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

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Chen J, Yu Q, Zhu Z, Peng Y, Fang F. Spatial summation revealed in the earliest visual evoked component C1 and the effect of attention on its linearity. *J Neurophysiol* 115: 500–509, 2016. First published November 11, 2015; doi:10.1152/jn.00044.2015.—In natural scenes, multiple objects are usually presented simultaneously. How do specific areas of the brain respond to multiple objects based on their responses to each individual object? Previous functional magnetic resonance imaging (fMRI) studies have shown that the activity induced by a multiobject stimulus in the primary visual cortex (V1) can be predicted by the linear or nonlinear sum of the activities induced by its component objects. However, there has been little evidence from electroencephalogram (EEG) studies so far. Here we explored how V1 responded to multiple objects by comparing the EEG signals evoked by a three-grating stimulus with those evoked by its two components (the central grating and 2 flanking gratings). We focused on the earliest visual component C1 (onset latency of ~50 ms) because it has been shown to reflect the feedforward responses of neurons in V1. We found that when the stimuli were unattended, the amplitude of the C1 evoked by the three-grating stimulus roughly equaled the sum of the amplitude of the C1s evoked by its two components, regardless of the distances between these gratings. When the stimuli were attended, this linear spatial summation existed only when the three gratings were far away from each other. When the three gratings were close to each other, the spatial summation became compressed. The results suggest that the earliest visual response in V1 follows a linear summation rule when attention is not involved and that attention can affect the earliest interactions between multiple objects.

attention; spatial summation; linearity; multiple objects; ERP; C1; V1; P1; N150; BESA source analysis

OBJECT RECOGNITION IS A BASIC function of the visual system. In natural scenes, objects are usually cluttered. Despite this, the majority of previously conducted studies have focused only on how a single object is processed in the visual system. As a result, although it is important to computational neuroscience, it is still unclear how the visual system responds to multiple objects based on its responses to each individual object. When computational models were established to predict the responses of neurons or brain areas to a multiobject stimulus, they often assumed that the response to this multiobject stimulus could be predicted as the sum of the individual responses to each of its components (Dumoulin and Wandell 2008; Walther et al. 2005). However, there has been little evidence for this summation, even in the earliest visual cortical area V1. Single-unit recording studies have focused on extrastriate areas (Gawne and Martin 2002; Luck et al. 1997; Oleksiak et al. 2011; Reynolds et al. 1997; Zoccolan et al. 2005) and showed that in these areas neuronal responses to a multiobject stimulus could be predicted by either the weighted average or the maximum response to its components. However, because the receptive fields of neurons in V1 are too small to cover multiple objects, very few electrophysiological studies have tried to tackle how V1 responds to multiple objects at the a ici a a e ded he i l ji) a d a e ded (i.e., a ici a a e ded a a f he i l ji) c di i . O e i a e f C1 i ha he C1 e ked b a i l i he e i al eld ha a ega i e ag i de he ea he C1 e ked b a i l i he l e i al eld ha a i e ag i de. T c he alidi f he ERP c e C1 e e a i ed a d he ge e ali abili f effec , e e f ed he a e e i b h he e (1) a d l e i al eld (2).

METHODS

T e - e a ici a (12 ale , 13 fe ale) a ici a ed i 1, a d 21 a ici a (13 ale , 8 fe ale) a ici a ed i 2. O e a ici a ' da a (ale) i 1 a d a ici a ' da a (1 ale a d 1 fe ale) i 2 e e di ca ded d e gal ha a e i hei EEG ig al (L ck 2005). All a ici a e e igh -ha ded a d e ed al c ec ed- al i i . Age a ged f 18 25. All a ici a ga e i e i f ed c e i acc da ce i h he ced e a d c l a ed b he h a a ici a e ie c i ee f Peki g U i e i .

E 1. All i li c i ed f ci c la i idal g a i g (dia e e = 2.36 ; a ial f e e c = 2.54 c/d; f ll c a ; ea l i a ce = 61.47 cd/ 2). The backg d had he a e l i a ce a he ea l i a ce f he g a i g . The ie a i f he g a i g i he ce e a ei he +45 −45 hile he ie a i f he a ki g g a i g e e i de e de l a d a d l elec ed f 0 180 f each ial.

Fi e i l c g a i e e ed: e g a i g (O e), cl e g a i g (T _cl e), di a g a i g (T _di a), h ee cl e g a i g (Th ee_cl e, c ea ed b c bi i g he e g a i g i h he cl e g a i g i ace), a d h ee di a g a i g (Th ee_di a , c ea ed b c bi i g he e g a i g i h he di a g a i g i ace) (Fig. 1A). The ce e -ce e di a ce be ee cl e g a i g a 2.48 , a d he di a ce be ee di a g a i g a 5.07 . The i l a ce e ed a 8 ecce ici i he e lef i al ad a . The a i a a i a he ce e f he c ee . A chi e a ed abili e he head ji . All i al i li e e di la ed a Vie S ic c l g a hic i (ef e h a e: 75 H ; e l i : 1,024 × 768; i e: 22 i .) i h a g a backg d a a ie i g di a ce f 73 c .

Each ial bega i h a i l (he i l) e e ed i he e lef i al eld f 500 . Thi i l a a d l elec ed f he e i l c g a i . Af e a bla k i e al (ji e ed be ee 200 a d 400), g a i g (he ec d i l) i h ie a i ligh l diffe e f he e ical e e e e ed f 100 . O e a e e ed i he a e ji a he ce al g a i g f he i l (i.e., e lef i al eld), a d he he a e e ed i he diag all ie ji he ce al g a i g f he i l (i.e., l e igh i al eld). The e g a i g e e a ac a ici a ' a e i he ad a ha a he a e a he ad a f he i l he ad a ha a diag all ie he ad a f he i l . S eci call , i he a e ded e i , a ici a e e i c ed j dge he ie a i f he e lef g a i g (lef igh , ela i e e ical ie a i) f he ec d i l , hich a ac ed hei a e i he a e ad a a he i l . I he a e ded e i , a ici a e e i c ed j dge he ie a i f he l e igh g a i g f he ec d i l , hich a ac ed hei a e i he diag all ie ad a f he i l . T da hed ci cle

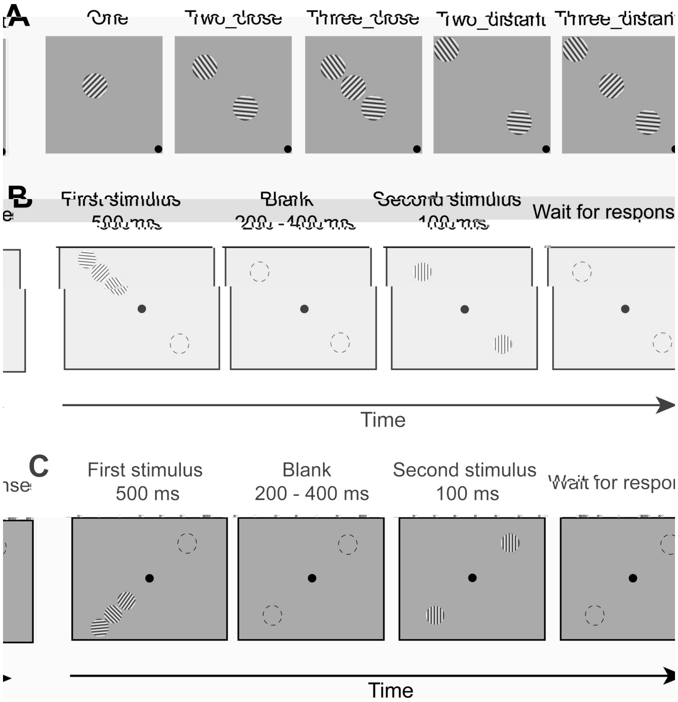

Fig. 1. S i li a d ced e f 1 a d 2. A: 5 g e c g a i e e ed a i li. B: ced e f a ial i b h he a e ded (i.e., a e ded he i l ad a) a d a e ded (i.e., a e ded a a f he i l ad a) e i f 1. I he a e ded e i , a ici a e e i c ed j dge he ie a i f he g a i g i he e lef i al eld f he ec d i l , hile i he a e ded e i , a ici a j dged he ie a i f he g a i g i he l e igh i al eld f he ec d i l . C: ced e f 2 a ide ical ha f 1. The l diffe e ce a i he ji f he a d ec d i li.

e e al a e e ed he c ee i dica e he ji f he g a i g (Fig. 1B). I h ld be ed ha he ced e i b h e i e e ide ical. The a ki b h e i e e i l - i ele a (i.e., i ele a he i l), e e i g a ic- i a f elec i el a e di g a eci c i l c g a- i . The diffe e ce be ee he ie a i f a k- ele a g a- i g (he e lef g a i g i he a e ded e i he l e igh g a i g i he a e ded e i) f he ec d i l a d he e ical ie a i a adj ed kee a ici a ' e f a ce le el a ~80% c ec .

The a e ded a d a e ded e i e e e f ed diffe e da i ac e bala ced de ac a ici a . The c l f he a i i a ed g ee i dica e he he a e i a a e ded a e ded (al c e bala ced ac a ici a), e ec i el . The e e e 20 bl ck i each e i . Each bl ck c i ed f 100 ial , 20 ial f each f he 5 i l c g a i , e e ed i a a d de . The ef e, f each i l c g a i , he e e e 400 ial i al. Al h gh e did ec d he ie a i f he a ki g g a i g f each c di i , he ie a i f he a ki g g a i g i he -g a i g c di i (i.e., T _cl e a d T _di a) a d h e i he h ee-g a i g c di i (i.e., Th ee_cl e a d Th ee_di a) h ld ha e bee bala ced, gi e ha he ie a i f he a ki g g a i g a i de e- de l a d a d l elec ed f 0 180 each ial a d he e e e 400 ial f each c di i . T e e e e a d he a ge l ca i , all bjec e e ai ed ai ai ai bef e he a ed he EEG e e i e . We e ea edl e ha i ed he i a ce f ai ai i g ai h gh he e i e . The e e e da a f a e bjec e e c llec ed he he e f ed he a e e e i e i h he a e ced e. The a i-

[illegible] deviation from the main position for all subjects was <1°, which suggests that these naive subjects can well maintain their gaze 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 the 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 separately. 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 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 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 extrastriate 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 with two gratings in the center (Two_close and Two_distant) [paired *t*-tests, all $t(23) > 2.43$, $P < 0.03$]. This is probably because the stimulus with a central grating served as a forward mask 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 ascribed 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 ERP 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 the three gratings overlapped the positions of the one grating

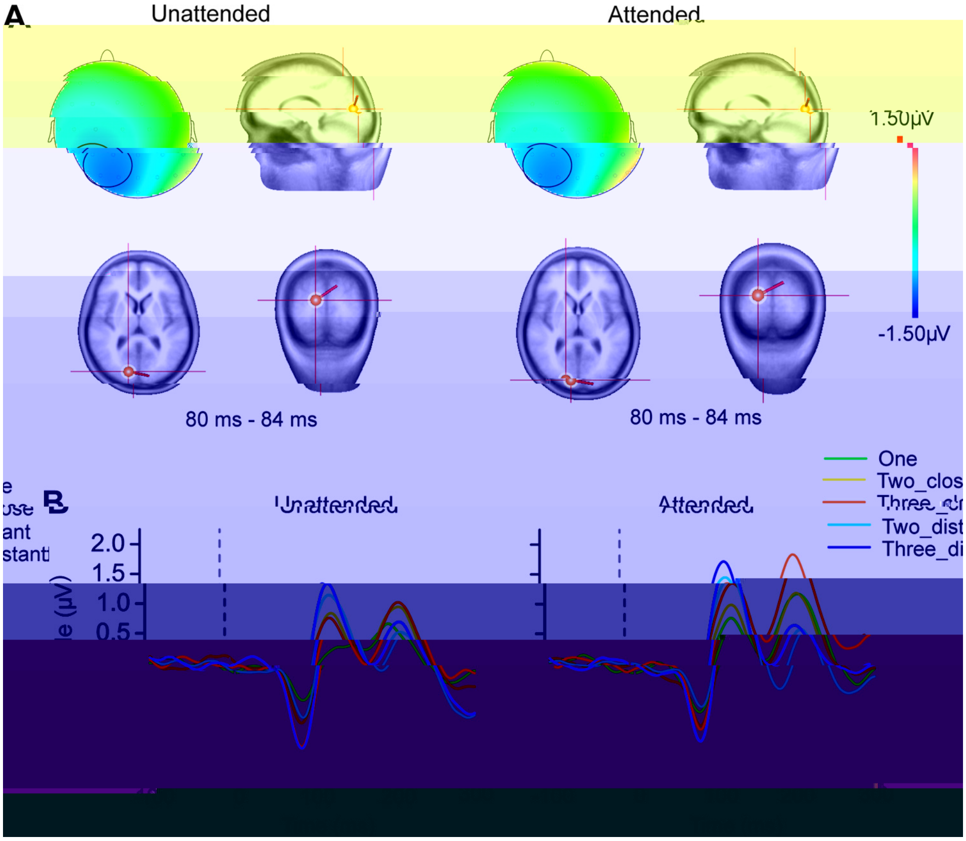

Fig. 2. Event-related potential (ERP) results for the unattended and attended sessions in *Experiment 1*. *A*: upper left: scalp topography of each panel shows the C1 topographies in response to the 1st stimulus was averaged over all 5 stimulus conditions and participants. Posterior electrodes, including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

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 interaction between close gratings. An alternative was, however, [illegible] the waveform of one grating and two gratings and the [illegible] the peak of the C1 for the summed waveform with the peak of C1 induced by the three gratings (Miller et al. 2015). In the current study, there was no significant late component 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 gratings (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 gratings [$t(23) =$

−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 ee cl e bjec , b di a bjec , a ea l a 80 af e i l e.

conditions were also very small, it is not clear whether or not 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: 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 conclusion 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 lower right visual fields, respectively (Fig. 1*C*).

Behavioral performance. 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-tests, 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 upcoming 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 site and the amplitude was positive (color map in Fig. 5*A*). The five electrodes with the largest C1 amplitude were P2, P4, P6, PO4, and PO8 (indicated by the black ellipse in Fig. 5A). The peak latencies of the C1 averaged acr-

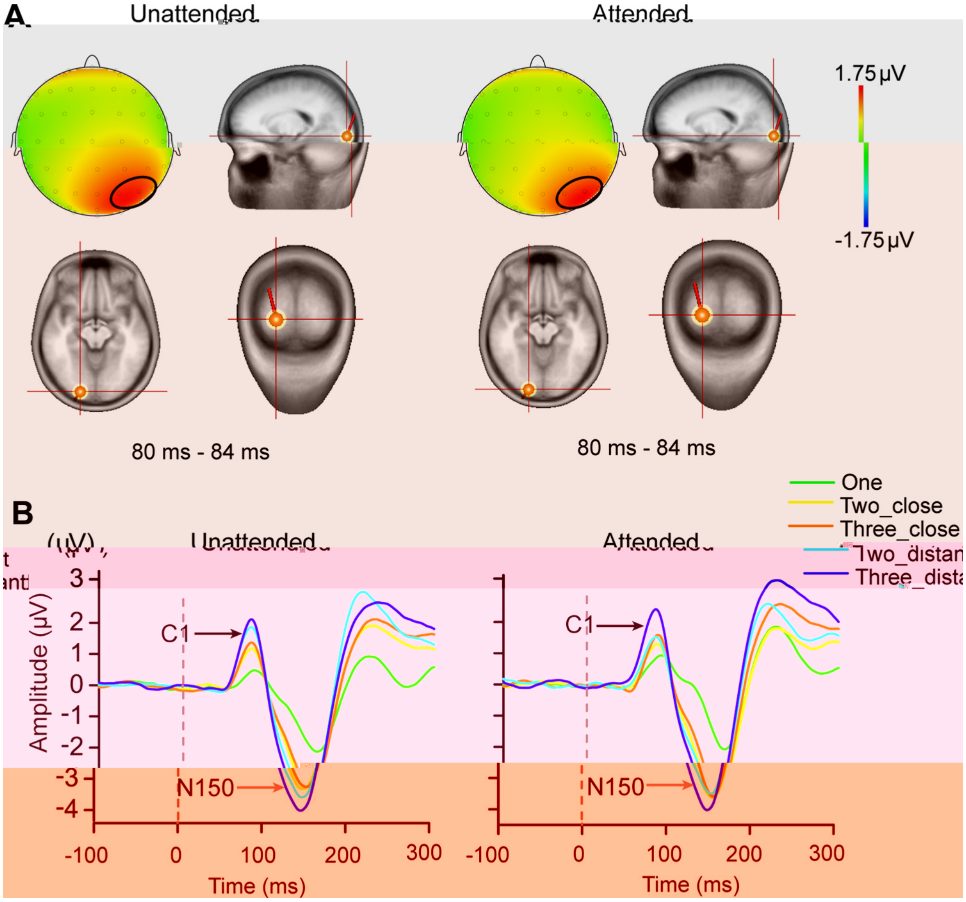

Fig. 5. ERP results for the attended and unattended sessions in *Experiment 2*. *A*: upper left quadrant of each panel shows the C1 topographies in response to the 1st stimulus averaged over all 5 stimulus conditions and participants. Posterior electrodes, including P2, P4, P6, PO4, and PO8 (within the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

participants for each stimulus configuration were between 80 and 84 ms after stimulus onset.

Despite the fact that neither the main effect of attention [$F_{(1,18)} = 0.06$, $p = 0.809$] nor the main effect of stimulus configuration [$F_{(4,72)} = 0.805$, $p = 0.526$] on C1 latency was significant, we analyzed the data using similar methods as in Experiment 1. We found that when the stimuli were not attended, C1 followed linear spatial summation regardless of the distance between gratings [$C1_{One} + C1_{Two}$ vs. $C1_{Three}$: close, $t(18) = 1.42$, $p = 0.17$; distant, $t(18) = 1.10$, $p = 0.29$]. However, when the stimuli were attended, $C1_{Three}$ was significantly smaller than $C1_{One} + C1_{Two}$ for close gratings [$t(18) = 3.63$, $p = 0.002$] but not for distant gratings [$t(18) = 0.24$, $p = 0.81$]. This suggests that there were nonlinear responses interaction between close gratings but not between distant gratings when the stimuli were attended (Fig. 6*A*). The nonlinear response index was also derived to examine how distance and attention influence the interaction between gratings (Fig. 6*B*). Unlike Experiment 1, the nonlinear response index should be positive because the C1 was positive. Fifteen out of the 19 participants showed a positive nonlinear response index in the close condition when the stimuli were attended, but fewer participants showed a positive nonlinear response index in the three other conditions (10 in the distant condition when the stimuli were attended, 12 and 9 in the close and distant conditions, respectively, when the stimuli were not attended). Repeated-measure ANOVA showed that the interaction between attention and distance was significant [$F_{(1,18)} = 4.57$, $p = 0.046$]. A paired t-test showed that the increase of nonlinear interaction caused by attention was close to significant between close gratings [$t(18) = 2.08$, $p = 0.051$] but was far from significant between distant gratings [$t(18) = -0.669$, $p = 0.512$]. When the stimuli were attended, i,c i (1a be la gel acc ed f b a i gle di le i V1, gge i g ha C1 a ai l ge e a ed i V1. Take ge he , e c cl de ha 1) he ea lie i al e ked c e C1, hich e ec he la i e e f e i V1, f ll li ea a ial a i he he i l i a e ded; a d 2) a e i ca d la e he i e ac i be- ee bjec i V1 a ea l a 80 af e i l e, e eciall he he bjec a e cl e each he i ace.

I h ld be ed ha al h gh a i ila de ig ha bee ed i e i d (Che e al. 2014), i hich e al ided e ide ce ha a ial a e i ca d la e he ea lie i e ac i be ee li le g a i g, he c e d i a i le e lica i f e i d. The c e d a de ig ed e a i e he he he ea lie i al ig al e ec ed i C1 f ll a li ea a ial a i le, he ea he e i d a de ig ed i e iga e he e al echa i f c di g. D e he e dif- fe e ce, e a ked a ici a e f diffe e a k i he e die. A he e i d a de ig ed e a i e he e al echa i f c di g (i.e., he dele e- i i e ce f he a ke he ec g i i f a a ge), a ici a e e a ked e f a a ge - ela ed a k (i.e., e di g he a ge ie a i) i he a e ded e i. The a k a e dif c l f he cl e c di ha f he di a c di i . Al h gh, k ledge, e ide ce ha h ha a k dif c l i e ce he ea lie i al ig al, i i ill h e i ga i l - ele a a k (ch a ha e ed i he c e d ha a ici a e d he ec d i ead f he i l). I hi ca e, he a k dif c l diffe e ce be ee diffe e c di i ld affec e l . M e e , i he c e d, e c d c ed e e i e i b h he e a d l e i al eld, hich ided e c i ci g c cl i .

1

O e l ha e i a i lica i i de a di g h he i al e i eg a e i e e i di id al bjec ge e a e e e a l i bjec i l (i.e., a ial a i). I e i e ea ch, f he i gle- i die ha e f c ed e a ia e a ea beca e he ece i e eld f V1 e a e all c e li le bjec . The h ed ha i V2 (L ck e al. 1997), V4 (Ga e a d Ma i 2002), V7a (Olek iak e al. 2011), IT (Z cc la e al. 2005), a d MT (Reca e e al. 1997), e al e e li le i li ca be edic ed b ei he he eigh ed a e age he a i f he e e f he c i e i li. S e e ea che ha e ed e e ec li- ca ed alg i h , ch a di i i e i hibi i (B i e a d He e 1999; Si celli a d Heege 1998). I a ca e, he e l gge ha a ial a i i e a ia e a ea f ll li ea le (a i , eigh ed a e age, di i i e i- hibi i).

Al h gh i i dif c l e l e h a i di id al e i V1 e d li le bjec , e ca e a i e h e i V1 e d li le bjec a he e al la i le el i h fMRI. Ha e e al. (2004) a e ed he li ea i f a ial a i b c a i g he ac i a i checke b a d edge a d i g i h f ac i a i hei c e a che a d f d ha he e e f el i V1 e e ell edic ed b li ea a ial a i (b al ee Pihlaja e al. 2008 a d Va i e al. 2005). H e e , a ece d (Ka e al. 2013) f d ha e i e a ial a i a be ed i V1 a d g e e ced i ela i el a e i e a ia e a ea . Thi i c i e i h he e i fMRI di g ha V1 h ed he alle diffe e ce be ee e e ial e e ai a d i la e e e a i a g V1 V4 (Ka e e al. 1998). I he highe -le el ca e- g - ele c i e i al a ea , ch a F if Face A ea (FFA) a d Pa ahi ca al Place A ea (PPA), Redd e al. (2009) f d ha he fMRI ig al i la e l e e ed ca e- g ie ca be edic ed b he eigh ed a e age f ig al i di id all e e ed ca eg ie . T , al h gh c ici g, a g a ea f V1 V4 a d he highe le el i al a ea , V1 ha bee h ha e he i ila e e a e li ea a ial a i .

O li ea a i e l e ealed i C1 a e c i e i h he af e e i ed fMRI e l (Ha e e al. 2004). Thi i ide c elli g c ide C1 a a ea e f ea l i al ig al i V1. M e e , he high e al e l i f EEG e e ha e l a e le likel be ca ed b feedback ig al f highe le el c ical a ea , c a ed i h he fMRI e l . O e l h ed ha al h gh li ea a ial a i de e i i V1, hi li ea ela i hi i c di i al: i de e d b h he a e i al a e f he a ici a a d he a ial la f he i li. Whe a e i i i l ed, he he a e ded bjec a e fa f each he , V1 e hibi li ea a i beha i ; h e e , he he a e ded bjec a e cl e each he , li ea a i di a ea .

I addi i , e l h ed ha li ea a i cc a ea l a 80 af e i l e b de e e i af e 122 , i.e., he li ea a i e l e e b e ed i P1 N150 i e e i e . A C1 e ec he ac i i i V1, a d P1 a d N150 e ec he ac i i i e a ia e i al c e (V2, V3, e c.), hi diffe e ce agai gge ha he li ea i f a ial a i di a ea g ad all f ia e e a ia e c e , hich i c i e i h e i e i- de ce (Mille e al. 2015). O e l a e al c i e i h e i ag e e ce hal g a h (MEG) (S ek e al. 1999) a d elec c ic g a h (EC G) e l (Wi a e e al. 2013). S eci call , S ek e al. (1999) b e ed li ea a ial a i 150 af e i l e i h MEG. Wi a e e al. (2013) e ed ha he i l -l cked c - e f EC G e e ha a a i a e li ea a ial a i , b he b adba d a ch c e f EC G e e i baddi i e. The gge ed ha he i - l -l cked c e f EC G e ec a b ief, a ie e e c a , i ila C1 e e, he ea he b adba d c e e ec al ge ai ed e e ha c e e e al a ie , e i d , i ila i h la e ERP c e ch a P1 a d N150.

A

O e l al ha e i a i lica i f he e al echa i f a ial a e i . O e ha d, he he a e i ca d la e C1 a li de ha l g bee a c - e (F e al. 2010; Kell e al. 2008; Ma i e e al. 1999). The eak i e ce f a e i C1 a li de f di d i c i e i h he e i e l (F e al. 2010; Kell e al. 2008; Ma i e e al. 1999). H e e , gi e ha a e i did d la e he e i e i e ac i 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 cie a ical e . O he he ha d, he g d la i f a e i ea l i e ac i be ee li le bjec e ealed i C1 gge ha a e i ca d la e i e ac i 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 ac i 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 ac i 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 ac i 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 de ig f e a i i g he effec f a e i (i.e., he e e e ak 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 ac i 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 ac i 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 ac i (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 l i ead f he i l . 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 ac i 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 ac i) 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 ac i 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 h e i gh 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 ai f ea b g a i g . I ha bee h ha he di ec i (i hibi i facili a i) f i e ac i 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 ac i . 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 hibi i . Ne e hele , c a i be ee he a li de f C1 i d ced b a li bjec i l 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 ac i be ee li le ie 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 ac i be ee high-le el i al i li ch a a i al , face , h e .

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