Behavioral/Cognitive

Attention-Dependent Early Cortical Suppression Contributes to Crowding

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Crowding, the identification difficulty for a target in the presence of nearby flankers, is ubiquitous in spatial vision and is considered a bottleneck of object recognition and visual awareness. Despite its significance, the neural mechanisms of crowding are still unclear. Here, we performed event-related potential and fMRI experiments to measure the cortical interaction between the target and flankers in human subjects. We found that the magnitude of the crowding effect was closely associated with an early suppressive cortical interaction. The cortical suppression was reflected in the earliest event-related potential component (C1), which originated in V1, and in the BOLD signal in V1, but not other higher cortical areas. Intriguingly, spatial attention played a critical role in the manifestation of the suppression. These findings provide direct and converging evidence that attention-dependent V1 suppression contributes to crowding at a very early stage of visual processing.

Key words: attention; crowding; event-related potential; fMRI; primary visual cortex

Introduction

When a target is presented ith nearb flankers in the peripheral visual field, it becomes harder to identif , hich is referred to as cro ding. Cro ding is a form of inhibitor interaction that is ubiquitous in spatial vision, and it has been reported to occur ith various kinds of stimuli and tasks (Levi, 2008; Whitne and Levi, 2011). Stud ing cro ding can advance our understanding of conscious vision and object recognition throughout the visual field.

Despite the significance of cro ding, its mechanisms are still unclear. Based on ps choph sical findings, various theories have been proposed to e plain cro ding at multiple levels. Some theories attribute cro ding to earl visual cortical interaction. The propose that cro ding occurs hen the target and flanker overlap ithin the same neural unit (Flom et al., 1963; Levi et al., 1985; Pelli, 2008) or are represented b different populations of neurons ith long-range hori ontal connections (Levi, 2008). These theories suggest that cro ding influences the representation of the target in earl visual processing stages. On the other hand, attention theories argue that cro ding could be ascribed to coarse resolution of spatial attention (He et al., 1996) or unfocussed spatial attention (Strasburger, 2005). The effect of cro ding on the target representation is in late processing stages.

To date, ver fe neuroph siological studies have attempted to investigate the neural mechanisms of cro ding (Fang and He, 2008; Bi et al., 2009; Freeman et al., 2011; Anderson et al., 2012; Millin et al., 2013). A major obstacle is the difficult in isolating neural signals induced b the target from those b flankers. This is because cortical areas responding to the peripheral target and flankers are hard to separate, especiall ith current brain imaging techniques. Several fMRI studies (Freeman et al., 2011; Anderson et al., 2012; Millin et al., 2013) sho ed that cro ding attenuated BOLD signals in earl visual corte , as earl as in V1. Ho ever, because of the lo temporal resolution of fMRI, it is unclear hether the attenuation originates in V1 or reflects top-do n feedback from higher cortical areas. Moreover, no e isting literature, e cept a conference presentation b Tjan et al. (2012) has investigated an important diagnostic criterion for cro ding,

Materials and Methods

Subjects. There ere 20 subjects (14 male) in E periment 1, 20 (12 male) in E periment 2, 10 (4 male) in E periment 3, and 10 (6 male) in E periment 4. All subjects ere right-handed and reported normal or corrected-to-normal vision. Ages ranged from 18 to 27 ears. The gave ritten, informed consent in accordance ith the procedures and protocols approved b the human subjects revie committee of Peking Universit .

Stimuli. All the targets and flankers ere circular sinusoidal gratings (diameter: 2.36°; spatial frequenc : 2.54 c cles/°; Michelson contrast: 1; mean luminance: 61.47 cd/m^2). The background luminance as also 61.47 cd/m^2. In all e periments, the target as centered at 8° eccentricit in the upper left visual quadrant. We presented the stimuli in the upper visual field, rather than the lo er visual field. This is because: (1) cro d-ing is stronger in the upper visual field than in the lo er visual field (He et al., 1996); and (2) it is easier to separate C1 and the follo ing positive P1 component ith upper visual field stimuli, as the C1 induced b stimuli in the upper visual field has a negative polarit , hereas the C1 induced b stimuli in the lo er visual field has a positive polarit (Clark et al., 1994). The orientation of the target as 45 ± θ°, either left or right tilted. θ as predetermined b a ps choph sical test (see belo). The orientations of the flankers ere independentl and randoml selected from 0° to 180° for each trial. Subjects ere asked to maintain fi ation on a black dot at the center of the displa throughout the e periments.

In E periment 1, there ere five stimuli: target onl (T), target ith nearb flankers (Near_T+F), target ith far flankers (Far_T+F), nearb flankers onl (Near_F), and far flankers onl (Far_F) (see Fig. 1*A*). The flankers ere positioned in the radial direction ith respect to fi ation. The center-to-center distance bet een the flankers and the target as 2.48° in the Near_T+F stimulus and 5.07° in the Far_T+F stimulus. E periment 2 also had five stimuli: target onl (T), target ith flankers positioned radiall (Rad_T+F), target ith flankers positioned tangentiall (Tan_T+F), radial flankers onl (Rad_F), and tangential flankers onl (Tan_F) (see Fig. 1*B*). In both the Rad_T+F and the Tan_T+F stimuli, the center-to-center distance bet een the flankers and the target as 2.36°. In E periments 3 and 4, the stimuli ere identical to those in E periments 1 and 2, respectivel , e cept T as not used.

θ as the orientation discrimination threshold (75% correct) for the target in the Far_T+F stimulus (E periments 1 and 3) and the Tan_T+F stimulus (E periments 2 and 4). To measure the threshold, a stimulus (Far_T+F or Tan_T+F) as presented for 250 ms. The orientation of the target as either 45+θ° or 45-θ°. Subjects ere asked to judge the orientation of the target relative to 45° (clock ise or counterclock ise). The θ varied trial b trial and as controlled b the QUEST staircase (Watson and Pelli, 1983).

ERP experiments. The procedures of E periments 1 and 2 ere identical, e cept that different stimuli ere used. Visual stimuli ere displa ed on a Vie Sonic color graphic monitor (refresh rate: 60 H ; resolution: 1024 × 768; si e: 22 inches) ith a gra background at a vie ing distance of 73 cm. A chin rest as used to stabili e subjects' head position.

Each trial began ith one of the five stimuli (T, Near_T+F, Far_T+F, Near_F, and Far_F in E periment 1 and T, Rad_T+F, Tan_T+F, Rad_F, and Tan_F in E periment 2) presented in the upper-left visual quadrant for 250 ms. Then, after a 450 650 ms blank interval, a grating hose orientation slightl deviated from the vertical as presented for 100 ms in the lo er-right visual quadrant. T o lo -contrast dashed circles, one at the same location as the target in the first stimulus and the other at the same location as the grating in the second stimulus, ere al a s presented on the screen to indicate the positions of the target and the second grating, respectivel (see Fig. 1*C*).

Both E periments 1 and 2 consisted of t o sessions: the attended session and the unattended session. In these t o sessions, subjects vie ed the same stimuli but performed different tasks. In the attended session, subjects ere instructed to pa attention to the upper left visual quadrant, respond to the first stimulus, and ignore the second stimulus. If the stimulus contained a target, subjects needed to press one of t o buttons to indicate the orientation of the target relative to 45° (clock ise or counterclock ise). If the stimulus contained onl the flankers, subjects pressed a button randoml . In the unattended session, subjects ere instructed to pa attention to the lo er right visual quadrant, ignore the first stimulus, and respond to the orientation of the second stimulus relative to the vertical (left or right). The t o sessions ere performed on different da s and ere counterbalanced across subjects. In each session, there ere 20 blocks of 100 trials, ith 20 trials for each of the five stimuli.

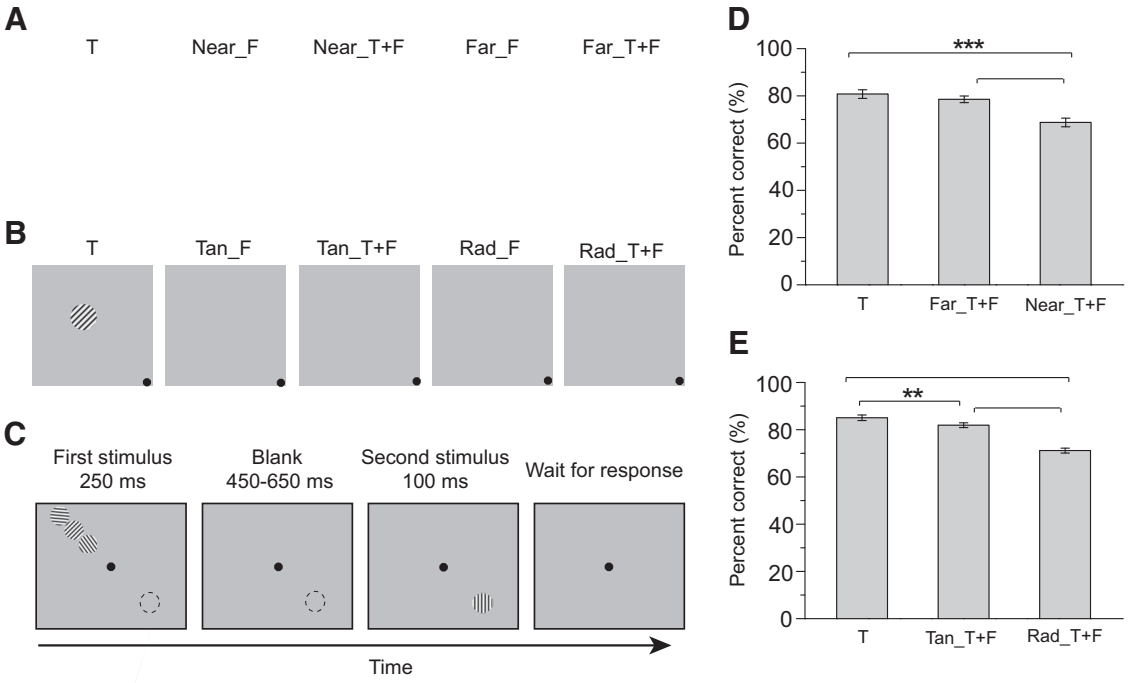
Scalp EEG as recorded from 64 Ag/AgCl electrodes positioned according to the e tended international 10 20 EEG s stem. Vertical electrooculogram as recorded from an electrode placed above the right e e. Hori ontal EOG as recorded from an electrode placed at the outer canthus of the left e e. Electrode impedance as kept <5 kΩ. EEG as amplified ith a gain of 500 K, bandpass filtered at 0.05 100 H , and digiti ed at a sampling rate of 1000 H . The signals on these electrodes ere referenced online to the nose and ere rereferenced offline to the average of the t o mastoids.

Offline data anal sis focused on the EEG signals induced b the first stimulus, using Brain Vision Anal er (Brain Products). EEG data ere first lo -pass filtered at 30 H and then epoched starting at 100 ms before stimulus onset and ending at 200 ms after stimulus onset. Each epoch as corrected for baseline over the 100 ms prestimulus interval. The epochs contaminated b e e blinks, e e movements, or muscle potentials e ceeding ±50 μV at an electrode ere e cluded from anal sis. Remaining epochs ere selectivel averaged according to the stimulus conditions. To select electrodes for the C1 amplitude and latenc anal sis, grand averaged ERPs ere made b averaging across subjects and stimulus conditions but separatel for the t o sessions. Five electrodes ith the largest C1 amplitudes ere chosen for further anal sis. To quantif the C1 amplitude and latenc for each stimulus and each subject, the aveforms at these five electrodes ere first averaged to obtain a mean aveform. The mean amplitude of the 11 sampling points around the C1 peak of the mean aveform as defined as the C1 amplitude. The C1 latenc as the peak latenc of the mean aveform.

Estimation of the dipole sources as performed using the BESA algorithm, as described b Clark et al. (1994). The C1 component as modeled on the grand-averaged aveforms elicited b all five stimuli. The aveform in the 3 ms interval around the peak amplitude (bet een 76 and 78 ms in E periment 1, 77 and 79 ms in E periment 2) as simulated ith one dipole ith free location and orientation.

fMRI experiments. E periment 3 used an event-related design and had t o sessions: the attended session and the unattended session. Each session consisted of eight functional runs of 128 continuous trials (2 s for each trial). In these t o sessions, subjects vie ed the same stimuli but performed different tasks. In the attended session, each run began ith a 12 s fi ation period and ended ith a 14 s fi ation period, thus lasting 282 s. The order of the three t pes of trials (blank, far, and nearb) in each run as balanced using M-sequence (Buracas and Bo nton, 2002). Specificall , a four condition M-sequence as adopted, ith one condition for far trials, one condition for nearb trials, and t o conditions for blank trials, such that subjects ould not feel time-pressed to perform the task. For each of the far and nearb conditions, there ere 32 trials in each run and 256 trials (32 × 8) in total. In a far trial, the Far_T+F and Near_F stimuli ere presented successivel in a random order, each for 0.25 s. In a nearb trial, the Near_T+F and Far_F stimuli ere presented in the same a (see Fig. 4*A*). In the follo ing 1.5 s, subjects performed the same orientation discrimination task ith the target as that in the ERP e periments. In a blank trial, onl the fi ation point as presented for 2 s. In the unattended session, subjects ere asked to ignore the stimuli and detect a brief luminance change at the fi ation point. A dashed circle at the location of the target as al a s presented on the screen to indicate the position of the target. The procedure of E periment 4 as identical to that of E periment 3, but different stimuli (Rad_T+F, Tan_T+F, Rad_F, and Tan_F) ere used. In a radial trial, the Rad_T+F and Tan_F stimuli ere presented. In a tangential trial, the Tan_T+F and Rad_F stimuli ere presented (see Fig. 6*A*).

Retinotopic visual areas (V1, V2, V3, and V4) ere defined b a standard phase-encoded method developed b Sereno et al. (1995) and Engel et al. (1997), in hich subjects vie ed rotating edge and e panding ring stimuli that created traveling aves of neural activit in visual corte . For both E periments 3 and 4, a block-design run as used to locali e the ROIs in V1-V4, LO corte LO, and IPS, corre-



sponding to the area covered b the four flankers and the target. The run consisted of 12 12-s stimulus blocks, interleaved ith 12 12-s blank intervals. In a given stimulus block, subjects passivel vie ed images of colorful natural scenes, hich had the same shape, si e, and location as the target and flankers (see Figs. 4*C* and 6*C*). The images appeared at a rate of 8 H .

MRI data ere collected using a 3T Siemens Trio scanner ith a 12-channel phase-arra coil. In the scanner, the stimuli ere back-projected via a video projector (refresh rate: 60 H ; spatial resolution: 1024 × 768) onto a translucent screen placed inside the scanner bore. Subjects vie ed the stimuli through a mirror located above their e es. The vie ing distance as 83 cm. BOLD signals ere measured ith an echo-planar imaging sequence (TE: 30 ms; TR: 2 s; FOV: 192 × 192 mm^2; matri : 64 × 64; flip angle: 90; slice thickness: 3 mm; gap: 0 mm; number of slices: 33, slice orientation: a ial). The fMRI slices covered the occipital lobe, most of the parietal lobe, and part of the temporal lobe. A high-resolution 3D structural dataset (3D MPRAGE; 1 × 1 × 1 mm^3 resolution) as collected in the same session before the functional runs. For both E periments 3 and 4, subjects under ent three sessions: the retinotopic mapping session, the attended session, and the unattended session.

The anatomical volume for each subject in the retinotopic mapping session as transformed into the AC-PC space and then inflated using BrainVo ager QX (Brain Innovation). Functional volumes in all sessions for each subject ere preprocessed, including 3D motion correction, linear trend removal, and high-pass (0.015 H) filtering using BrainVo - ager QX. The images ere then aligned to the anatomical volume in the retinotopic mapping session. A GLM procedure as used for selecting ROIs. The ROIs in V1-V4, LO, and IPS ere defined as areas that responded more strongl to the natural scene images than to a blank screen ($p < 10^{-4}$, uncorrected).

Event-related BOLD signals ere calculated separatel for each subject, follo ing the method used b Kourt i and Kan isher (2000). For each event-related run, the time course of the MR signal intensit as first e tracted b averaging the data from all the vo els ithin the predefined ROI. The average event-related time course as then calculated for each t pe of trial. Specificall , in each run, e averaged the signal intensit across the trials for each trial t pe at each of 9 corresponding time points (volumes) starting from the stimulus onset. These event-related time courses of the signal intensities ere then converted to time courses of percentage signal change for each t pe of trial b subtracting the corresponding value for the blank trials and then being divided b that value. The resulting time course for each t pe of trial as then averaged across runs for each subject and then across subjects. In the ps choph sical, ERP, and fMRI data anal ses, Bonferroni correction as applied ith *t* tests involving multiple comparisons.

Results

Experiment 1: C1 suppression and the target–flanker distance

It is ell kno n that the cro ding one e tends to appro imatel half the target eccentricit (Bouma, 1970, 1973). That is, cro d-ing is significantl stronger hen the target is presented ith nearb flankers than ith far flankers. If the cortical suppression bet een the target and flankers contributes to cro ding, e predict a stronger suppression in the nearb condition relative to the far condition. We conducted the first ERP e periment to test this.

Five stimuli (Fig. 1*A*) ere used, including target onl (T), target ith nearb flankers (Near_T+F), target ith far flankers (Far_T+F), nearb flankers onl (Near_F), and far flankers onl (Far_F). The target as centered at 8 eccentricit in the upper left visual quadrant, and its orientation as ~45 . The orientations of the flankers ere randoml selected for each trial. In a given trial, one of the five stimuli as presented for 250 ms. Then, after a 450 650 ms blank interval, a grating as presented for 100 ms in the lo er-right visual quadrant. The orientation of the grating slightl deviated from the vertical (Fig. 1*C*).

E periment 1 consisted of t o sessions: the attended session and the unattended session. In these t o sessions, subjects vie ed the same stimuli but performed different tasks. In the attended session, subjects al a s paid attention to the upper left visual quadrant and

2D). In the attended session, the suppression inde for the nearb condition as significantl lo er than that for the far condition ($t_{(19)} = 2.65$, $p < 0.05$). Ho ever, there as no significant difference bet een the t o conditions in the unattended session ($t_{(19)} = 0.33$, $p = 0.75$). The suppression indices ere submitted to a repeated-measures ANOVA ith attention status (attended and unattended) and distance (far and nearb) as ithin-subject factors. We found a significant interaction bet een attention status and distance ($F_{(1,19)} = 4.37$, $p < 0.05$). These findings demonstrate that, parallel to the behavioral cro ding effect, suppression can be modulated b target flanker distance. Moreover, spatial attention pla ed a significant role in the manifestation of this suppression.

We further e plored the link bet een the C1 suppression and the perceived cro ding (rather than the ph sical stimuli). We first ranked the strength of cro ding (i.e., the response accurac difference bet een the Near_T+F and Far_T+F stimuli) in 20 EEG blocks of the attended session for each subject. Then, these 20 blocks ere split into t o groups: 10 blocks ith the largest differences in the strong cro ding group and the remaining blocks in the eak cro ding group. For the strong and eak cro ding groups, the mean accurac differences ere 20.1 ± 1.61% and −0.20 ± 1.46%, respectivel . Subjects vie ed almost identical stimuli in the t o groups (because the orientations of the flankers and target ere randomi ed). The difference in the strength of cro ding could then be attributed to the fluctuation of perceptual processing. Suppression indices ere calculated for both groups. Onl in the strong cro ding group, the C1 suppression as found to be modulated b the target flanker distance (strong cro ding group: $t_{(19)} = 3.09$, $p < 0.01$; eak cro ding group: $t_{(19)} = 1.44$, $p = 0.17$; Figure 2E). The suppression indices ere submitted to a repeated-measures ANOVA ith cro ding strength (strong and eak) and distance (far and nearb) as ithin-subject factors. We found a significant interaction bet een cro ding strength and distance ($F_{(1,19)} = 5.88$, $p < 0.05$). These results suggest a close relationship bet een the C1 suppression and the perceived cro ding.

We also e amined the effect of attention on C1 amplitude and latenc . Paired *t* tests sho ed that there as no significant difference bet een the attended and unattended sessions for all five stimuli. This result sho ed that, although attention could modulate the interaction bet een the target and flankers, its effect on C1 amplitude and latenc as ver eak.

Experiment 2: C1 suppression and the radial–tangential anisotropy

The radial tangential anisotrop , hich refers to the phenomenon that radiall positioned flankers can induce a stronger cro ding effect than tangentiall positioned ones, is considered a diagnostic criterion of cro ding (Whitne and Levi, 2011). In the second ERP e periment, e e amined hether the C1 suppression as also related to the radial tangential anisotrop . If this ere the case, the C1 suppression ith radiall positioned flankers should be stronger than that ith tangentiall positioned ones. This e periment also had five stimuli: target onl (T), target ith flankers positioned radiall (Rad_T+F), target ith flankers positioned tangentiall (Tan_T+F), radial flankers onl (Rad_F), and tangential flankers onl (Tan_F) (Fig. 1B). The procedure and data anal sis ere similar to those used in the first ERP e periment.

In the attended session, subjects' response accuracies ith the T, Tan_T+F, and Rad_T+F stimuli ere 85%, 81.9%, and 71.2%, respectivel (Fig. 1E). The performance differences bet een the stimulus conditions ere significant, demonstrating that the presentation of flankers led to cro ding (Tan_T+F vs T: $t_{(19)} = 3.72$, $p < 0.01$; Rad_T+F vs T: $t_{(19)} = 8.76$, $p < 0.001$) and that the radial tangential anisotrop as evident (Rad_T+F vs Tan_T+F: $t_{(19)} = 8.08$, $p < 0.001$).

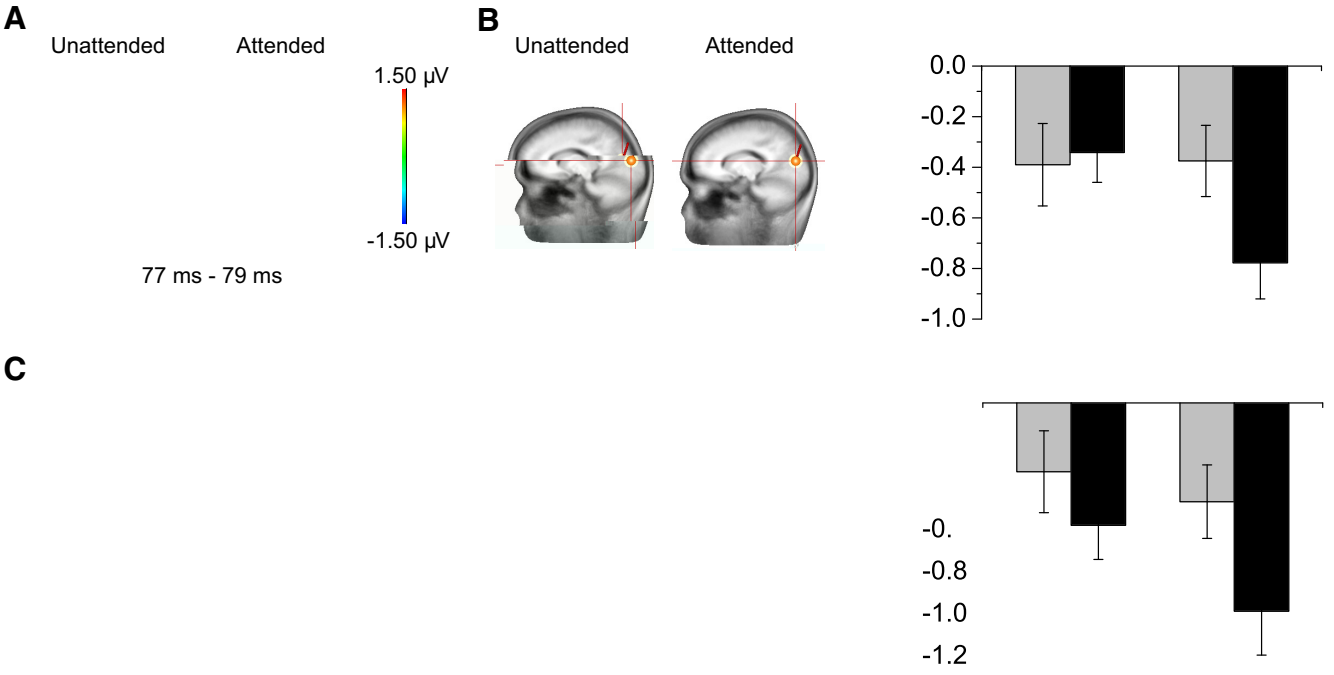
Figure 3A sho s C1 topographies averaged over all the five stimuli in the unattended and attended sessions. The C1 component had a peak latenc of ~78 ms. CP1, CPZ, P1, P3, and P had the largest C1 amplitudes. Dipole modeling confirmed that the intracranial source of the C1 component as located in V1 (Fig. 3B; Table 1). Computed from the C1 amplitudes sho n in Figure 3C, the suppression indices ere negative (Fig. 3D). In the attended session, the suppression inde for the radial condition as significantl lo er than that for the tangential condition ($t_{(19)} = 2.55$, $p < 0.05$), suggesting a stronger suppression ith the radial flankers than ith the tangential flankers, hich is consistent ith our prediction. Ho ever, in the unattended session, there as no significant difference bet een the t o conditions ($t_{(19)} = 0.29$, $p = 0.78$). The suppression indices ere submitted to a repeated-measures ANOVA ith attention status (attended and unattended) and orientation (radial and tangential) as ithin-subject factors. We found a significant interaction bet een attention status and orientation ($F_{(1,19)} = 5.66$, $p < 0.05$).

Similar to E periment 1, 20 EEG blocks ere split into t o groups: the strong radial tangential anisotrop group and the eak radial tangential anisotrop group. For the t o groups, the mean response accurac differences bet een the Rad_T+F and Tan_T+F stimuli (i.e., the magnitude of the radial tangential anisotrop) ere 20.5 ± 1.32% and 0.85 ± 1.35%, respectivel . Onl in the strong anisotrop group, the suppression inde for the radial condition as significantl lo er than that for the tangential group (strong group: $t_{(19)} = 2.97$, $p < 0.01$; eak group: $t_{(19)} = 1.38$, $p = 0.18$; Figure 3E). The suppression indices ere submitted to a repeated-measures ANOVA ith anisotrop strength (strong and eak) and orientation (radial and tangential) as ithin-subject factors. We found a significant interaction bet een anisotrop strength and orientation ($F_{(1,19)} = 4.49$, $p < 0.05$). Attention also had little effect on C1 amplitude and latenc for all the five stimuli in this e periment. Overall, these results suggest that the C1 suppression closel mirrors the radial tangential anisotrop of cro ding.

Experiment 3: cortical suppression and the target–flanker distance

Although the C1 suppression found in the ERP e periments suggests an earl V1 contribution to cro ding, the role of intermediate and high cortical areas in cro ding is still unclear. Parallel to the ERP e periments, t o event-related fMRI e periments ere designed to investigate the relationships bet een cortical suppression in different visual areas and the target flanker distance (E periment 3) as ell as the radial tangential anisotrop (E periment 4).

Because the target and flankers ere small and ere presented in peripher , it is difficult to use fMRI to separate their cortical representations and directl measure the effect of cro ding on the representation of the target. We modified the paradigm developed b Kastner et al. (1998) and Beck and Kastner (2005) to solve this problem. E periment 3 had t o trial t pes (conditions): far and nearb trials. In a far trial, the Far_T+F and Near_F stimuli ere presented successivel in a random order, each for 0.25 s. In a nearb trial, the Near_T+F and Far_F stimuli ere presented in the same a (Fig. 4A). Integrated over time, the ph sical stimulations in each location of the target and flankers ere identical in the t o conditions. Ho ever, relative to the far condition, subjects should e perience a stronger cro ding effect in the nearb condition because the target as presented ith the nearb flankers. Subjects under ent t o sessions: the attended session and the unattended session. In the attended



session, subjects performed the same orientation discrimination task ith the target as that in the ERP e periments. As predicted, their performance as better in the far condition (72.1%) than in the nearb condition (61.7%) ($t_{(9)} = 4.13$, $p < 0.01$, Fig. 4*B*). In the unattended session, subjects ere asked to ignore the stimuli and detect a brief luminance change at the fi ation point.

ROIs ere defined as cortical areas representing the locations of the target and flankers (Fig. 4*C*) in V1, V2, V3, V4, LO, and IPS. We anal ed BOLD signals in these ROIs in the nearb and far conditions (Fig. 5*A*). An signal difference bet een the t o conditions might be largel the result of different levels of cortical suppression bet een the target and flankers, rather than the ph sical stimuli per se (Beck and Kastner, 2005). We defined a suppression inde as $(BOLD_{Far}\text{-}BOLD_{Near})/(BOLD_{Far}+BOLD_{Near})$, here $BOLD_{Far}$ and $BOLD_{Near}$ are the peak amplitudes of BOLD signals in the far and nearb conditions, respectivel . If the mutual suppression bet een the target and flankers in the nearb condition is stronger than that in the far condition, $BOLD_{Far}$ should be larger than $BOLD_{Near}$. Thus, the suppression inde should be above ero; the

larger the inde , the stronger the suppression. We found that, in the attended session, the suppression indices ere significantl larger than ero in V1 ($t_{(9)} = 6.58, p < 0.001$), V2 ($t_{(9)} = 4.58, p <$

mutual suppression bet een the target and flankers in the radial condition is stronger than that in the tangential condition, $BOLD_{Tan}$ should be larger than $BOLD_{rad}$. Thus, the suppression inde should be above ero; the larger the inde , the stronger the suppression. We found that, in the attended session, V1 had the largest inde and onl the inde in V1 as significantl larger than ero (V1: $t_{(9)} = 4.58, p < 0.01$; Fig. 7*B*). In the unattended session, no area sho ed a significantl positive inde (all $t_{(9)} < 1.22$, $p > 0.25$) (Fig. 7*C*). For all the ROIs, e also performed a repeated-measures ANOVA of the peak amplitudes ith attention status (attended and unattended) and orientation (radial and tangential) as ithin-subject factors. V1 and V2 e hibited a significant interaction bet een attention status and orientation (both $F_{(1,9)} > 8.46$, $p < 0.05$), hich is generall in line ith the *t* test results.

Similar to E periment 3, e ranked the strength of the radial tangential anisotrop (i.e., the response accurac differ- ence bet een the radial and tangential conditions) in eight fMRI runs for each subject, then split these eight runs into the strong anisotrop group and the eak anisotrop group, ith four runs in each group. For the strong and eak anisotrop groups, the mean accurac differences ere $17.13 \pm 1.95\%$ and $2.24 \pm 2.75\%$, respectivel . Suppression indices ere calculated for both groups in V1. The suppression inde for the strong anisotrop group as significantl larger than that for the eak ansiotrop group ($t_{(9)} = 3.06, p < 0.05$) (Fig. 7*D*). We also performed a repeated-measures ANOVA of the peak amplitudes ith cro ding strength (strong and eak) and orientation (radial and tangential) as ithin-subject factors. V1 e hibited a significant interaction bet een cro ding strength and orientation ($F_{(1,9)} = 16.22, p < 0.01$). These results demonstrate a tight coupling bet een the cortical suppression in V1 and the radial tangential anisotrop of cro ding

Discussion

With a combination of ERP and fMRI approaches, e demonstrated that the orientation cro ding effect as closel associated ith the inhibitor interaction bet een the target and flankers, as manifested in the suppression of the C1 component and the V1 BOLD signal. Furthermore, the suppression as largel dependent on spatial attention. These results strongl suggest that attention-dependent V1 suppression contributes to cro ding at a ver earl stage of visual processing.

Our findings are of unique significance to understanding the neural mechanisms of cro ding. First, e provide the first piece of neuroph siological evidence regarding the temporal evolution of cro ding, hich goes significantl be ond previous fMRI studies (Fang and He, 2008; Bi et al., 2009; Freeman et al., 2011; Anderson et al., 2012; Millin et al., 2013). The ver short peak latenc (77 78 ms) of the C1 component unequivocall supports that cro ding originates in earl visual corte , as earl as V1. Second, e not onl sho that the earl cortical suppression is associated ith the target flanker distance and the radial tangential anisotrop but also demonstrate a close link bet een the suppression and the perceived cro ding. Third, our evidence is strong and converging. The fMRI observation that V1 is the onl area ith the suppression tightl tied to the strength of the perceived cro ding supports that the cro ding-related BOLD signal in V1 is unlikel feedback from higher cortical areas, consistent ith the ERP findings.

In a ver recent fMRI stud , Millin et al. (2013) manipulated the target flanker distance to modulate the strength of cro ding. The found that cro ding induced BOLD signal suppression in V1, even hen subjects ere performing a fi ation task and did not pa attention to the stimuli. Ho ever, e failed to find such suppression in the unattended session of E periment 3. Our and their e periments are different in man aspects, including stimulus, e perimental design, and data anal sis. Their stimuli ere presented closer to fi ation and longer than ours, hich could induce stronger BOLD signals. The block design used b them is more effective to detect BOLD signal changes than the event-related design e used here. Taking into account all these evidence, e suggest that the cro ding-induced cortical suppression could be modulated b at-

pla a role in this kind of cro ding (Louie et al., 2007). In the future, it ould be important to investigate hether our conclusion can be generali ed to other conditions and stimuli.

References

Anderson EJ, Dakin SC, Sch ar kopf DS, Rees G, Green ood JA (2012) The neural correlates of cro ding-induced changes in appearance. Curr Biol 22:1199 1206. CrossRef Medline

Bao M, Yang L, Rios C, He B, Engel SA (2010) Perceptual learning increases the strength of the earliest signals in visual corte . J Neurosci 30:15080 15084. CrossRef Medline

Beck DM, Kastner S (2005) Stimulus conte t modulates competition in human e trastriate corte . Nat Neurosci 8:1110 1116. CrossRef Medline

Bi T, Cai P, Zhou T, Fang F (2009) The effect of cro ding on orientation-selective adaptation in human earl visual corte . J Vis 9:1 10. CrossRef Medline

Bouma H (1970) Interaction effects in parafoveal letter recognition. Nature 226:177 178. CrossRef Medline

Bouma H (1973) Visual interference in the parafoveal recognition of initial and final letters of ords. Vision Res 13:767 782. CrossRef Medline

Buracas GT, Bo nton GM (2002) Efficient design of event-related fMRI e periments using M-Sequences. Neuroimage 16:801 813. CrossRef Medline

Clark VP, Hill ard SA (1996) Spatial selective attention affects earl e trastriate but not striate components of the visual evoked potential. J Cogn Neurosci 8:387 402. CrossRef Medline

Clark VP, Fan S, Hill ard SA (1994) Identification of earl visual evoked potential generators b retinotopic and topographic anal ses. Hum Brain Mapp 2:170 187. CrossRef

Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci 3:201 215. CrossRef Medline

Ding Y, Mart ne A, Qu Z, Hill ard SA (2013) Earliest stages of visual cortical processing are not modified b attentional load. Hum Brain Mapp

Dumoulin SO, Wandell BA (2008) Population receptive field estimates in human visual corte . Neuroimage 39:647 660. CrossRef Medline

Engel SA, Glover GH, Wandell BA (1997) Retinotopic organi ation in human visual corte and the spatial precision of functional MRI. Cereb Corte 7:181 192. CrossRef Medline

Fang F, He S (2008) Cro ding alters the spatial distribution of attention modulation in human primar visual corte . J Vis 8:1 9. CrossRef Medline

Flom MC, We mouth FW, Kahneman D (1963) Visual resolution and contour interaction. J Opt Soc Am 53:1026 1032. CrossRef Medline

Freeman E, Sagi D, Driver J (2001) Lateral interactions bet een targets and flankers in lo -level vision depend on attention to the flankers. Nat Neurosci 4:1032 1036. CrossRef Medline

Freeman J, Donner TH, Heeger DJ (2011) Inter-area correlations in the ventral visual path a reflect feature integration. J Vis 11:1 23. CrossRef Medline

Fu S, Fedota JR, Green ood PM, Parasuraman R (2010) Dissociation of visual C1 and P1 components as a function of attentional load: an event-related potential stud . Biol Ps chol 85:171 178. CrossRef Medline

Gandhi SP, Heeger DJ, Bo nton GM (1999) Spatial attention affects brain activit in human primar visual corte . Proc Natl Acad Sci U S A 96: 3314 3319. CrossRef Medline

Gilbert C, Ito M, Kapadia M, Westheimer G (2000) Interactions bet een attention, conte t and learning in primar visual corte . Vision Res 40: 1217 1226. CrossRef Medline

He S, Cavanagh P, Intriligator J (1996) Attentional resolution and the locus of visual a areness. Nature 383:334 337. CrossRef Medline

Kastner S, De Weerd P, Desimone R, Ungerleider LG (1998) Mechanisms of directed attention in the human e trastriate corte as revealed b functional MRI. Science 282:108 111. CrossRef Medline

Kell SP, Gome -Ramire M, Fo e JJ (2008) Spatial attention modulates initial afferent activit in human primar visual corte . Cereb Corte 18:2629 2636. CrossRef Medline

Kourt i Z, Kan isher N (2000) Cortical regions involved in perceiving object shape. J Neurosci 20:3310 3318. Medline

Levi DM (2008) Cro ding an essential bottleneck for object recognition: a mini-revie . Vision Res 48:635 654. CrossRef Medline

Levi DM, Klein SA, Aitsebaomo AP (1985) Vernier acuit , cro ding and cortical magnification. Vision Res 25:963 977. CrossRef Medline

Li W, Piech V, Gilbert C (2004) Perceptual learning and top-do n influences in primar visual corte . Nat Neurosci 7:651 657. CrossRef Medline

Li W, Piech V, Gilbert CD (2006) Contour salienc in primar visual corte . Neuron 50:951 962. CrossRef Medline

Liu T, Pestilli F, Carrasco M (2005) Transient attention enhances perceptual performance and fMRI response in human visual corte . Neuron 45:469 477. CrossRef Medline

Louie EG, Bressler DW, Whitne D (2007) Holistic cro ding: selective interference bet een configural representations of faces in cro ded scenes. J Vis 7:1 11. CrossRef Medline

Luck SJ, Chela i L, Hill ard SA, Desimone R (1997) Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual corte . J Neuroph siol 77:24 42. Medline

Mart ne A, Anllo-Vento L, Sereno MI, Frank LR, Bu ton RB, Dubo it DJ, Wong EC, Hinrichs H, Hein e HJ, Hill ard SA (1999) Involvement of striate and e trastriate visual cortical areas in spatial attention. Nat Neurosci 2:364 369. CrossRef Medline

Miller EK, Gochin PM, Gross CG (1993) Suppression of visual responses of neurons in inferior temporal corte of the a ake macaque b addition of a second stimulus. Brain Res 616:25 29. CrossRef Medline

Millin R, Arman AC, Chung STL, Tjan BS (2013) Visual cro ding in V1. Cereb Corte 7:1 9. CrossRef Medline

Moran J, Desimone R (1985) Selective attention gates visual processing in the e trastriate corte . Science 229:782 784. CrossRef Medline

Nand AS, Tjan BS (2012) Saccade-confounded image statistics e plain visual cro ding. Nat Neurosci 15:463 469. CrossRef Medline

Pelli DG (2008) Cro ding: a cortical constraint on object recognition. Curr Opin Neurobiol 18:445 451. CrossRef Medline

Pourtois G, Grandjean D, Sander D, Vuilleumier P (2004) Electroph siological correlates of rapid spatial orienting to ards fearful faces. Cereb Corte 14:619 633. CrossRef Medline

Sereno MI, Dale AM, Reppas JB, K ong KK, Belliveau JW, Brad TJ, Rosen BR, Tootell RB (1995) Borders of multiple visual areas in humans revealed b functional magnetic resonance imaging. Science 268:889 893. CrossRef Medline

Smith AT, Singh KD, Williams AL, Greenlee MW (2001) Estimating receptive field si e from fMRI data in human striate and e trastriate visual corte . Cereb Corte 11:1182 1190. CrossRef Medline

Stettler DD, Das A, Bennett J, Gilbert CD (2002) Lateral connectivit and conte tual interactions in macaque primar visual corte . Neuron 36: 739 750. CrossRef Medline

Strasburger H (2005) Unfocussed spatial attention underlies the cro ding effect in indirect form vision. J Vis 5:1024 1037. CrossRef Medline

Tjan BS, K on M, Millin R, Bao P (2012) Cro ding modulates activit in V1. J Vis 12:598. CrossRef

Watson AB, Pelli DG (1983) Quest: a Ba esian adaptive ps chometric method. Percept Ps choph s 33:113 120. CrossRef Medline

Whitne D, Levi DM (2011) Visual cro ding: a fundamental limit on conscious perception and object recognition. Trends Cogn Sci 15:160 168. CrossRef Medline