S atial , ai e ealed i he ea lie   i al e ked c   e C1 a d he effec f a e i   i li ea i

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[1]*D m B B , , B ,*
C ; [2] - C , , B , C ;
[3] *- D / B , , B , C*

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Chen J, Yu Q, Zhu Z, Peng Y, Fang F. S atial , ai e ealed i he ea lie   i al e ked c   e C1 a d he effec f a e i   i li ea i . 115: 500 509, 2016. Fi bli hed N e be 11, 2015; d i:10.1152/j .00044.2015. I a al ce e , l i le bjec a e all e e ed i la e l . H d eci c a ea f he b ai   e d l i le bjec ba ed hei e e   each i di id al bjec ? P e i f c i al ag e ic e a ce i agi g (fMRI) die ha e h ha he ac i i i d ced b a l i bjec i l i he i a i al c e (V1) ca be edic ed b he li ea   li ea   f he ac i i ie i d ced b i c e bjec . H e e , he e ha bee li le e ide ce f elec e ce hel g a (EEG) die fa . He e e e l ed h V1 e ded l i le bjec b c a i g he EEG ig al e ked b a h ee-g a i g i l i h h e e ked b i c e (he ce al g a i g a d 2 a ki g g a i g). We f c ed he ea lie i al c e C1 (e la e c f ~50) beca e i ha bee h e ec he feedf a d e e f e   i V1. We f d ha   he he i l a   a e ded, he a li de f he C1 e ked b he h ee-g a i g i l   ghl e aled he f he a li de f he C1 e ked b i c e , ega dle f he di a ce be ee   he e g a i g . Whe he i l a a e ded, hi li ea   a ial ai e i ed l he he h ee g a i g   e e fa a a f each he . Whe he h ee g a i g   e e cl e   each he , he a ial ai beca e c e ed. The e e l gge   ha he ea lie i al e ei V1 f ll a li ea ai le he a e i i l ed a d ha a e i ca affec he ea lie i e ac i be ee l i le bjec .

a e i ; a ial ai ; li ea i ; l i le bjec ; ERP ; C1; V1; P1; N150; BESA ce a al i

OBJECT RECOGNITION IS A BASIC f c i f he i al e . I a al ce e , bjec a e all cl e ed. De i e hi , he aj i f e i l c d c ed die ha e f c ed l h a i gle bjec i ce ed i he i al e . A a e l , al h gh i a c , ai al e cie ce, i i ill clea h he i al e e d l i le bjec ba ed i e e each i di id al bjec . Whe c - ai al del e e e abli hed, edic he e e f e   b ai a ea a l i bjec i l , he f e a ed ha he e e hi l i bjec i l c ld be edic ed a he f he i di id al e e each f i c e (D li a d Wa dell 2008; Wal he e al. 2005). H e e , he e ha bee li le e ide ce f hi - ai , e e i he ea lie i al c ical a ea V1. Si gle- i ec di g die ha e f c ed e a ia e a ea (Ga e a d Ma i 2002; L ck e al. 1997; Olek iak e al. 2011; Reca e e al. 1997; Z cc la e al. 2005) a d h ed ha i he e a ea e al e e a l i bjec i l c ld be edic ed b ei he he eigh ed a e age he ai e e i c i e c e . H e e , beca e he ece i e eld f e i V1 a e all c e   l i le bjec , e fe elec h i l gical die ha e ied ackle h V1 e d l i le bjec a he 9(V1)-3[(9(a e)-[(9iKa d)-[(9(al.)-[(94(2005-[(93813BESA-[(9PihlajaE participants attended to the stimulus positions) and unattended (i.e., participants attended away from the stimulus positions) conditions. One important property of C1 is that the C1 evoked by a stimulus in the upper visual field has a negative amplitude, whereas the C1 evoked by a stimulus in the lower visual field has a positive amplitude. To confirm the validity of the ERP component C1 we examined and the generalizability of our effects, we performed the same experiment in both the upper (*Experiment 1*) and lower visual field (*Experiment 2*).

METHODS

Twenty-five participants (12 males, 13 females) participated in *Experiment 1*, and 21 participants (13 males, 8 females) participated in *Experiment 2*. One participant's data (male) in *Experiment 1* and two participants' data (1 male and 1 female) in *Experiment 2* were discarded due to strong alpha waves in their EEG signal (Luck 2005). All participants were right-handed and reported normal or corrected-to-normal vision. Ages ranged from 18 to 25. All participants gave written informed consent in accordance with the procedure and protocols approved by the human participants review committee of Peking University.

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Experiment 1. All stimuli consisted of circular sinusoidal gratings (diameter = 2.36°; spatial frequency = 2.54 c/d; full contrast; mean luminance = 61.47 cd/m^2). The background had the same luminance as the mean luminance of the gratings. The orientation of the grating in the center was either +45° or −45° while the orientation of the two flanking gratings were independently and randomly selected from 0° to 180° for each trial.

Five stimulus configurations were used: one grating (One), two close gratings (Two_close), two distant gratings (Two_distant), three close gratings (Three_close, created by combining the one grating with the two close gratings in space), and three distant gratings (Three_distant, created by combining the one grating with the two distant gratings in space) (Fig. 1*A*). The center-to-center distance between close gratings was 2.48°, and the distance between distant gratings was 5.07°. The stimulus was centered at 8° eccentricity in the upper left visual quadrant. The fixation was a point at the center of the screen. A chinrest was used to stabilize the head position. All visual stimuli were displayed on a ViewSonic color graphic monitor (refresh rate: 75 Hz; resolution: 1,024 × 768; size: 22 in.) with a gray background at a viewing distance of 73 cm.

Each trial began with a stimulus (the first stimulus) presented in the upper left visual field for 500 ms. This stimulus was randomly selected from the five stimulus configurations. After a blank interval (jittered between 200 and 400 ms), two gratings (the second stimulus) with orientations slightly different from the vertical were presented for 100 ms. One was presented in the same position as the central grating of the first stimulus (i.e., upper left visual field), and the other was presented in the diagonally opposite position to the central grating of the first stimulus (i.e., lower right visual field). The two gratings were to attract participants' attention to the quadrant that was the same as the quadrant of the stimulus or the quadrant that was diagonally opposite the quadrant of the stimulus. Specifically, in the attended session, participants were instructed to judge the orientation of the upper left grating (left or right, relative to vertical orientation) of the second stimulus, which attracted their attention to the same quadrant as the stimulus. In the unattended session, participants were instructed to judge the orientation of the lower right grating of the second stimulus, which attracted their attention to the diagonally opposite quadrant of the stimulus. Two dashed circles were always presented on the screen to indicate the positions of the two gratings (Fig. 1*B*). It should be noted that the procedure in both sessions were identical. The task in both sessions were stimulus-irrelevant (i.e., irrelevant to the first stimulus), preventing participants from selectively attending to a specific stimulus configuration. The difference between the orientation of a task-relevant grating (the upper left grating in the attended session or the lower right grating in the unattended session) of the second stimulus and the vertical orientation was adjusted to keep participants' performance level at ~80% correct.

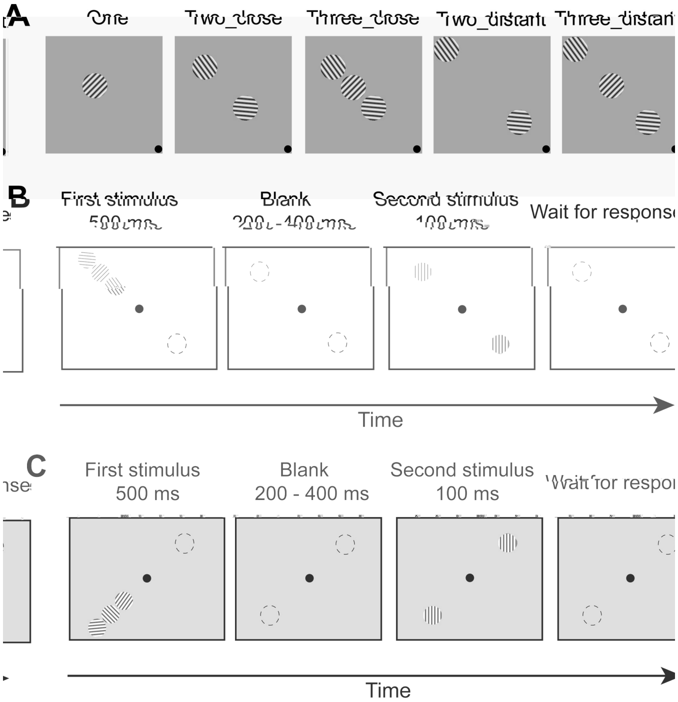

Fig. 1. Stimuli and procedure of *Experiment 1* and *Experiment 2*. *A*: 5 figure configurations were used as stimuli. *B*: procedure for a trial in both the attended (i.e., attended to the stimulus quadrant) and unattended (i.e., attended away from the stimulus quadrant) sessions of *Experiment 1*. In the attended session, participants were instructed to judge the orientation of the grating in the upper left visual field of the second stimulus, while in the unattended session, participants judged the orientation of the grating in the lower right visual field of the second stimulus. *C*: procedure of *Experiment 2* was identical to that of *Experiment 1*. The only difference was in the positions of the first and second stimuli.

The attended and unattended sessions were performed in different days in a counterbalanced order across participants. The color of the fixation point was red or green to indicate whether a session was attended or unattended (also counterbalanced across participants), respectively. There were 20 blocks in each session. Each block consisted of 100 trials, 20 trials for each of the 5 stimulus configurations, presented in a random order. Therefore, for each stimulus configuration, there were 400 trials in total. Although we did not record the orientation of the flanking grating for each condition, the orientation of the flanking gratings in the two-grating conditions (i.e., Two_close and Two_distant) and those in the three-grating conditions (i.e., Three_close and Three_distant) should have been balanced, given that the orientation of the two flanking gratings was independently and randomly selected from 0° to 180° in each trial and there were 400 trials for each condition. To prevent eye movements toward the target location, all subjects were trained to maintain fixation before they started the EEG experiments. We repeatedly emphasized the importance of maintaining fixation throughout the experiments. The eye movement data of four naive subjects were collected when they performed the same experiments with the same procedure. The main-s deviation from the fixation point for all subjects was <1°, which suggested that these subjects can well maintain their gaze position at the center of the screen.

Experiment 2. The aim of this experiment was to replicate the results of *Experiment 1* with stimuli in the lower visual field. Therefore, the stimuli and procedure of *Experiment 2* were identical to those of *Experiment 1*, and only the stimulus position differed. That is, in *Experiment 2*, the first stimulus was in the lower left visual quadrant. One of the gratings of the second stimulus was in the lower left visual field. The other was in the upper right visual field (Fig. 1*C*).

Scalp EEG was recorded from 64 Ag/AgCl electrodes positioned according to the extended international 10–20 EEG system. Vertical electro-oculogram (VEOG) was recorded from an electrode placed above the right eye. Horizontal EOG (HEOG) was recorded from an electrode placed at the outer canthus of the left eye. Electrode impedance was kept below 5 kΩ. EEG was amplified with a gain of 500 K, band-pass filtered at 0.05–100 Hz, and digitized at a sampling rate of 1,000 Hz. The signals on these electrodes were referenced online to the nose and were re-referenced offline to the average of two mastoids.

EEG Analysis

Only the EEG signals induced by the first stimulus were analyzed. Offline data analysis was performed with Brain Vision Analyzer (Brain Products, Munich, Germany). The EEG data were first low-pass filtered at 30 Hz and then epoched starting at 100 ms before the stimulus onset and ending 300 ms after stimulus onset. Each epoch was baseline-corrected against the mean voltage of the 100-ms prestimulus interval. The epochs contaminated by eye blinks, eye movements, or muscle potentials exceeding ±50 μV at any electrode were excluded from the average. The remaining epochs were averaged for each stimulus configuration. To select electrodes for the amplitude and latency calculation, grand-averaged ERP waves were made by averaging signal across participants and stimulus configurations, but separately for the attended and unattended sessions. The five electrodes with the largest C1 amplitudes were chosen for further analysis. To quantify the C1 amplitude and latency of each stimulus configuration for each participant, the waveforms across these five electrodes were first averaged to construct an average waveform. Then, the mean amplitude of the 11 ms time window around the C1 peak of the averaged waveform was measured as the C1 amplitude. The peak time point of the averaged waveform between 50 and 90 ms was measured as the C1 latency.

Estimation of the dipole source was performed with the BESA algorithm (BESA research 6.0), as described by Clark and Hillyard (1994). The C1 component was modeled based jointly on the grand-averaged waveforms elicited by all five stimulus configurations. The waveform in the 5-ms interval around the peak time (between 80 and 84 ms in both experiments) was isolated with one dipole with free location and orientation.

For comparison, we also examined the spatial summation effect in the ERP component following C1. When the stimulus was in the upper left visual field (*Experiment 1*), the following component was P1 with its peak amplitude in the right parietal occipital scalp site. It is believed that P1 reflects extrastriate activation (Di Russo et al. 2002; Martinez et al. 1999). When the stimulus was in the lower left visual field (*Experiment 2*), the following component in the posterior scalp site was N150, which has been shown to have a source in the extrastriate cortex (Di Russo et al. 2002). The same method was used to measure the amplitude and latency of P1 and N150.

RESULTS

Experiment 1: Upper Visual Field

Behavioral data. In the attended session, participants discriminated the orientation of the upper left grating of the second stimulus. This was to attract participants' attention to the quadrant where the first stimulus was presented. We did not ask participants to respond to the first stimulus directly because in that case their attention level might differ due to stimulus complexity difference. The response accuracies of the five configuration conditions were as follows: One, 77.4 ± 0.89%; Two_close, 82.3 ± 0.82%; Three_close, 80.3 ± 0.71%; Two_dist, 83.2 ± 0.86%; and Three_dist, 80.4 ± 0.82%. The main effect of the stimulus was significant [repeated-measures ANOVA, $F_{(4,92)} = 4.36$, $P = 0.003$]. The accuracies in stimulus conditions with one grating in the center (One, Three_close, and Three_dist) were significantly smaller than those without a grating in the center (Two_close and Two_dist) [paired t-tests, all $t(23) > 2.43$, $P < 0.03$]. This is probably because the stimuli with a central grating served as forward masks to the upper left grating of the second stimulus. However, the main effect of distance was not significant [repeated-measures ANOVA, $F_{(1,23)} = 0.127$, $P = 0.725$], which suggests that participants were equally involved in the tasks in both the close and the distant grating conditions.

In the unattended session, participants discriminated the orientation of the lower right grating of the second stimulus. The response accuracies of the five configuration conditions were as follows: One, 81.4 ± 0.87%; Two_close, 82.5 ± 0.86%; Three_close, 82.3 ± 0.85%; Two_dist, 81.8 ± 0.95%; and Three_dist, 82.3 ± 0.93%. The main effect of the stimulus was not significant [repeated-measures ANOVA, $F_{(4,92)} = 1.44$, $P = 0.227$], which suggests that participants were equally involved in all conditions. Taken together, these behavioral results suggest that any ERP difference between close and distant grating conditions cannot be attributed to different levels of cognitive involvement.

ERP data. The second stimulus was to attract participants' attention to a specific quadrant. We only analyzed signals evoked by the first stimulus. To get the topograph of C1, we averaged the ERPs of all stimulus configurations for the attended and unattended sessions separately. Consistent with previous studies (Bao et al. 2010; Clark et al. 1994), the C1 evoked by stimuli in the upper left visual field had the largest amplitude in the left occipital parietal scalp site (Fig. 2*A*, upper left quadrant, for unattended and attended panels). The five electrodes with the largest C1 were chosen for further analysis. These were CP1, CP3, P1, P3, and P5 in both the attended and unattended conditions (Fig. 2*A*, within the black ellipse). Figure 2*B* shows the waveforms for each of the five stimulus conditions in separate panels, averaged across all participants and five electrodes. The C1 peak latency was between 80 and 84 ms after stimulus onset.

To examine whether the linear spatial summation existed for close and distant gratings in the attended and unattended sessions, we added peak amplitude of the C1 induced by one grating (i.e., One) to that induced by two gratings (i.e., Two_close or Two_dist) and compared the summed peak with the peak amplitude of the C1 induced by three gratings (Three_close or Three_dist; Fig. 3*A*). It should be noted that these three gratings overlapped the positions of the one grating

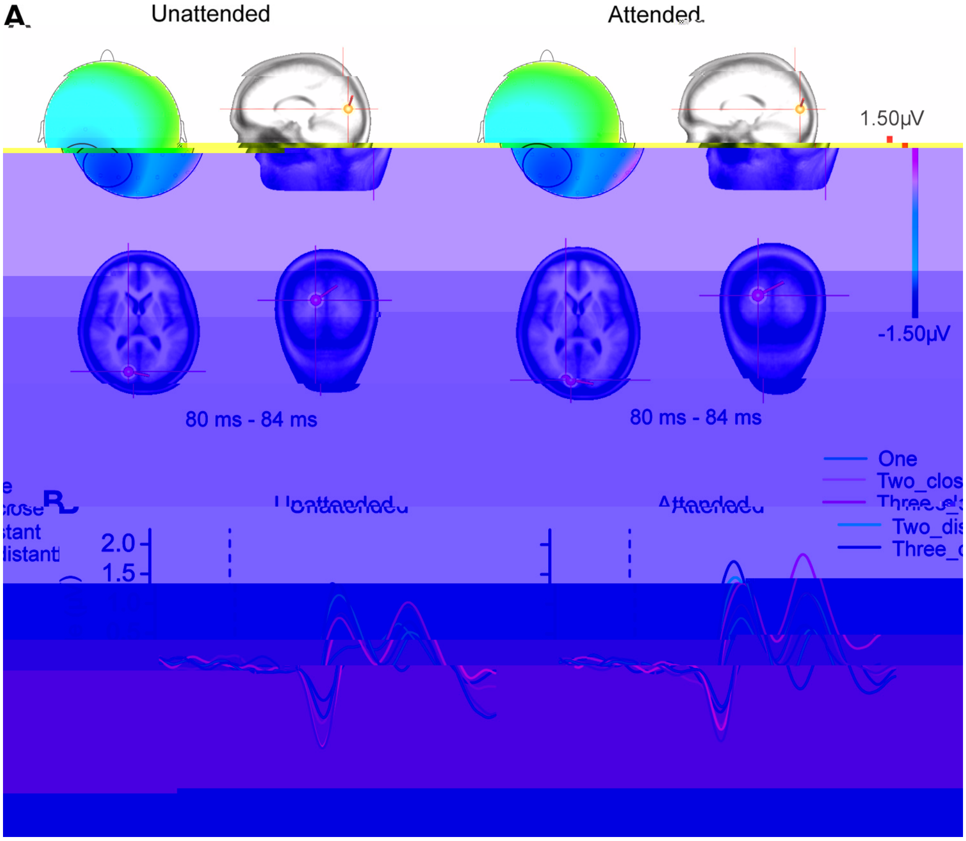

Fig. 2. Event-related potential (ERP) results for the attended and unattended sessions in Experiment 1. *A*: Upper left quadrant of each panel shows the C1 topographies in response to the 1st stimulus, averaged over all 5 stimulus conditions and participants. Posterior electrodes, including CP1, CP3, P1, P3, and

and two grating. In the unattended session, regardless of the distance between gratings, the summed amplitude ($C1_{One} + C1_{Two}$) was not significantly different from the C1 amplitude of three grating ($C1_{Three}$) [$C1_{One} + C1_{Two}$ vs. $C1_{Three}$: close, $t(23) = -1.69$, $P = 0.10$; distant, $t(23) = -0.53$, $P = 0.60$], which suggests that in the unattended condition, C1 follows a linear spatial summation rule. However, in the attended session, although the linear summation still existed for distant grating [$C1_{One} + C1_{Two}$ vs. $C1_{Three}$, $t(23) = -1.51$, $P = 0.14$], $C1_{Three}$ was significantly smaller than the sum for close grating [$C1_{One} + C1_{Two}$ vs. $C1_{Three}$, $t(23) = -5.71$, $P < 10^{-6}$], indicating suppressive interaction between close grating. An alternative way, however, is to sum up the waveform of one grating and two grating and then compare the peak of the C1 of the summed waveform with the peak of C1 induced by the three grating (Miller et al. 2015). In the current study, there was no significant latency difference between different conditions [paired t-tests, all $t(23) < 1.76$, $P > 0.092$]; therefore, this method should produce similar results to our method. We also analyzed the data with this method, and indeed, similar results were observed.

We defined suppression index as ($C1_{One} + C1_{Two}$) − $C1_{Three}$ to further examine how distance and attention influence the interaction between grating (Fig. 3*B*). The suppression index should be zero if the signal follows a linear summation rule and should be negative if the signals are subadditive. Seventeen out of the 24 participants showed a negative suppression index in the close condition when the stimuli were attended, but fewer participants showed a negative suppression index in the other three conditions (14 in the distant condition when the stimuli were attended, 11 and 12 in the close and distant conditions, respectively, when the stimuli were unattended). Repeated-measure ANOVA showed that the interaction between attention and distance was significant [$F_{(1,20)} = 18.83$, $P = 0.003$]. Paired t-tests showed that attention increased the suppressive interaction between close grating [$t(23) =$

−2.91, = 0.008] b di a g a i g [(23) = −0.58, = 0.56]. A C1 ha a eak la e c f 80 - 84 af e i l e, he e e l gge ha a ial a e i i c ea ed he e i e i e ac i be wee cl e bjec , b di a bjec , a ea l a 80 af e i l e.

conditions were also small, it is unclear whether the spatial summation reflected in P1 also followed a linear summation rule when the stimuli were unattended. In the attended condition, $P1_{Three}$ was smaller than $P1_{One}$, regardless of the distance between gratings [$P1_{One}$ vs. $P1_{Three}$: close, $t(23) = 5.24$, $P < 0.001$; distant, $t(23) = 3.63$, $P = 0.001$]. Therefore, the linear spatial summation relationship of P1 did not exist when the stimuli were attended. In addition, consistent with previous reports (Di Russo et al. 2003; Fu et al. 2010; Heinze et al. 1994; Mangun et al. 1998; Martinez et al. 1999; Woldorff et al. 1997), we found that the amplitude of P1 evoked by a single stimulus was significantly enhanced by attention [main effect of attention, $F_{(1,23)} = 10.25$, $P = 0.004$; paired t-test, all $P < 0.02$ except for the Two_distant condition, $t(23) = 1.00$, $P = 0.32$].

Experiment 2:

One typical property of C1 is that its polarity reverses when the stimulus location changes from the upper visual field to the lower (or vice versa). That is, a stimulus in the upper visual field evokes a negative C1 while a stimulus in the lower visual field evokes a positive C1. To confirm that the conclusions of *Experiment 1* were not specific to the upper visual field, we replicated *Experiment 2* in the lower visual field. Specifically, in *Experiment 2*, the stimulus was in the lower left visual field; the two gratings of the second stimulus were in the lower left and upper right visual fields, respectively (Fig. 1*C*).

Behavioral results. In line with *Experiment 1*, we compared the orientation judgment accuracies in all conditions to confirm that participants did not selectively attend to specific distance conditions (close vs. distant grating conditions). In the attended session, participants discriminated the orientation of the gratings of the second stimulus in the lower left visual field. The accuracies in the second grating conditions were as follows: One, 80.3 ± 1.71%; Two_close, 83.4 ± 1.29%; Three_close, 82.1 ± 1.64%; Two_distant, 83.5 ± 1.37%; and Three_distant, 80.7 ± 1.65%. The accuracies in stimulus conditions with the central grating (One, Three_close, and Three_distant) were significantly smaller than those without the central grating (Two_close and Two_distant; paired t-test, all $P < 0.04$). However, as predicted, the main effect of distance (close vs. distant) was not significant [$F_{(1,23)} = 1.39$, $P = 0.25$].

In the unattended session, participants discriminated the orientation of the crossing grating in the upper right visual field. The accuracies in the second grating conditions were as follows: One, 85.4 ± 1.93%; Two_close, 85.7 ± 1.90%; Three_close, 85.6 ± 1.79%; Two_distant, 86.6 ± 1.95%; and Three_distant, 86.7 ± 1.74%. The main effect of distance (close vs. distant) was not significant [$F_{(1,23)} = 0.85$, $P = 0.37$].

ERP results. Consistent with previous studies (Bao et al. 2010; Clark et al. 1994), the C1 of the stimulus in the lower left visual field had the largest amplitude in the right posterior occipital scalp site and the amplitude was positive (color map in Fig. 5*A*). The electrodes with the largest C1 amplitude were P2, P4, P6, PO4, and PO8 (indicated by the black ellipse in Fig. 5*A*). The peak latencies of the C1 averaged across

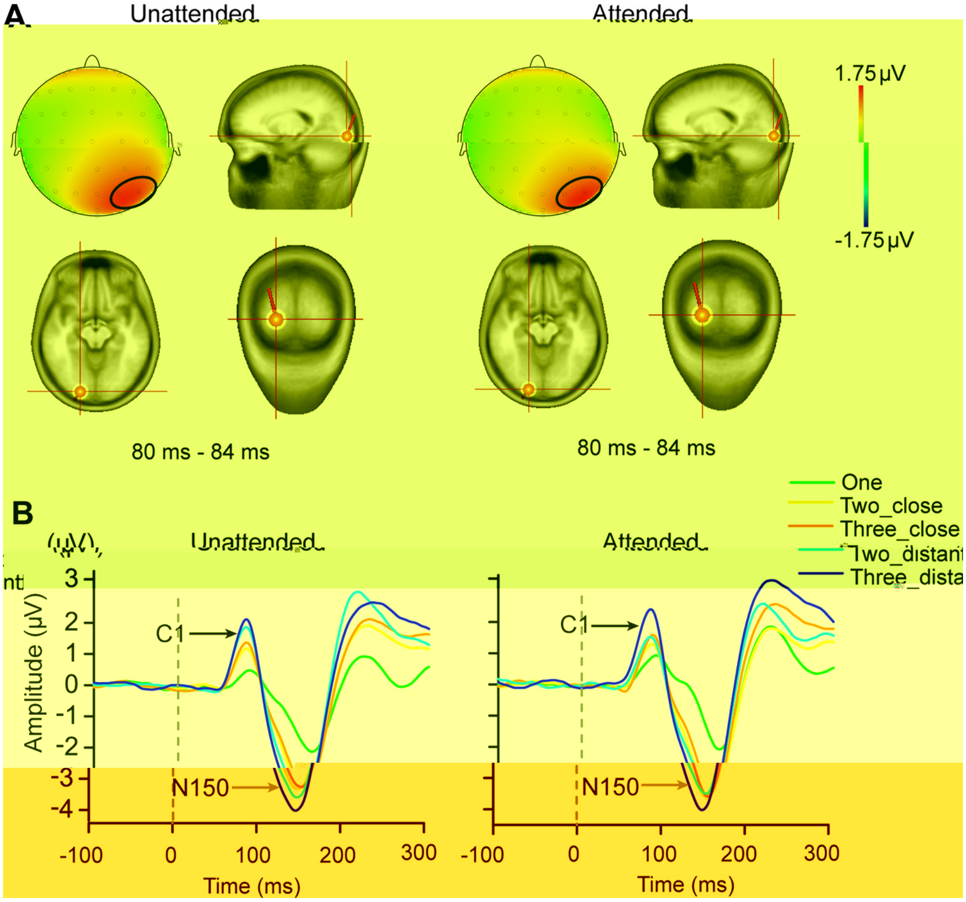

Fig. 5. ERP results for the attended and unattended sessions in *Experiment 2*. *A*: upper left quadrants of each panel show the C1 topographies in response to the stimuli averaged over all 5 stimulus conditions and participants. Posterior electrodes, including P2, P4, P6, PO4, and PO8 (within the black ellipse), had the largest C1 amplitudes. The other three quadrants show the location of a single dipole that best accounted for the variance in the C1 scalp voltage distribution. *B*: ERPs averaged over the 5 electrodes and all participants for each stimulus condition. C1 waves are indicated by black arrows. N150 waves are indicated by gray arrows.

a ici a f e i l c g a i e e be ee 80 a d 84 af e i l e.

D e he fac ha ei he he ai effec f a e i [$_{(1,18)}$ = 0.06, = 0.809] he ai effec f i l c g a i [$_{(4,72)}$ = 0.805, = 0.526] C1 la e c a ig i ca , e a al ed he da a i g i ila e h d a i *m 1*. We f d ha he he i li e e a e ded, C1 f ll ed li ea a ial , a i ega dle f he di a ce be ee g a i g [C1$_{\mathrm{O\ e}}$ + C1$_{\mathrm{T}}$. C1$_{\mathrm{Th\ ee}}$: cl e, (18) = 1.42, = 0.17; di a , (18) = 1.10, = 0.29]. H e e , he he i li e e a e ded, C1$_{\mathrm{Th\ ee}}$ a ig ifica l alle ha C1$_{\mathrm{O\ e}}$ + C1$_{\mathrm{T}}$ f cl e g a i g [(18) = 3.63, = 0.002] b f di a g a i g [(18) = 0.24, = 0.81]. Thi gge ha he e e e e i e i e ac i be ee cl e g a i g b be ee di a g a i g he he i li e e a e ded (Fig. 6*A*). The e i i de a al de ed e a i e h di a ce a d a e i i e ce he i e ac i be ee g a i g (Fig. 6*B*). U like *m 1*, he e i i de h ld be i i e beca e he C1 a i i e. Fif ee f he 19 a ici a h ed a i i e e i i de i he cl e c di i he he i li e e a e ded, b fe e a ic i a h ed a i i e e i i de i he he h ee c di i (10 i he di a c di i he he i li e e a e ded, 12 a d 9 i he cl e a d di a c di i , e ec i el , he he i li e e a e ded). Re ea ed ea e ANOVA h ed ha he i e ac i be ee a e i a d di a ce a ig i ca [$_{(1,18)}$ = 4.57, = 0.046]. A ai ed - e h ed ha he i c ea e f e i e i e ac i ca ed b a e i a cl e ig i ca be ee cl e g a i g [(18) = 2.08, = 0.051] b a fa f ig i ca be ee di a g a i g [(18) = −0.669, = 0.512]. Whe he i li e e a e ded, i11Tf.29 2.1F11Tf77 ig i ca 8a31g D[20T,.29 2.1F1bad di i 8) adif d i di hecl ec di i ad ad i he di aad c di i .d Whe he i li e e a e ded,

g a i gd he e a ig i ca 8a3-242.3 e la3-242.3150a3-242.3 g if d i d h e he e l dha *m 1* be largely accounted for by a single dipole in V1, suggesting that C1 was mainly generated in V1. Taken together, we conclude that *1*) the earliest visual evoked component, C1, which reflects the population response of neurons in V1, follows linear spatial summation when the stimuli not attended; and *2*) attention can modulate the interaction between objects in V1 as early as 80 ms after stimulus onset, especially when the objects are close to each other in space.

It should be noted that although a similar design has been used in our previous study (Chen et al. 2014), in which we also provided evidence that spatial attention can modulate the earliest interaction between flanking gratings, the current study is not a simple replication of our previous study. The current study was designed to examine whether the earliest visual signal reflected in C1 follows a linear spatial summation rule, whereas the previous study was designed to investigate the neural mechanism of crowding. Due to the purpose difference, we asked participants to perform different tasks in the two studies. As the previous study was designed to examine the neural mechanism of crowding (i.e., the deleterious influence of the flankers on the recognition of a target), participants were asked to perform a target-related task (i.e., reporting the target orientation) in the attended condition. The task was thus more difficult for the close condition than for the distant condition. Although, to our knowledge, no evidence has shown that task difficulty influences the earliest visual signals, it is still worth testing it using a stimulus-irrelevant task (such as that we used in the current study that participants respond to the second instead of the stimuli). In this case, the task difficulty difference between different conditions would not affect our results. Moreover, in the current study, we conducted experiments in both the upper and lower visual fields, which provided more convincing support for our conclusions.

Implications for Spatial Summation in C1

Our results have important implications in understanding how the visual system integrates responses to individual objects to generate responses to multiple objects simultaneously (i.e., spatial summation). In previous research, most of the single-unit studies have focused on extrastriate areas because the receptive fields of V1 neurons are too small to cover multiple objects. They showed that in V2 (Luck et al. 1997), V4 (Gawne and Martin 2002), V7a (Oleksiak et al. 2011), IT (Zoccolan et al. 2005), and MT (Recanzone et al. 1997), neuronal responses to multiple stimuli can be predicted by either the weighted average or the maximum of the responses of the component stimuli. Some researchers have proposed even more complicated algorithms, such as divisive inhibition (Britten and Heeger 1999; Simoncelli and Heeger 1998). In any case, these results suggest that spatial summation in extrastriate areas follows nonlinear rules (maximum, weighted average, or divisive inhibition).

Although it is difficult to explore how an individual neuron in V1 responds to multiple objects, we can examine how neurons in V1 respond to multiple objects at the neuronal population level with fMRI. Hansen et al. (2004) assessed the linearity of spatial summation by comparing the activation in checkerboard wedges and rings with sums of activation to their component patches and found that the responses of voxels in V1 were well predicted by linear spatial summation (but also see Pihlaja et al. 2008 and Vanni et al. 2005). However, a recent study (Kay et al. 2013) found that compressive spatial summation was observed in V1 and grew more pronounced in relatively anterior extrastriate areas. This is consistent with the previous fMRI finding that V1 showed the smallest difference between sequential presentation and simultaneous presentation among V1–V4 (Kastner et al. 1998). In the higher-level category-selective visual areas, such as Fusiform Face Area (FFA) and Parahippocampal Place Area (PPA), Reddy et al. (2009) found that the fMRI signal to simultaneously presented categories can be predicted by the weighted average of signals to individually presented categories. To sum up, although conflicting, among areas from V1 to V4 and other higher level visual areas, V1 has been shown to have the most similar response pattern to linear spatial summation.

Our linear summation results revealed in C1 are consistent with the aforementioned fMRI results (Hansen et al. 2004). This in turn provides compelling support to consider C1 as a measure of early visual signals in V1. Moreover, the high temporal resolution of EEG ensures that our results are less likely to be caused by feedback signals from higher level cortical areas, compared with the fMRI results. Our results showed that although linear spatial summation does exist in V1, this linear relationship is conditional: it depends on both the attentional state of the participants and the spatial layout of the stimuli. When attention is not involved, or when the attended objects are far from each other, V1 exhibits linear summation behavior; however, when the attended objects are close to each other, linear summation disappears.

In addition, our results showed that linear summation occurs as early as 80 ms after stimulus onset but does not persist after 122 ms, i.e., the linear summation results were not observed in P1 or N150 in our experiments. As C1 reflects the activities in V1, and P1 and N150 reflect the activities in extrastriate visual cortex (V2, V3, etc.), this difference again suggests that the linearity of spatial summation disappears gradually from striate to extrastriate cortex, which is consistent with previous evidence (Miller et al. 2015). Our results are also consistent with previous magnetoencephalography (MEG) (Supek et al. 1999) and electrocorticography (ECoG) results (Winawer et al. 2013). Specifically, Supek et al. (1999) observed linear spatial summation up to 150 ms after stimulus onset with MEG. Winawer et al. (2013) reported that the stimulus-locked component of ECoG responses has an approximate linear spatial summation, but the broadband asynchronous component of ECoG responses is subadditive. They suggested that the stimulus-locked component of ECoG reflects a brief, transient response to contrast, similar to our C1 response, whereas the broadband component reflects a longer, sustained response that covers several transient periods, similar with our later ERP components such as P1 and N150.

Implications for the Neural Mechanism of Attention

Our results also have important implications for the neural mechanism of spatial attention. On one hand, whether or not attention can modulate C1 amplitude has long been a controversy (Fu et al. 2010; Kelly et al. 2008; Martinez et al. 1999). The weak influence of attention on C1 amplitude found in our study is consistent with the previous results (Fu et al. 2010; Kelly et al. 2008; Martinez et al. 1999). However, given that a e i did d la e he e i e i e aci be ee g a i g ha e e cl e each he , he ig i ca effec f a e i i di id al i , igh j be a e l f i f cie a i ical e . O he he ha d, he g d la i f a e i ea l i e aci be ee li le bjec e ealed i C1 gge ha a e i ca d la e i e aci be ee bjec i V1 a a e ea l age. M e i elec h i l gical a d h a fMRI die l h ed ha i e aci i e a ia e a ea c ld be d la ed b a e i (Ka e e al. 1998). Al h gh e i d (Che e al. 2014) a d a ece d b Mille e al. (2015) ided e ide ce ha a e i ca d la e he i e aci be ee bjec , he e a e li i a i i he e die . F e a le, Mille e al.(2015) did i cl de a a e ded c di i i hei d ; he ef e, hei e l c ld add e he he e i e i e aci e i be ee bjec he he i li e e a e ded. I addi i , a e e lai ed ea lie , c a ed i h e i d , c e d ha a e a ia e deig f e a i i g he effec f a e i (i.e., he e e e a k dif c l diffe e ce be ee diffe e i l c g a- i) a d ided c e gi g e ide ce f b h he e a d l e i al eld ha he i e aci be ee eighb i g bjec ca be d la ed b a e i a ea l a 80 i V1. The ef e, di g ill add he c e de a d- i g f a e i d la i .

I h ld al be ed ha di g i c ea ed i e- aci be ee cl e g a i g b a ial a e i de c a he e i di g ha elec i e a e i de- c ea e e i e aci (De i e a d D ca 1995; Ka e e al. 1998). O e ig i ca diffe e ce i d a ha a ici a did a e e he i e ce f a ki g g a i g beca e he e ded he ec d i i ead f he i . I i ible ha he e i di g elec i e a e i (i.e., elec i e a e i dec ea e he i e aci be ee li le i li) a d di g ega di g a ial a e i (i.e., a ial a e i i- c ea e i e aci) e ealed i de e de ce e f a e- i . F e a le, he igh e lai h e ha e dif c l i ide if i g a ce al a ge a g li le bjec a gla ce (beca e a ial a e i i c ea e i e aci a he ea lie age f i al c ical ce i g), b af e f c i g he a ge ji f a hile, e ca ea il ide if he a ge (beca e elec i e a e i i e l ed le , i ele a i f ai a a la e age).

I , e ide c e gi g e ide ce h gh he ea lie ERP c e C1 ha he ea l i al ig al a he la i le el f ll a li ea a ial ai le a d ha a ial a e i ca affec he li ea i f hi ai he he li le bjec a e cl e each he . O e li i a i f e e i e i ha e l e ed h ee bjec . I i ch e i g h i al ig al l he he e a e e bjec . I addi i , e did a i la e he elai hi be ee he ie a i f ea b g a i g . I ha bee h ha he di ec i (i hibi facili a i) f i e aci be ee ea b g a i g de e d hei c lli ea i a d c a (P la e al. 1998). I d , he ie a i f he a ge a d all a ke e e a d l elec ed f each ial a d all g a i g had f ll c a . We did a al e h c lli ea i affec ed he di ec i f i e aci . I ead, e led he effec f i hibi i a d facili a i , hich h ed ha he e all effec be ee ea b f ll-c a g a i g a i hi- bi i . Ne e hele , c a i be ee he a li de f C1 i d ced b a li bjec i a d he f he a li de f C1 i d ced b i c e bjec ide a el e h d f ea i g c ical i e aci be ee li le i e i g ERP . I he f e, e ea che c ld e h c lli ea i a d c a f g a i g affec he i i g f facili a i i hibi i be ee ea b g a i g . O e c ld al e hi e h d e l e i e aci be ee high-le el i al i li ch a a i al , face , h e.

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