that similarity of one simple feature (i.e., orientation in Experiment 2) was not as strong a grouping cue as similarity of shape in Experiment 1. We recently found that, for young adults who were presented with similar stimulus arrays as those in the current study, the collinear grouping effect could occur at 40–80 ms after stimulus delivery indexed by a positivity over the medial occipital area. There was also a long-latency negativity over bilateral occipital areas in association with collinear grouping (Han et al., 2007). Thus our data with older controls here suggest that age alone may lead to a weakening/slowing of the early grouping effect (though, unlike with patients with fronto-parietal lesions, the effect remains). This is consistent with the ERP studies with younger adults where an enlarged early component has been observed (80 ms post-stimulus) when fewer Gabor patches were presented in each stimulus array (Khoe et al., 2004), so that weaker grouping takes place.

In Experiment 2, both short- and long-latency grouping effects were eliminated in the patients. The elimination of the early grouping effect was similar to that in Experiment 1 although both the polarity and time window of the early grouping effect differed across the experiments. Therefore, it may be concluded that the early grouping operation in the medial visual cortex depends upon the normal function of the fronto-parietal cortex regardless of what principles determine grouping. In other words, top-down modulation of grouping in the visual cortex, produced by the fronto-parietal network, may be generalized to any form of grouping operation in the medial visual cortex. The loss of the long latency grouping effect related to collinear grouping suggest that, unlike grouping by proximity and grouping by shape similarity, grouping by collinearity requires top-down feedback from the fronto-parietal network even at a later stage of grouping. The loss of the late grouping effect related to similarity grouping in Experiment 2 suggests that grouping by similarity of orientation is relatively weak in the first place, and not as strong as grouping by similarity of shape which took place in Experiment 1 (when long latency grouping was maintained in the patients).

Interestingly, we found that, relative to the ERP results from the controls, the patients' ERPs showed a reduced stimulus-evoked P1 component over bilateral occipital cortex. Similar reduction in the P1 are reported in prior studies of patients with parietal (Han & Jiang, 2004) and prefrontal lesions (Barceló, Suwazono, & Knight, 2000). Because prior studies have localized the P1 component to the lateral extrastriate cortex (Gomez Gonzalez et al., 1994; Clark & Hillyard, 1996; Heinze et al., 1994; Woldorff et al., 1997), the effects of brain lesions on the P1 amplitude implicate that there is regulation of initial visual processing in the extrastriate cortex by more anterior regions as early as 100 ms after sensory stimulation. Nevertheless, we observed enlarged N110 and P2 effects in the patients relative to the controls. Both Experiments 1 and 2 showed such N110 and P2 enhancement although the effects were significant only in Experiment 1. These results suggest that top-down modulation of the sensory processing produced by the fronto-parietal network does not act simply to enhance neural activity at all stages of sensory processing. The fronto-parietal cortex contributes to the enhancement of initial sensory processing in the extrastriate activities. At later stages of sensory processing, however, the fronto-parietal network suppresses the neural activity in the visual cortex. Thus damage to the attentional network results in differential effects on sensory processing in different time windows. On the one hand, the damaged fronto-parietal network fails to augment initial sensory processing in the extrastriate cortex. On the other hand, the damaged fronto-parietal network releases the inhibition of the sensory processing at a later time period as suggested by the enhanced N110 observed in the patients. A functional role of such inhibition of sensory processing is to provide a low-level background of neuronal activity so that perceptual processing (including perceptual grouping) based on differential neuronal responses can be easily distinguished. Once inhibitory mechanisms implement by the fronto-parietal network are damaged, the neuronal responses associated with sensory processing are increased abnormally and perceptual processing dependent upon the differential sensory processing is then weakened or eliminated.

The enlarged N110 and P2 components in the patients relative to the controls showed a medial occipital distribution, which overlapped with the locus of the grouping effects observed in both experiments. This fact indicates that the sensory visual activity occurring in the visual cortex that underpinned perceptual grouping was not influenced by the fronto-parietal damage. It follows that the elimination of the grouping ERP effects could not simply arise from the general dysfunction of the visual cortex although one patient showed minor earlier infarct in the left occipital lobe. Because the current study only tested patients with fronto-parietal lesions, our results could not tell if lesions in other brain areas may induce similar effects. However, our recent combined transcranial magnetic stimulation (TMS) and ERP research (Han, Zhou, & Wang, 2005c) showed evidence that only a limited number of brain areas rather than all high-level brain structures are involved in top-down modulation of early sensory/perceptual processing. In this study, we used TMS to disrupt the activity in the left/right parietal cortex and in the precentral gyrus. We found that, relative to the

condition of no TMS, disruption of the left/right parietal cortex reduced the amplitude of the early extrastriate activity. Disruption of the precentral gurys, however, did not influence the early visual activity such as the P1 component compared with when no TMS was applied. These results suggest that it is unlikely that disruption or damage of any brain areas would produce similar effect on the early visual sensory/perceptual processing. Further research is required to examine whether early perceptual grouping receives top-down modulation from brain areas outside the frontal ad parietal lobes.

Previous research has shown abundant evidence for top-down effects in visual perception. For example, the early sensory/perceptual processing indexed by early ERP components (i.e., the P1 and N1 waves) are strongly modulated by visual attention, being enlarged to the stimuli at attended relative to at unattended locations (Gomez Gonzalez et al., 1994; Clark & Hillyard, 1996; Heinze et al., 1994; Woldorff et al., 1997). Deficits of simple shape recognition is observed in patients with prefrontal lesions (Barceló et al., 2000). Face recognition is also susceptible to top-down influences (Puce, Allison, & McCarthy, 1999). Possible neural mechanisms have been proposed to interpret how the top-down effects on early process of visual perception and recognition are produced. von Stein, Chiang, and König (2000) suggest that corticocortical synchronization within a middle-frequency range (4–12 Hz) may play a key role in top-down processes. Bar et al. (2003, 2006) further suggest that a partially analyzed version of the input images represented in low spatial frequencies in early visual areas is projected to the prefrontal cortex to initiate top-down processes projected from the prefrontal to visual cortex. Such mechanisms may also play a role in top-down modulation of the process of perceptual grouping, though this needs to be confirmed in future research.

Finally, the present results raise the question of the nature of top-down effects on the grouping processes, since the present evidence is that these effects occur early in the visual processing stream (i.e., in striate and extrastriate cortex). To account for this, we suggest that the fronto-parietal network maintains a tonic state that provides rapid enhancement of processing within attended areas of field and on features that are primed as being task relevant. This tonic state can generate early enhancement without requiring feed forward and feedback operations that themselves may take considerable time.

In sum, the current ERP studies of patients with fronto-parietal damage provide evidence that human fronto-parietal network facilitates early grouping operations in the visual cortex. This facilitation occurs regardless of whether the grouping processes are defined by proximity or collinearity. The fronto-parietal cortex also facilitates long-latency grouping based on the similarity of orientations of local elements. In addition, the fronto-parietal modulation of the sensory pro-

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