Neural mechanisms of attentional modulation of perceptual grouping by collinearity

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Psychophysical research showed that detection of an oriented visual target is facilitated when the target is grouped with collinear visual flankers. However, this collinear grouping effect is evident only when the flankers are attended. This study examined neural mechanisms underlying the interaction between attention and grouping by collinearity. Event-related potentials were recorded from study participants who judged whether oriented Gabor patches (i.e. visual elements consisting of a sinusoidal contrast modulation convolved with a Gaussian function) along the cued orientation were collinear or orthogonal. Event-related potentials showed an enhanced negativity over the posterior occipital cortex at 48–72 ms when collinear patches were congruent rather than incongruent with the cued orientation. A negative shift bee tie 503(x0-175 The long-latency effect, however, was evident only when the collinear patches were allocated along 45°. The event-related potential results suggest that the interaction between attention and collinear grouping may take place as early as in the primary visual cortex and is independent of global orientations of perceptual groups. *NeuroReport* 16:567–570 © 2005 Lippincott Williams & Wilkins.

Key words: Attention; Collinear grouping; Event-related potential; Orientation

INTRODUCTION

Our perception of an ordered visual world is based on grouping processes that integrate local elements into global configurations. It is widely accepted that such grouping operations occur at early stages of visual perception [1]. Human neural correlates of grouping processes have been investigated in neuroimaging studies. For example, event-related brain potential (ERP) studies found that perceptual grouping defined by proximity (i.e. integration of spatially close objects into a whole) results in enhanced neural activities at 100 ms after sensory stimulation [2]. Functional magnetic resonance imaging (fMRI) studies further identified generators of such early grouping activity in the human primary visual cortex [3]. Similarly, there has been evidence for the engagement of the primary visual cortex in the grouping process defined by collinearity (i.e. integration of oriented visual elements of which orientations match the global orientation of a virtual line drawn through all elements). Neuronal responses in monkeys' primary visual cortex are enhanced when stimuli inside and outside the neurons' receptive fields form a collinear group [4]. Collinear grouping also facilitates the detection of central Gabor patches (a Gabor patch consists of a sinusoidal contrast modulation convolved with a Gaussian function) in humans [5] and is associated with an increased activity at 80–140 ms over the middle occipital area [6], suggesting the involvement of the human primary visual cortex in collinear grouping.

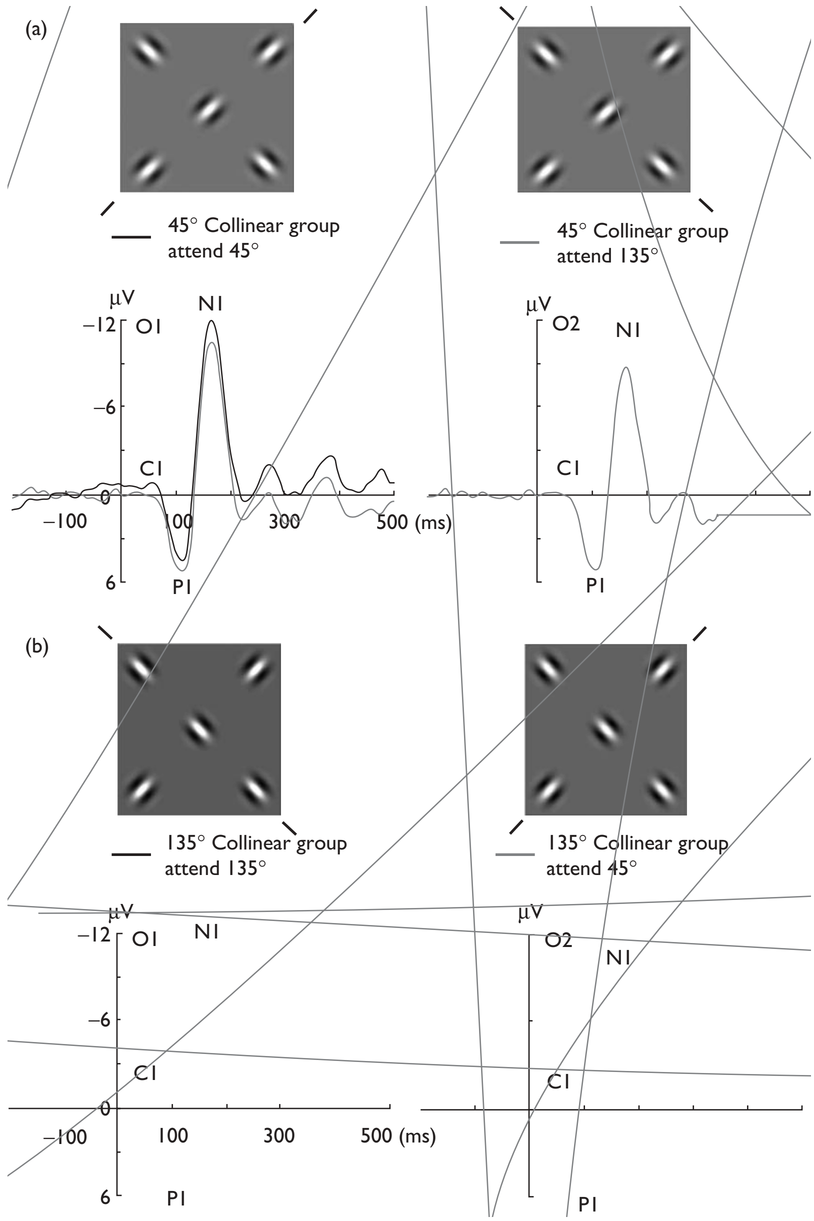
It has been argued that grouping processes may take place independent of focal attention [7]. However, recent research has shown evidence for the interaction between attention and perceptual grouping in the human primary visual cortex [3]. Neural activities in the primary visual cortex around the calcarine sulcus associated with proximity grouping are strengthened when stimulus arrays are of high task relevance and fall inside attended areas. Similarly, a recent psychophysical study showed that collinear flankers facilitate the detection of a central Gabor patch when flankers are attended but not when flankers are ignored [8]. This lateral interaction possibly reflects attentional modulation of flanker-target grouping defined by collinearity. The current study investigated neural mechanisms underlying the interaction between attention and grouping by collinearity using a cueing paradigm similar to that used in prior psychophysical experiments [8,9]. Study participants were cued to allocate their attention along a specific orientation (45° or 135°) before they were shown a stimulus array of Gabor patches, as illustrated in Fig. 1. Neural mechanisms underlying attentional modulation of grouping by collinearity were investigated by comparing ERPs with stimulus arrays between the conditions when attentional allocation was either congruent or incongruent with the orientation of perceptual groups formed by collinear Gabor patches.

MATERIALS AND METHODS

Study participants: Sixteen undergraduate and graduate students (nine women, seven men; 18–27 years of age, mean 22 years) from Peking University participated in this study. All participants were right-handed and had normal or corrected-to-normal vision. Informed consent was obtained from all the participants. Four of them were excluded from data analyses because of excessive eye blinks during electrophysiological data recording.

Stimuli and procedure: Stimuli were displayed on a gray background (25.1 cd/m^2). Each stimulus array consisted of a configuration of Gabor patches (see Fig. 1). The central Gabor patch was orientated either 45° or 135° and was flanked by two pairs of patches in an 'X' configuration. The flankers were either collinear with or orthogonal with the central Gabor patch. At a viewing distance of 120 cm, each Gabor patch had a wavelength (λ) and Gaussian distribution equal to 0.45° of visual angle (spatial frequency, 2.2 cycles per degree), with center-to-center separation of 4.2λ between the central Gabor and each flanker. Target stimulus arrays consisted of Gabor patches with carrier wavelength and Gaussian distribution of contrast envelope both equal to 0.36° of the visual angle (spatial frequency, 2.8 cycles per degree). Center-to-center separation between center and flanker was 3.7λ. The target stimulus arrays were 70% smaller than the nontarget stimulus arrays.

Participants pressed a button with the left or right index finger to start each block of trials. On each trial, the fixation cross (0.6$^\circ \times$ 0.6°



collinear group was allocated along 45° or 135°, indicating that response speeds were independent of the global orientations of perceptual groups.

The neural mechanisms of attentional modulation of grouping by collinearity were indexed by the differences in ERPs between the conditions when attentional allocation was either congruent or incongruent with the global orientations of perceptual groups composed of collinear Gabor patches. We found that nontarget stimulus arrays elicited an early negative wave peaking between 40 and 80 ms after stimulus onset, which was enlarged by attention allocated along the collinear group in stimulus displays. Both the time course and morphology suggest that this negativity is the C1 component that has been identified to have neural generators in the human primary visual cortex around the calcarine sulcus [10,11]. Because stimulus arrays were identical in the congruent and incongruent conditions, the C1 effect could not arise from any difference in stimulus features. Thus, our ERP results suggest that attention along the collinear group resulted in enhancement of neural activities in the primary visual cortex as early as 50 ms after stimulus onset, providing electrophysiological evidence for the interaction between attention and grouping by collinearity in the primary visual cortex. Because the task used in the current study emphasized the global orientation of a perceptual group rather than the orientation of the central Gabor patch, the C1 effect suggests that the integration of collinear Gabor patches involved neural mechanisms in the primary visual cortex, possibly through long-range horizontal connections linking neurons with common orientation tunings [12].

Prior ERP studies have shown that the C1 component evoked by stimulus arrays is modulated by whether local elements in the stimulus display are grouped into columns or rows by proximity [13]. In addition, the proximity-grouping-related activity in the calcarine cortex is modulated by whether stimulus arrays are of high task relevance and are located inside an attended area [3]. In accordance with the previous findings, the current ERP results suggest that the interaction between attention and grouping operations defined by different principles, such as proximity and collinearity, may share a common neural mechanism in the primary visual cortex.

The current ERP study also showed evidence for a long-latency effect of the interaction between attention and grouping by collinearity. A negative shift was observed in the congruent rather than incongruent conditions at the occipital–parietal areas at 200–420 ms. Because the long-latency effect was observed in ERPs to nontarget stimuli that did not require behavioral responses, it is unlikely that this effect reflected the process after perceptual processing such as response selection or execution. Interestingly, the long-latency effect depended upon the global orientation of collinear groups, being significant only when collinear Gabor patches were allocated along 45°. This effect has not been reported in prior psychophysical studies [8,9] and cannot be simply accounted for by attentional allocation, which was decided by peripheral cues that appeared before the presentation of Gabor patch displays. A possible interpretation of this orientation-dependent long-latency effect is that the long-latency process of collinear grouping along 135° was less perceptually salient than that along 45° and, thus, was less sensitive to the prior allocation of spatial attention. This proposal is consistent with the fact that behavioral responses to the perceptual groups were slower when the perceptual group required to be identified was along 135° than when along 45°. However, this proposal needs further evidence. Whatever the case, our ERP results complement previous psychophysical research by showing that there might be two distinct phases of interaction between spatial attention and grouping by collinearity.

CONCLUSION

The early interaction between spatial attention and collinear grouping may have occurred in the primary visual cortex and was independent of globalne9(i-337.5((prnt)Ah1(of)-447.5(percep