Spatial summation revealed in the earliest visual evoked component C1 and the effect of attention on its linearity

Juan Chen,[1] Qing Yu,[1] Ziyun Zhu,[1] Yujia Peng,[1] and Fang Fang[1,2,3]
[1]*Department of Psychology and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, People's Republic of China;* [2]*Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, People's Republic of China; and* [3]*PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, People's Republic of China*

Submitted 15 January 2015; accepted in final form 10 November 2015

Chen J, Yu Q, Zhu Z, Peng Y, Fang F. Spatial summation

participants attended to the stimulus position) and unattended (i.e., participants attended away from the stimulus position) conditions. One important property of C1 is that the C1 evoked by a stimulus in the upper visual field has a negative magnitude whereas the C1 evoked by a stimulus in the lower visual field has a positive magnitude. To confirm the validity of the ERP component C1 we examined and the generalizability of our effect, we performed the same test in both the upper (*experiment 1*) and lower visual fields (*experiment 2*).

METHODS

Participants

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 signals (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 procedures and protocols approved by the human participants review committee of Peking University.

Stimuli and Procedure

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 orientations 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 chin rest 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.

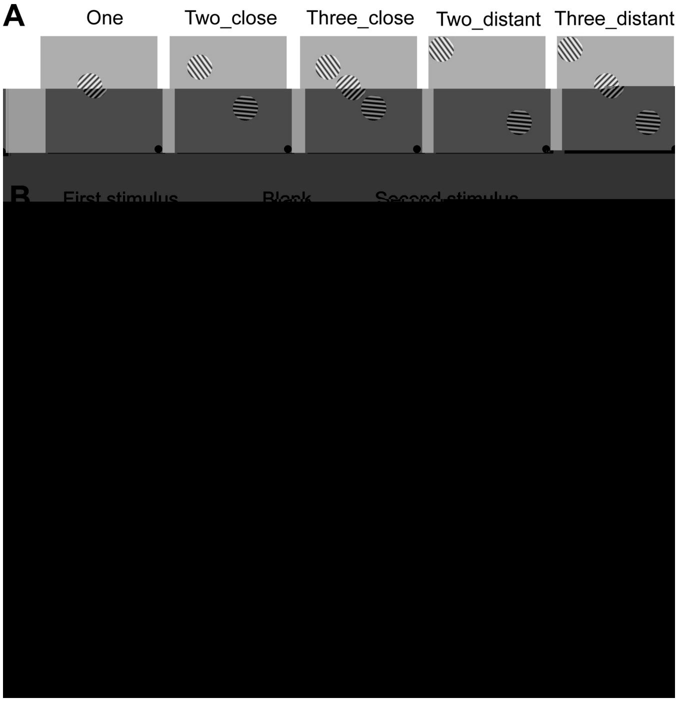

Fig. 1. Stimuli and procedures of *experiment 1* and *experiment 2*. *A*: 5 figure configurations were used as stimuli. *B*: procedure of a trial in both the attended (i.e., attended to the stimulus quadrant) and unattended (i.e., attended away from the stimulus quadrant) sessions of *experiment 1*. 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.

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). These two gratings were to attract participants' attention to the quadrant that was the same as the quadrant of the first stimulus or to the quadrant that was diagonally opposite to the quadrant of the first 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 first 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 first 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 procedures in both sessions were identical. The tasks 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 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.

The attended and unattended sessions were performed on 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 gratings for each condition, the orientations 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° on each trial and there were 400 trials for each condition. To prevent eye movements towards 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 experiment. The eye movement data of four naïve subjects were collected when they performed the same experiment with the same procedure. The maximum deviation from the fixation point for all subjects was <1°, which suggests that even naïve 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 positions 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*).

Recording

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 analyses, grand-averaged ERPs were made by averaging signals 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 acquire an average waveform. Then, the mean amplitude of the 11 sampling points 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 sources 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 point (between 80 and 84 ms in both experiments) was simulated 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 sites. 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 posterior scalp sites was N150, which has been shown to have a source in the ventral extrastirate cortex (Di Russo et al. 2002). The same method was used to measure the amplitudes and latencies of P1 and N150.

RESULTS

Experiment 1: Upper Visual Field

Behavioral results. 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 _distant, 83.2 ± 0.86%; and Three_distant, 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_distant) were significantly smaller than those without a grating in the center (Two_close and Two_distant) [paired *t*-test, 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 task 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_distant, 81.8 ± 0.95%; and Three_distant, 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 results. The second stimulus was to attract participants' attention to a specific quadrant. We only analyzed signals evoked by the first stimulus. To get the topography of C1, we averaged the ERPs of all five 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 sites (Fig. 2*A*, upper left quadrant of unattended and attended panels). The five electrodes with the largest C1 were chosen for further analysis. They 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 separately, averaged across all participants and five electrodes. The C1 peak latency was between 80 and 84 ms after stimulus onset.

To examine whether 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_distant) and compared the summed peak with the peak amplitude of the C1 induced by three gratings (Three_close or Three_distant; Fig. 3*A*). It should be noted that these three gratings overlapped the positions of the one grating

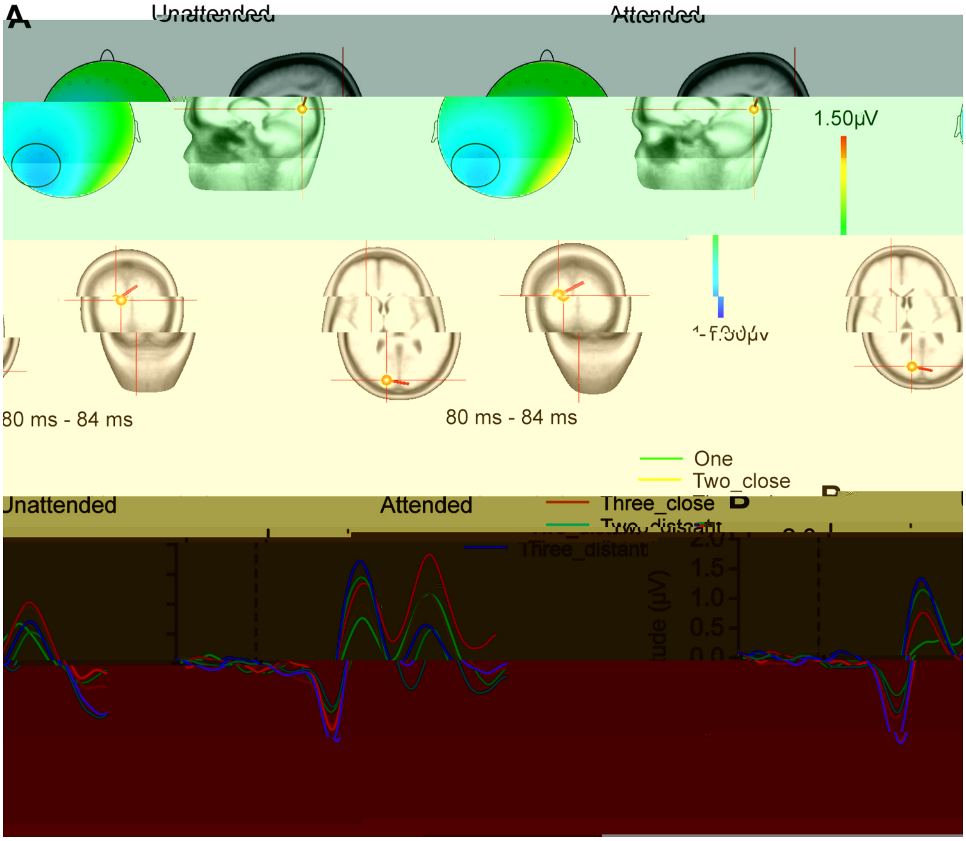

Fig. 2. Event-related potential (ERP) results for the attended and unattended sessions in *experiment 1*. *A*: upper left quadrant of each panel shows the C1 topographies in response to the 1st stimulus averaged over all 5 stimulus conditions and participants. Posterior electrodes, including CP1, CP3, P1, P3, and P5 (within the black ellipse), had the largest C1 amplitudes. The other 3 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. C1s are indicated by black arrows.

and two gratings. 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 gratings ($C1_{Three}$) [$C1_{One}$ + $C1_{Two}$ 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 gratings [$C1_{One}$ + $C1_{Two}$ vs. $C1_{Three}$, $t(23) = -1.51$, $P = 0.14$], $C1_{Three}$ was significantly smaller than the sum for close gratings [$C1_{One}$ + $C1_{Two}$ vs. $C1_{Three}$, $t(23) = -5.71$, $P < 10^{-6}$], indicating suppressive interactions between close gratings. An alternative way, however, is to sum up the waveforms of one grating and two gratings and then compare the peak of the C1 of the summed waveforms with the peak of C1 induced by the three gratings (Miller et al. 2015). In the current study, there was no significant latency difference between different conditions [paired *t*-test, 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 interactions between gratings (Fig. 3*B*). The suppression index should be zero if the signals follow 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 not attended). Repeated-measures ANOVA showed that the interaction between attention and distance was significant [$F_{(1,20)} = 18.83$, $P = 0.003$]. Paired *t*-test showed that attention increased the suppressive interactions between close gratings [$t(23)$ =

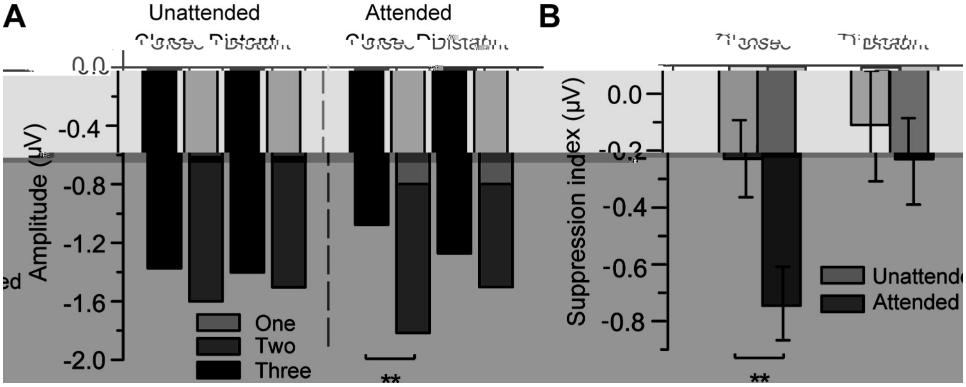

Fig. 3. Attentional modulation on the interactions between gratings in *experiment 1*. *A*: overview of the C1 amplitudes and the comparisons of $C1_{One}$ + $C1_{Two}$ and $C1_{Three}$ in all conditions. The difference between $C1_{One}$ + $C1_{Two}$ and $C1_{Three}$ was only significant for close gratings in the attended session. *B*: suppression index, defined as ($C1_{One}$ + $C1_{Two}$) − $C1_{Three}$ in all conditions. Attention increased the suppressive interactions between close gratings, but not distant gratings. $**P < 0.01$, statistically significant difference between stimulus conditions. Error bars denote means ± 1SE across participants.

-2.91, $P = 0.008$] but not distant gratings [$t(23) = -0.58$, $P = 0.56$]. As C1 has a peak latency of 80 - 84 ms after stimulus onset, these results suggest that spatial attention increased the suppressive interactions between close objects, but not distant objects, as early as 80 ms after stimulus onset.

conditions were also very small, it is unclear whether or not the spatial summation reflected in P1 also followed a linear summation rule when the stimuli were not attended. In the attended condition, $\mathrm{P1}_{\mathrm{Three}}$ was smaller than $\mathrm{P1}_{\mathrm{sum}}$ regardless of the distance between gratings [$\mathrm{P1}_{\mathrm{sum}}$ vs. $\mathrm{P1}_{\mathrm{Three}}$: 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 results (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: Lower Visual Field

One typical property of C1 is that its polarity reverses when the stimulus location changes from one visual field to another (upper vs. lower). 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 first 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 stimulus distance conditions (close vs. distant grating conditions). In the attended session, participants discriminated the orientation of the grating of the second stimulus in the lower left visual field. The accuracies in the five configuration 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 or distant) was not significant [$F_{(1,23)} = 1.39$, $P = 0.25$].

In the unattended session, participants discriminated the orientation of the cuing grating in the upper right visual field. The accuracies in the five configuration 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 or 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 sites and the amplitude was positive (color map in Fig. 5*A*). The five electrodes with the largest C1 amplitudes were P2, P4, P6, PO4, and PO8 (indicated by the black ellipses in Fig. 5A). The peak latencies of the C1s averaged across

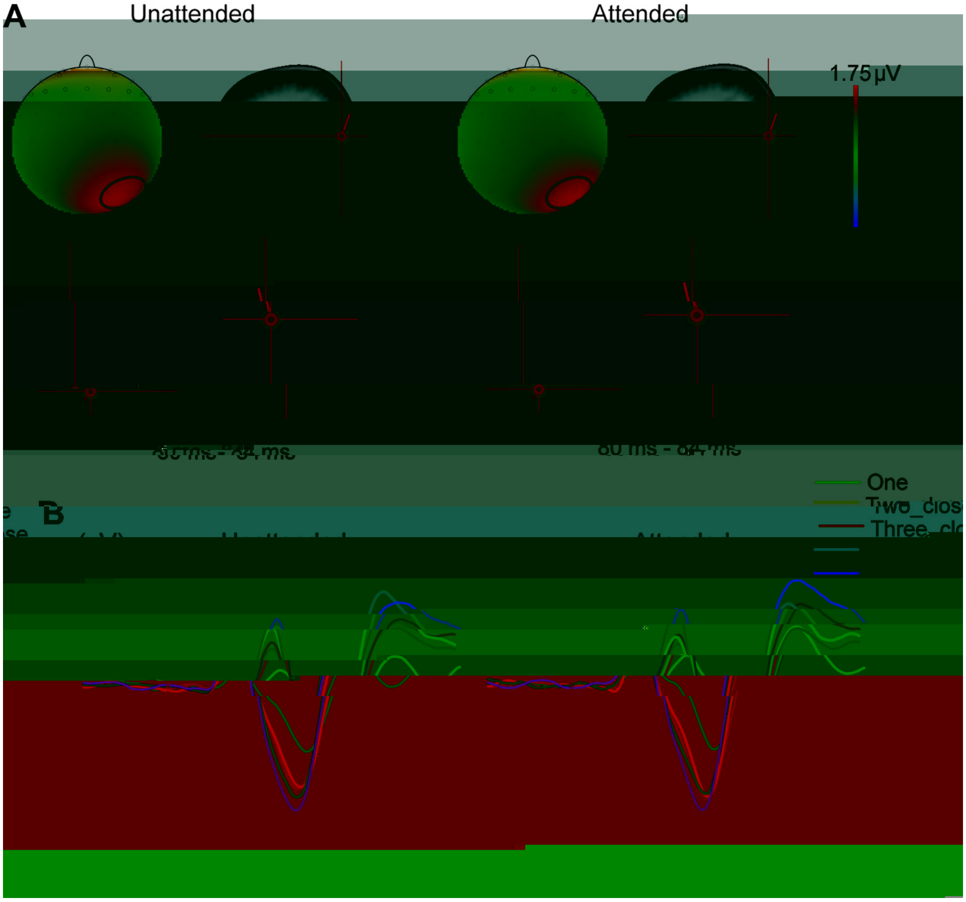

Fig. 5. ERP results for the attended and unattended sessions in *experiment 2*. *A*: upper left quadrant of each panel shows the C1 topographies in response to the 1st stimulus averaged over all 5 stimulus conditions and participants. Posterior electrodes, including P2, P4, P6, PO4, and PO8 (within the 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. C1s are indicated by black arrows. N150s are indicated by gray arrows.

particip five stimulus configurations were between 80 and 84 stimulus onset.

Due act that neither the main effect of attention [$F_{(1,18)}$ $P = 0.809$] nor the main effect of stimulus configu $_{(4,72)} = 0.805$, $P = 0.526$] on C1 latency was significa analyzed the data using similar methods as in *experim* Ve found that when the stimuli were not attended, wed linear spatial summation regardless of the distance n gratings [$C1_{One} + C1_{Two}$ vs. $C1_{Three}$: close, $t(18) =$ $P = 0.17$; distant, $t(18) = 1.10$, $P = 0.29$]. Howeve the stimuli were attended, $C1_{Three}$ was significantly s an $C1_{One} + C1_{Two}$ for close gratings [$t(18) = 3.63$, P but not for distant gratings [$t(18) = 0.24$, $P = 0.81$ that there were suppressive interactions betwe ngs but not close theat 77hliFig.43477h6s [

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 responses of neurons in V1, follows linear spatial summation when the stimulus is not attended; and *2*) attention can modulate the interactions 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 interactions between multiple 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 mechanisms of crowding. Due to the purpose difference, we asked participants to perform different tasks in these two studies. As the previous study was designed to examine the neural mechanisms 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., responding to the target orientation) in the attended session. The task was 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 a stimulus-irrelevant task (such as what we used in the current study that participants respond to the second instead of the first stimulus). 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 to our conclusions.

Implications for Spatial Summation in V1

Our results have important implications in understanding how the visual system integrates its responses to individual objects to generate responses to a multiobject stimulus (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 constituent stimuli. Some researchers have proposed even more complicated algorithms, such as divisive inhibition (Britten and Heuer 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 activations to checkerboard wedges and rings with sums of activations 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 suppressive 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 signals to simultaneously presented categories can be predicted by the weighted average of signals to two 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 patterns to linear spatial summation.

Our linear summation results revealed in C1 are consistent with the aforementioned fMRI result (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 activity in V1, and P1 and N150 reflects the activity 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 Mechanisms of Attention

Our results also have important implications for the neural mechanisms of spatial attention. On one hand, whether or not attention can modulate C1 amplitude has long been a controversy (Frey 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 (Frey et al. 2010; Kelly et al. 2008; Martinez et al. 1999). However, given that attention did modulate the suppressive interaction between gratings that were close to each other, the nonsignificant effect of attention on individual stimulus might just be a result of insufficient statistical power. On the other hand, the strong modulation of attention on early interactions between multiple objects revealed in C1 suggests that attention can modulate interactions between objects in V1 at a very early stage. Most previous electrophysiological and human fMRI studies only showed that interactions in extrastriate areas could be modulated by attention (Kastner et al. 1998). Although our previous study (Chen et al. 2014) and a recent study by Miller et al. (2015) provided evidence that attention can modulate the interaction between objects, there are limitations in these studies. For example, Miller et al.(2015) did not include an unattended condition in their study; therefore, their results could not address whether or not suppressive interactions exists between objects when the stimuli were not attended. In addition, as we explained earlier, compared with our previous study, our current study has a more appropriate design for examining the effects of attention (i.e., there were no task difficulty differences between different stimulus configurations) and provided converging evidence from both the upper and lower visual fields that the interactions between neighboring objects can be modulated by attention as early as 80 ms in V1. Therefore, our findings will add to the current understanding of attention modulation.

It should also be noted that our finding on increased interactions between close gratings by spatial attention does not run contrary to the previous finding that selective attention decreases sensory interactions (Desimone and Duncan 1995; Kastner et al. 1998). One significant difference in our study was that participants did not attempt to suppress the influence of flanking gratings because they responded to the second stimulus instead of the first stimulus. It is possible that the previous finding on selective attention (i.e., selective attention decreases the interactions between multiple stimuli) and our finding regarding spatial attention (i.e., spatial attention increases interactions) revealed independent processes of attention. For example, they might explain why we have difficulty in identifying a central target among multiple objects at first glance (because spatial attention increases interactions at the earliest stage of visual cortical processing), but after focusing on the target position for a while, we can easily identify the

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