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Research Report
Interactions between attention and perceptual grouping in human visual cortex
W. Khoe^{a,*}, E. Freeman^b, M.G. Woldorff^c, G.R. Mangun^d
^aDepartment of Neurosciences, 0608, University of California, San Diego, La Jolla, CA 92093-0608, USA^bInstitute of Cognitive Neuroscience, University College London, London, UK^cCenter for Cognitive Neuroscience and Department of Psychiatry, Duke University, Durham, NC 27708, USA^dCenter for Mind and Brain, Departments of Psychology and Neurology, University of California, Davis, CA 95616, USA

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ABSTRACT

Freeman et al. (Freeman, E., Sagi, D., Driver, J., 2001. Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. *Nat. Neurosci.* 4, 1032-1036) demonstrated that detection sensitivity for a low contrast Gabor stimulus improved in the presence of flanking, collinearly oriented grating stimuli, but only when observers attended to them. By recording visual event-related potentials (ERPs) elicited by a Gabor stimulus, we investigated whether this contextual cueing effect involves changes in the short-latency afferent visual signal from V1 that have a stimulus onset latency between 60 and 80 ms and/or longer-latency changes from visual cortex. Under dual-task conditions, the subjects performed contrast discrimination for a central Gabor and an orientation judgment for a pre-specified subset of the flanking Gabors. On random trials, the central Gabor could be collinearly or orthogonally oriented with respect to the attended flankers. Subjects showed improvements in discriminating the contrast of the central grating when it was oriented collinearly with the attended flankers. The ERP difference between attending to collinear versus orthogonal flankers manifested as a positive polarity response at occipital electrodes with a latency of 180–250 ms after stimulus onset. No shorter-latency contextual cueing differences were observed in the ERPs. The ERP latency profile of the contextual cueing effect argues against the hypothesis that short-latency afferent activity from V1 is the stage of processing at which attention can influence neuronal lateral interactions. However, the scalp voltage distribution of the longer-latency contextual cueing effect is similar to the one generated by the early phasic stimulus onset activity from V1. These findings leave open the possibility that V1 is involved in the attentional modulation of lateral interactions but that this has a longer time course, likely being mediated by re-afferent inputs from later stages of the visual pathway.

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1. Introduction

The role of visual attention during visual processing has been investigated using a variety of psychophysical and physiological methods (reviewed by Hopfinger et al., 2005). In particular,

there has been increasing interest in the question of whether attention can interact with perceptual grouping processes (Baylis and Driver, 1992; Moore and Egeth, 1997). Recent data from monkey physiology (Ito and Gilbert, 1999; Gilbert et al., 2000) and from human psychophysics (Freeman et al., 2001)

* Corresponding author.

E-mail address: wkhoe@sdepl.ucsd.edu (W. Khoe).

suggest that attention may influence facilitatory lateral interactions between neighboring collinearly configured stimuli. Such lateral interactions are thought to reflect the functioning of fundamental contour grouping processes in primary visual cortex (Gilbert et al., 2000; Polat et al., 1998).

The psychophysical paradigm of Freeman et al. (2001) (see also Freeman et al., 2003) investigated the effects of attention on lateral interactions, a phenomenon thought to reflect the integrative architecture of horizontal connections in V1. In the original lateral interactions paradigm, developed by Polat and Sagi (1993, 1994), contrast detection of a target improves in the context of a single pair of collinear high-contrast flankers. Modifying this paradigm for the purpose of measuring attentional modulation effects, Freeman et al. (2001) presented stimuli comprising of two pairs of flanker patches arranged on two intersecting axes around a central patch (see Fig. 1). This central patch could be oriented so that it was either collinear with the left-oblique flanking axis (Figs. 1a, b), or with the right-oblique axis (Figs. 1c, d). Attention was manipulated to left- or right-oblique flankers pairs (illustrated by the ellipses in Fig. 1), yielding two attentional conditions in which the central patch was either collinear or orthogonal to the attended flankers (Figs. 1a and c versus Figs. 1b and d, respectively). Freeman et al. (2001) found that contrast sensitivity for an identical central target (in an identical stimulus context) improved when it was collinear with the attended flankers (i.e., compare Fig. 1a with b, and c with d).

This finding was taken to imply that attention can influence lateral interactions depending on their behavioral relevance. However, in order to infer that attention can modulate the neural mechanisms of lateral interactions in early visual cortex, a physiological correlate of this behavioral effect still needs to be demonstrated convincingly in humans. In the present study, we recorded event-related potentials (ERPs) in a replication of the original behavioral paradigm. To date, ERP studies have found little evidence for attention influencing sensory processing in V1 (Di Russo et al., 2003; Martinez et al., 1999), despite data from animal physiology (e.g., McAdams and Maunsell, 1999; Motter, 1993) and human functional imaging (e.g., Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999; Watanabe et al., 1998). However, the ERP studies did not investigate the role of attention under specific conditions such as those promoting lateral interactions phenomena that might predict a locus of activity in V1 (although see Wu et al., 2005). As the groundwork for the present study, we (Khoe et al., 2004) recently confirmed that a stimulus-driven electrophysiological correlate of collinear versus orthogonal lateral interactions could be found in

humans, having a scalp topology consistent with a V1 source and an early onset (80–120 ms). The present study used a similar experimental method, but now with a modified version of Freeman et al.'s (2001) attentional paradigm, which allowed us to test whether the correlates of lateral interactions could be modulated by selective attention to the flankers.

In contrast to hemodynamic measures of attention in early vision (e.g., Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999), only electrophysiological methods currently offer the temporal precision necessary to specify the precise latency at which attention affects visual processing. Such latency information may provide important clues for understanding the mechanism by which attention may be involved in early perceptual grouping processes. For example, if contextual cueing can modulate lateral interactions during the early feedforward stage of stimulus processing, then we might find attentional modulation of the early waveforms that we found in our previous study (Khoe et al., 2004). However, if selective attention to the flankers modulates lateral interactions in V1 or other early visual areas via re-afferent projections, then a difference in the ERP waveforms might be observed only at relatively longer latencies (e.g., later than 120 ms).

Some modifications to Freeman et al.'s (2001) original stimulus set and paradigm were required to render it suitable for recording ERPs (see Fig. 2). Instead of performing two simultaneous two-interval forced-choice tasks, we used two randomly interleaved Go/No-Go tasks in single-interval trials. In some trials, a central pedestal patch was presented selected randomly from one of two orientations (Figs. 2a and b). The subjects' primary task was then to detect the presence of a higher contrast central target superimposed on this lower contrast pedestal (i.e., a small contrast increment), pressing one key whenever the target increment was present (see Fig. 3 for an illustration of the correct responses associated with each display). In the secondary task, flanker displays were presented without any central patch (e.g., Figs. 2c–e), and subjects hit a separate key whenever they detected a rotation in the attended flanker pair (Figs. 2c and d; see also Fig. 3). Because central target detection trials and flanker-only rotation trials were presented randomly, optimum performance of both tasks required subjects to simultaneously attend to the task-relevant flankers and the central target pedestal.

A further modification of the paradigm was to present the stimuli in the perifovea (see Khoe et al., 2004 and illustrations in Fig. 3). Presenting target stimuli at fixation (as in the original lateral interactions paradigm) may lead to equal stimulation

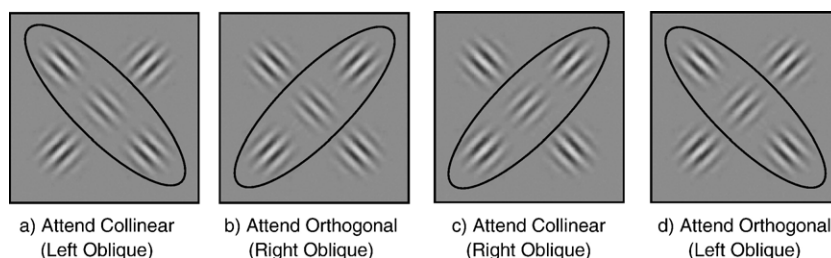


Fig. 1 – Attend-collinear versus attend-orthogonal conditions. For identical stimuli (a and b, c and d), the central stimulus can be considered to be in either a collinear (a, c) or orthogonal configuration (b, d), depending on which pair of flankers are attended: left-oblique flankers (a and d) or right-oblique (b and c). The attended set is outlined here with dashed ellipses, and the contrast of the central patch is enhanced for the purpose of illustration.

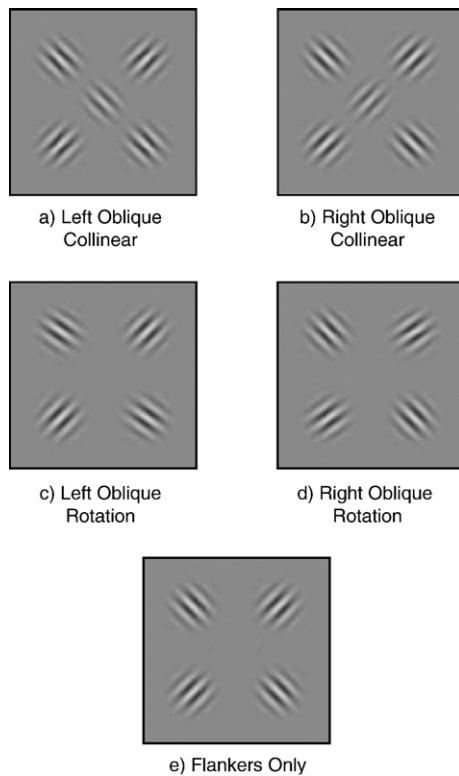


Fig. 2 – Stimulus configurations used in Experiments 1 and 2. The central stimulus was oriented collinearly with flankers on the left-oblique axis (a) or the right-oblique axis (b). The flanker rotation targets consisted of flanker elements rotated on the left-oblique axis (c) or the right-oblique axis (d). Trials with non-rotated flankers only were also included (e). Contrast of the central patch has been increased for illustration purposes.

of both banks of the calcarine sulcus, thus eliciting dipoles of opposite polarity, which may cancel each other at the scalp (Clark et al., 1995). To avoid this, the whole stimulus array was slightly displaced to the right and above of fixation.

Experiment 1 presents a behavioral confirmation that, despite these changes, reliable attentional modulation of central target thresholds could still be readily obtained. In Experiment 2, we present ERP data showing attentional modulation of only relatively late ERP components, which nevertheless have a topology consistent with a locus in V1. In the General discussion section, we consider reasons why our findings differ from a similar study by Wu et al. (2005), who recently reported early components of attentional modulation.

2. Results

2.1. Experiment 1

In this first experiment, we collected only behavioral data to confirm whether the present modified paradigm could replicate the attentional effects observed previously.

Estimates of perceptual sensitivity (d') for the central target contrast discrimination task were entered into a repeated

measure ANOVA with the following factors: attended target-flanker configuration (collinear vs. orthogonal) and attended axis (left-oblique vs. right-oblique). The main effect of contrast discrimination showed significantly greater d' 's for targets that were oriented collinearly to the attended flankers compared to the orthogonal configuration [$F(1,11) = 6.34, P < 0.03$, see Table 1]. The main effect of attending between the two axes was not significant [$F < 1$]: contrast discrimination when attending to the left-oblique axis was equivalent to attending to the right-oblique axis. No significant interactions between the two factors were found. For the flanker-rotation task, d' was entered into a two-tailed t test ($\alpha = 0.05$). There was no significant difference in sensitivity between the two attended axes [$P < 0.09$].

The results from Experiment 1 provide evidence that the modified paradigm with perifoveal targets replicated the original attentional effects from Freeman et al. (2001) with foveal targets. Detection sensitivity for a central target improved when the target was collinear with the attended flankers, compared to when the target was orthogonal to the attended flankers. The consistently high sensitivity for the secondary flanker rotation task suggests that subjects attended successfully to the cued axis.

2.2. Experiment 2

Having validated the paradigm behaviorally, we now recorded ERPs (and concurrent behavioral data) to the various presented stimuli. In order to reveal the effects of contextual cueing on the central pedestal, a series of subtractions were performed on the ERP data to extract the responses to the central pedestals (see also Busse et al., 2005; Khoe et al., 2004), as according to the following logic. A pedestal that is collinear with the attended flankers can be defined as P_c and the four flankers under that condition as F_c . The entire compound stimulus configuration can be written as $(P_c + F_c)$. The corresponding flanker-only trials can be written as F_c' . An analogous convention can be used for the identical stimulus in the case where the central pedestal is orthogonal ($P_o + F_o$). The flanker-only trials can be written as F_o' . Next, the linear contributions from the flankers to the compound stimulus response can be removed by subtracting the flanker-only trials. The result from this subtraction is the activity elicited by the central pedestal for the collinear or orthogonal context. Removing the activity elicited by the flankers alone reveals any non-linear effects of lateral interactions between the pedestal and the flankers. A second subtraction between the attend-orthogonal condition and the attend-collinear condition then isolates the critical effects of attentional modulation of lateral interactions on the pedestal response.

$$[(P_c + F_c) - F_c'] - [(P_o + F_o) - F_o'] = P_c - P_o \quad (1)$$

$$P_c - P_o = \text{Effect of attention and lateral interactions.} \quad (2)$$

However, if F_c' and F_o' elicit similar visual evoked potentials (which can be tested separately—see below), the algebra is such that Eq. (1) becomes:

$$(P_c + F_c) - (P_o + F_o) = \text{Effect of attention and lateral interactions} \quad (3)$$

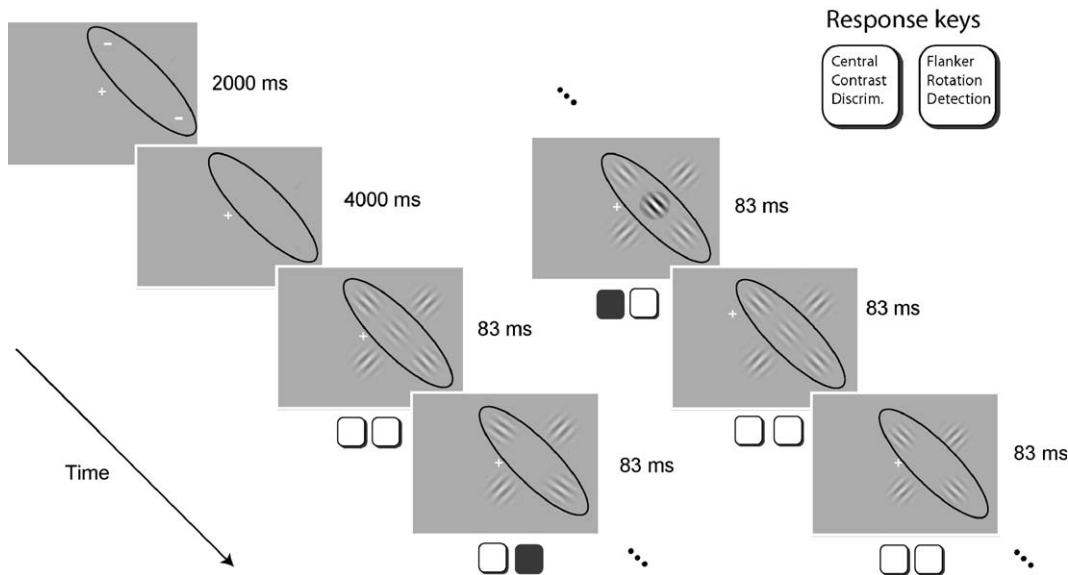


Fig. 3 – Sample sequence of trials in Experiment 1 and 2. In this example, attention is directed to the flankers on the left-oblique axis (ellipses are shown here for illustration purposes only). The block begins with a fixation cross and peripheral markers and is followed by a random sequence of stimulus displays. Collinear and orthogonal stimulus configurations were randomized within an experimental block. Correct key-presses are displayed schematically under each frame (gray colored keys). One key (illustrated here on the left) is for indicating detection of a contrast increment in the central target; the other key is for indicating detection of flanker rotation on the attended flanking axis. Contrast of the central patch has been increased for illustration purposes.

2.2.1. Behavior

Analysis of behavioral data (d') proceeded as in Experiment 1. A main effect of attention for target–flanker configuration was significant [$F(1,12) = 6.48, P < 0.03$]. Similar to Experiment 1, contrast discrimination for the central target was greater when the attended flankers were collinear versus an orthogonal configuration (see Table 1). The size of the contextual cueing effect did not vary between the two axes [$F < 1$]. Interactions between the factors were non-significant. For the rotation discrimination judgment, there was no significant difference in rotation discriminability between the two flanker pairs [$t(12) = 0.09, P > 0.4$] (Table 1).

2.2.2. ERPs: long latency effects of attention on lateral interactions

The comparison in Eq. (2) concerning the effects of attention on lateral interactions is only valid if the ERPs for flanker-only stimuli are equivalent for the different attention conditions (i.e., $F_c' = F_o'$). Thus, the ERPs for these flanker-only trials when attending to one axis versus the other were compared.

The mean amplitudes for these ERPs between 0 and 300 ms for the two flanker pairs were entered into an ANOVA using a sliding time window analysis (20 ms intervals). At midline and lateral electrodes, the ERPs evoked by the two flanker-only trials were not significantly different ($F < 1$).

The ERPs for the central pedestal in a collinear or orthogonal context are superimposed in Fig. 4. Since the above analysis showed no significant difference between attending left and right-oblique axes, the ERPs elicited by the attention to the different axis were collapsed. The waveforms for the two stimuli configurations begin to diverge at the peak and descending edge of the N1 component, with the ERP for attended collinear flankers showing a greater positivity between 190 and 230 ms. The effect of contextual attention can be seen more clearly as difference waves (Fig. 5), obtained by subtracting the ERPs elicited by the pedestal in the orthogonal context from the pedestal in the collinear context on a point-by-point basis across the waveforms.

At midline electrode sites, a main effect of attention was significant in the latency range of 190–230 ms [$F(1,13) = 5.85, P < 0.03$]. Pedestals in a collinear context elicited a greater positivity compared to when the pedestal was in an orthogonal context. There were no significant effects of axis or any significant interaction between attention and axis. A sliding time window analysis starting at time zero revealed that the first 20 ms window to show an effect of attention for context was between 190 and 210 ms [$F(1,12) = 4.97, P < 0.05$]. The five succeeding time windows were also significant. The final window that showed statistical significance was 230–250 ms [$F(1,12) = 7.65, P < 0.02$]. At occipital midline electrode sites, the effect of attention for context to oriented flankers persisted from 190 to 250 ms (Table 2).

Table 1 – Experiments 1 and 2: subject accuracy (d')

Axis attended	Orientation of pedestal		Orientation discrimination
	Collinear	Orthogonal	
Experiment 1			
Left-oblique	1.94	1.00	3.35
Right-oblique	2.12	1.77	3.68
Experiment 2			
Left-oblique	2.12	1.98	3.46
Right-oblique	2.29	1.99	3.37

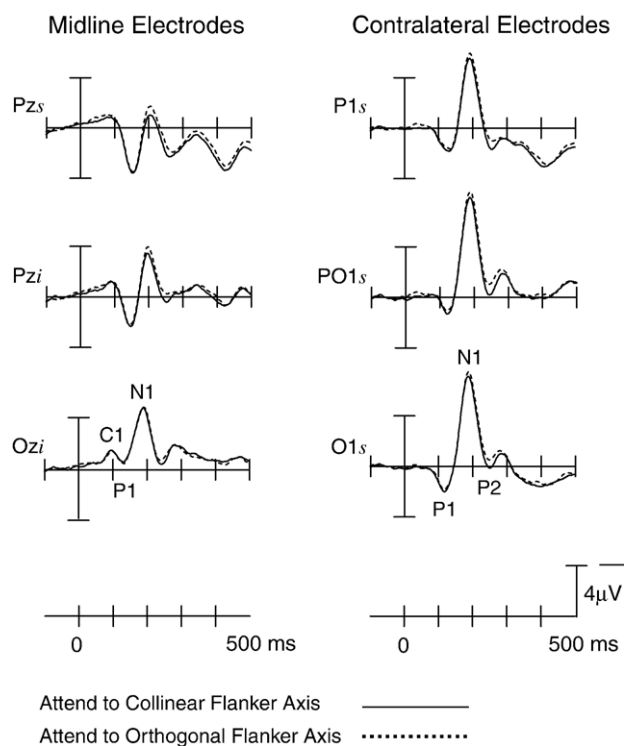


Fig. 4 – Experiment 2 Event-related potentials (ERPs) for occipital midline and contralateral electrodes re-referenced to the average mastoid. ERPs recorded from attending to collinear and orthogonal flanker configurations for pedestal trials only. At midline electrode sites, the ERPs contain C1, P1, and N1 components. At the lateral electrode sites, the ERPs contain P1, N1, and P2 components.

At lateral electrode sites, a similar attention effect for context was observed between approximately 230 ms and 280 ms. A main effect of attention was significant [$F(1,12) = 10.44, P < 0.01$]. Again, attention to collinear flankers elicited a larger positivity than orthogonal flankers. A hemisphere \times electrode interaction was also significant [$F(2,24) = 6.53, P < 0.005$]. The sliding window analysis revealed that the first time window to show a statistically significant effect of attention on context was between 190 and 210 ms [$F(1,12) = 5.85, P < 0.04$]. The subsequent windows were significant up until the 250–270 ms time window [$F(1,12) = 8.19, P < 0.02$]. At lateral occipital electrode sites, the effect of attention on context effect appeared between 190 and 270 ms (Table 2).

2.2.3. Scalp voltage topographies of the attentional effects

A comparison of the two longer-latency contextual attention effects revealed different voltage distributions (Fig. 6). The effect occurring between 190 and 230 ms was largest at midline occipital sites. Afterwards, the effect occurring between 230 and 280 ms was distributed with bilaterally symmetrical foci over lateral electrode sites.

We performed a further analysis comparing the scalp distribution during the occipital midline effect (i.e., the first time window in which the ‘attentional effect’ of attend-collinear versus attend-orthogonal was greatest, see above and Fig. 6), with that of the sensory C1 component (shown in Fig. 7, top panel), which is thought to originate in V1 (Di Russo et al., 2003).

This comparison was intended to test the hypothesis that the attention effect represented a modulation of the same V1 neural generators underlying the C1 component. For the scalp voltage analysis, component (C1 vs. late attention effect), electrodes (Pzs vs. Pzi vs. Ozi), and subject were specified as factors. A time window between 63 and 113 ms was specified to calculate the mean amplitude of the C1 component. A time window between 180 and 230 ms was used to calculate the mean amplitude of the midline attention effect. Main effects of component [$F(1,12) = 22.86, P < 0.0004$] and electrode [$F(2,24) = 3.90, P < 0.03$] were significant. However, the component \times electrode interaction [$F < 1$] was not significant, which would reflect a significant distributional difference. The lack of a significant interaction suggests the attention to context effect and the C1 may share a common neural generator. Moreover, the distribution of the attention effect occurring at 190–230 ms has a different topography in comparison to the sensory P1 and N1 components (Fig. 7), which both have a bilateral occipital scalp distribution. The difference in topography argues against extrastriate contributions to the attention effect observed at 190–230 ms.

3. General discussion

3.1. Summary

The present study recorded psychophysical performance and ERPs to a central target that was either collinearly or orthogonally oriented with respect to a pair of attended flanking elements. In Experiment 1, we found that contrast discrimination was better when the central target was collinearly vs.

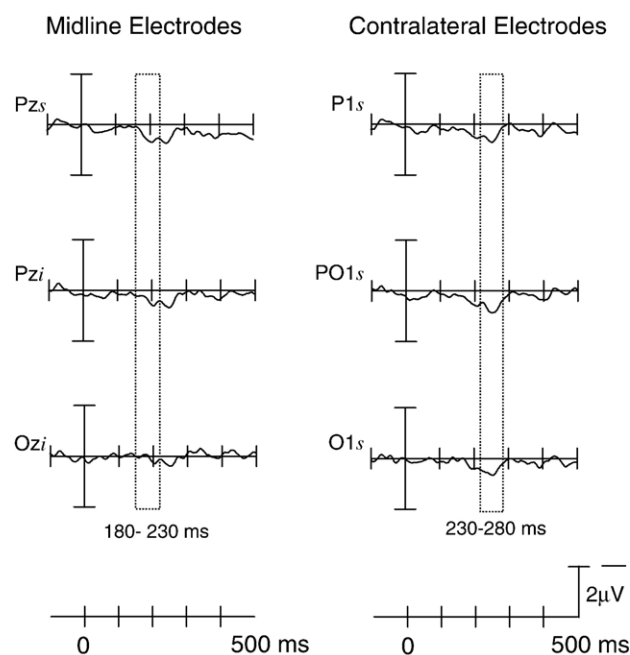


Fig. 5 – Experiment 2 ERP difference waves for attend-collinear minus attend-orthogonal (see main text for Eq. (3)). The right column shows midline occipital electrodes. The left column shows contralateral electrodes. The dotted boxes indicate the time window where the effect of attention to context was statistically significant.

Table 2 – Experiment 2: onset of collinearity difference (mean voltage, μV) for midline and lateral occipital electrodes (* indicates statistical significance)

Window (ms)	Midline			Lateral		
	F value	P value	Difference (μV)	F value	P value	Difference (μV)
0–20	<1	–	0.20	1.98	0.18	0.15
10–30	1.25	0.29	0.30	2.93	0.12	0.15
20–40	1.16	0.30	0.17	1.69	0.22	0.11
30–50	<1	–	0.28	1.11	0.31	0.09
40–60	<1	–	0.30	0.86	0.37	0.10
50–70	<1	–	0.28	<1	–	0.07
60–80	<1	–	0.25	<1	–	0
70–90	<1	–	0.21	<1	–	0
80–100	<1	–	0.16	<1	–	0.04
90–110	<1	–	0.11	<1	–	0.05
100–120	<1	–	0.07	<1	–	0.05
110–130	<1	–	0.08	<1	–	0.1
120–140	<1	–	0.09	<1	–	0.07
130–150	<1	–	0.07	<1	–	0.03
140–160	<1	–	0.09	1.70	0.21	0.06
150–170	<1	–	0.10	3.71	0.08	0.11
160–180	<1	–	0.20	2.75	0.12	0.17
170–190	1.02	0.33	0.38	2.37	0.15	0.27
180–200	2.60	0.13	0.55	3.17	0.10	0.36
190–210	4.97	0.047*	0.64	5.85	0.037*	0.42
200–220	5.86	0.032*	0.63	5.65	0.035*	0.44
210–230	6.20	0.028*	0.57	5.52	0.037*	0.46
220–240	6.57	0.024*	0.58	5.81	0.033*	0.54
230–250	7.65	0.017*	0.66	7.95	0.016*	0.63
240–260	7.63	0.017*	0.54	9.99	0.0082*	0.69
250–270	3.93	0.071	0.44	8.19	0.014*	0.66
260–280	2.05	0.17	0.35	4.42	0.057*	0.50
270–290	<1	–	0.13	2.27	0.15	0.30
280–300	<1	–	0.10	1.09	0.31	0.15

orthogonally oriented with respect to the task-relevant (i.e., attended) flankers, replicating [Freeman et al. \(2001, 2003\)](#) but with perifoveal target stimuli. In Experiment 2, we found electrophysiological evidence that attending to collinear flankers influences the processing of the central target differently compared to when attending to the orthogonal flankers. Two ERP amplitude differences were revealed between attending to the collinear versus the orthogonal

flankers. The first statistically significant effects of attention to collinear versus orthogonal flankers occurred between 190 and 230 ms with a scalp distribution focused over midline parietal-occipital sites. The second attentional difference occurred at an even longer latency between 230 and 280 ms with a lateral occipital distribution.

In our previous study ([Khoe et al., 2004](#)), we reported ERPs to collinear versus orthogonal flanker–target interactions, in

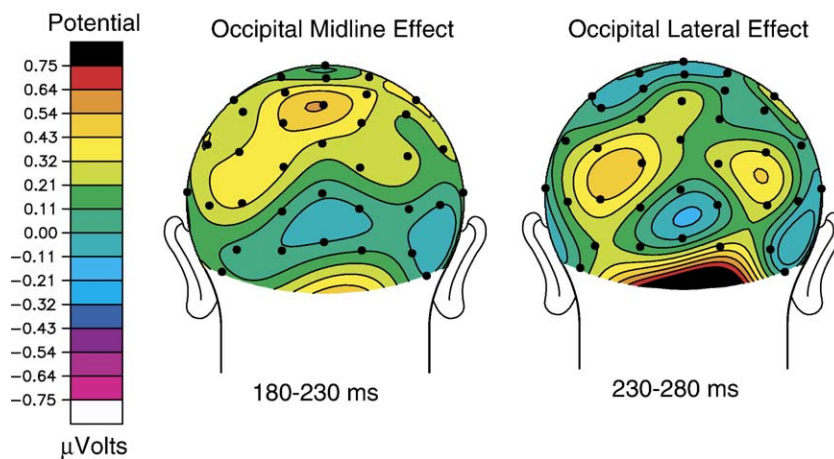


Fig. 6 – Scalp topographic voltage maps of the attend-collinear minus attend-orthogonal difference wave (rear view of head, referenced to the right mastoid). An occipital midline effect develops first (180–230 ms) followed by an occipital lateral effect (230–280 ms).

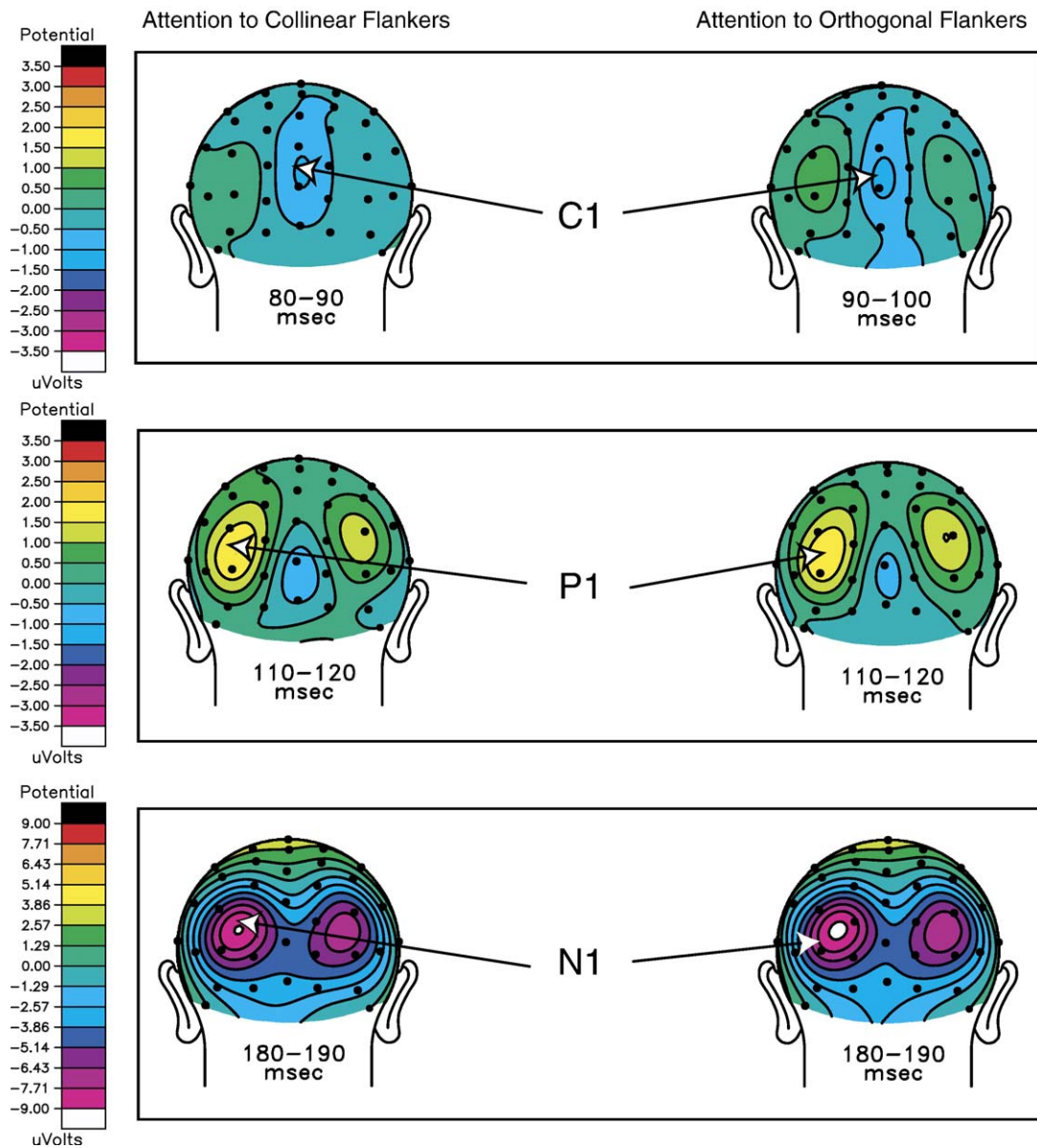


Fig. 7 – Scalp topographic voltage maps of the C1, P1, and N1 visual ERP components for attention to collinear and orthogonal flankers, in the rear view of the head, referenced to the right mastoid. The voltage scales corresponding to each figure pair is shown to the left of the pair.

the absence of any explicit manipulation of attention. There we found an earlier attention-independent or sensory effect between 80 and 140 ms. The scalp topography and early timing of that effect resembled that of the characteristic C1 component, which is thought to reflect the initial stimulus phasic response in V1 (Di Russo et al., 2003). The present finding of only relatively longer-latency (190–230 ms) attentional components suggests that attention does not modulate processing of lateral interactions during the initial stimulus-evoked afferent in V1. However, the scalp topography of this later attentional effect was statistically indistinguishable from the topography associated with the sensory C1 component. Given this close similarity, the present results are consistent with a model in which attention modulates lateral interactions at the neuroanatomical level of V1 via longer-

latency re-afferent activity from later visual processing stages.

3.2. Related studies

Past ERP and MEG (magnetoencephalography) studies of attention have shown the short-latency evoked C1 response to be invariant with attention (Di Russo et al., 2003; Martinez et al., 1999; Noesselt et al., 2002). This would be consistent with the present results. In apparent contradiction to this, however, Wu et al. (2005) recently reported an early effect of contextual cueing for the C1 component (48–72 ms) in a related lateral interaction paradigm based on Freeman et al. (2001). Their interpretation of this apparent early latency cueing effect was that attention may be modulating lateral interactions during the initial sensory

processing in V1. Wu et al.'s result clearly conflicts with ours as we found no such early component associated with attentional modulation of lateral interactions. A further difference is that they failed to find a reliable later effect in the N1 component, while we did. However, we have reason to question Wu et al.'s (2005) results and in particular whether their early attentional effect was indeed related to the classical C1 as they claimed.

To begin with, on inspection of Wu et al.'s Fig. 1, it appears that the difference between their attend-collinear and attend-orthogonal conditions is no larger in their early component (48–72 ms) than in the pre-stimulus period. As Wu et al. (2005) did not reference their averaged ERPs to a pre-stimulus baseline (as we did), it is unclear to what extent their effects represent signal or merely residual noise, though at best the signal-to-noise ratio for the early component must in any case be very small. A low signal-to-noise ratio might also explain why Wu et al. found no significant attentional effect in the later N1 component, though the trend appears in their Fig. 1. Secondly, it is difficult to assess whether the morphology of their claimed C1 attention effect is consistent with a V1 source. Numerous studies have reported that the C1 component is largest over midline parieto-occipital sites, in line with the orientation of the neural generators of the C1 in human calcarine cortex (Di Russo et al., 2003). However, in Wu et al.'s data, their claimed C1 component appears to onset 50 ms pre-stimulus and is statistically stronger at lateral occipital sites compared to midline occipital site Oz, while no significant effects were reported for occipital–parietal midline sites, which are also typically implicated in the classical C1 component. Scalp topographies might have helped to localize the source of the effect and its reliability with respect to nearby electrodes, but these were not shown in the Wu et al. paper. These concerns lead us to question Wu et al.'s conclusion that attention can modulate lateral interactions in V1 during the initial sensory evoked response.

The present study also goes beyond previous studies by providing both human electrophysiological and behavioral correlates of attentional modulation of lateral interactions, using standardized psychophysical procedures. This again contrasts with Wu et al., who used reaction time to index collinear and orthogonal flanker–target interactions. Several investigators have suggested that reaction time patterns associated with attentional cueing tasks could arise from either changes in perceptual or post-perceptual decision criteria (e.g., Hawkins et al., 1988). This study and past studies of lateral interactions have thus tended to use detection or discrimination measures that index sensory processes independent of subject decision criterion variability (Freeman et al., 2001, 2003; Polat and Sagi, 1993, 1994).

The longer-latency attention effects (i.e., 190–230 ms) in the present study are consistent with past studies that reported longer-latency modulations of sensory processing in V1 (Di Russo et al., 2003; Martinez et al., 1999; Noesselt et al., 2002) and V2/V3 (Woldorff et al., 2002). For example, Noesselt et al. (2002) found that spatial attention to left versus right hemifields modulates V1 sensory processing at a relatively late latency between 189 and 224 ms. They also found an additional source in right temporo-parietal cortex that contributed to the attention-related effects at that latency. In the present study, the contextual cueing effects peaked at 230 ms over occipital midline sites, with no effect being observed at temporo-parietal

electrode sites. Other fMRI studies of spatial attention cueing studies have implicated right temporo-parietal cortex for shifting attention between visual fields (i.e., Corbetta et al., 2000). The absence of parietal cortex participation in the present study might therefore be explained because the present experimental design did not require subjects to shift their spatial attention across the visual hemifields. Another apparent discrepancy is that Noesselt et al. observed attention-related modulations in extrastriate visual cortex (80–130 ms) prior to the longer-latency V1 attention effect (attended stimuli elicited a larger P1 component than did unattended stimuli), while no such attentional enhancements within the P1 time range were found in the present study. However, the present experiment did not manipulate attention between opposite hemifields, as did Noesselt et al. (2002), which would likely explain the observed absence of such lateralized P1 attentional components.

Because the spatial attention task demands between the different cueing conditions were effectively constant and the stimuli identical, we can attribute the longer-latency ERP differences to contextual cueing. This late attentional modulation likely reflects feedback projections from higher order visual areas, instead of a modulation of the initial feedforward activity from V1.

3.3. Physiology of lateral interactions

Several studies have found that neurons in the primary visual cortex of cats and monkeys are sensitive to the cues that result in perceptual grouping (Nelson and Frost, 1985; Gilbert et al., 2000; Kapadia et al., 1995; Polat et al., 1998). Studies of contour integration have shown that the response properties of V1 neurons are sensitive to the orientation of stimuli presented outside the boundaries of the receptive field; collinear stimuli presented outside the receptive field enhance the neuronal response (Kasamatsu et al., 2001; Mizobe et al., 2001). These context-specific effects are thought to be mediated via the long-range lateral connections that connect cortical columns of similar orientation preference within V1 (Ts'o et al., 1986). Attention has been shown to modulate the resulting contextual interactions. For example, Ito and Gilbert (1999) reported that focal attention to a collinear stimulus configuration increased the activity of V1 neurons by a factor of three compared to a divided attention condition. In addition, data from single unit physiology have shown that attentional modulation of V1 sensory processing occurs relatively late (Mehta et al., 2000; Vidyasagar, 1998). In particular, Roelfsema et al. (1998) reported enhanced longer-latency V1 activity for attended contiguous line segments. In that study, attentional enhancement occurred approximately 235 ms, well after the initial V1 sensory transient occurring at 35 ms. Roelfsema et al. (1998) interpreted this longer-latency effect as the result of feedback from higher order visual areas.

There is also physiological evidence suggesting that feedback signals from extrastriate visual areas amplify, or enhance the gain, of V1 neurons (Bourne et al., 2002; Hupe et al., 1998). In particular, Grossberg and Raizada (2000) have proposed that these feedback projections may allow attention to influence surround-receptive field interaction via the network of long-range horizontal connections. In the case of a collinear surround,

the interaction between attention and horizontal connections would perhaps be similar to attention increasing the effective contrast of a stimulus (Reynolds et al., 2000). Another possibility for the longer-latency effects observed could be due to the slow-conducting nature of the horizontal connections in relation to the initial feedforward input in V1 (Girard et al., 2001).

3.4. Conclusion

In conclusion, our human ERP results are broadly consistent with past physiological evidence for the role of attention in modulating fundamental perceptual grouping processes in early visual cortex. In further agreement with past animal studies, the present results argue in favor of the hypothesis that attention modulates lateral interaction only via feedback from higher cortical areas, rather than during the initial sensory transient in V1. The present combination of electrophysiology with robust psychophysical procedures provides a critical bridge necessary to understand the consequences of such attentional feedback for human perceptual grouping and performance.

4. Experimental procedures

4.1. Subjects

Twenty-two right-handed adults with normal or corrected vision from the university community served as paid volunteers. Ten of these participated in Experiment 1 (5 males and 5 females; age range 18–35, mean = 22 years); the remaining twelve participated in Experiment 2 (4 males and 8 females; age range 17–24, mean = 20 years). All were naive to the purpose of the study and had not previously experienced the stimuli or the task.

4.2. Stimulus display

Stimuli were displayed as a gray level modulation on a 12 in. NEC MultiSync E750 color CRT monitor, in 8-bit RGB mode with software gamma correction. The display was viewed at a distance of 120 cm under mesopic conditions (2.62 cd/m^2). A software look-up table was used for the gamma correction, based on display calibration data acquired shortly before to the first experimental session using a Minolta Chroma CS-100 photometer and Matlab software. Stimulus display and behavioral data acquisition was controlled by a PC running Neurobehavioral Systems Presentation software. The display consisted of a light gray central fixation cross (41.6 cd/m^2 , 0.2° of visual angle) on a gray background (36.0 cd/m^2). Gabor signals with wavelength (λ) and Gaussian distribution (σ) equal to 0.15° of visual angle (spatial frequency, 6.28 cycles per degree), and zero phase were generated using Matlab software. The location of the central target was 0.75° to the right of fixation and 0.09° above fixation. This variable-contrast target was superimposed on an identical 'pedestal' of fixed contrast (see below) in the same position. The positions of the flankers relative to fixation were as follows: top left flanker: 0.11° right, 0.74° above; top right flanker: 0.75° right, 0.74° above; bottom right flanker: 0.75° right, 0.55° below; bottom left flanker: 0.11°

right, 0.55° below fixation. The distance between the central stimulus and flankers was 5λ .

Dual-axis stimulus configurations were constructed with a central Gabor pedestal/target surrounded by two flanker pairs in an 'X' configuration. The central stimulus could be oriented collinearly with the pair of flankers on the left-oblique axis (Fig. 1a) or the right-oblique axis (Fig. 1b). Because of the dual-axis configuration, the central stimulus was oriented orthogonally to the other pair of flankers. The central pedestal contrast was fixed at 0.1 Michelson contrast [$C = (L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$], while the target contrast varied from 0.18 to 0.3. The contrast of the flankers was held constant at 0.2. The appropriate luminances to display were obtained from the look-up table described above. For the secondary flanker rotation discrimination task, elements in the left-oblique (Fig. 2c) or right-oblique (Fig. 2d) flanker pair were rotated 5° clockwise. Only the flankers were displayed in these rotated-flankers stimuli (i.e., zero-contrast central stimulus). The elements on the opposite flanker axis remained unchanged. Lastly, one stimulus configuration consisted of non-rotated flankers only (zero-contrast central stimulus), which were included for the ERP subtractions performed in Experiment 2 (Fig. 2e).

4.3. Design and procedure

At the start of each experimental block, two bar markers (0.8°) were presented for 2000 ms to cue the flanker pair to be attended for a possible rotation. Following a delay of 4000 ms, the pedestal, target, rotated flanker targets, and flanker-only trials were presented in a randomized sequence each for a duration of 83 ms. The inter-stimulus interval was randomly jittered between 800 and 1200 ms. The orientation of the pedestals (and superimposed targets) was randomized with respect to whether they were collinear or orthogonal to the task-relevant flankers. Each block consisted of 120 stimuli divided equally among the six stimulus types: collinear target, orthogonal target, collinear pedestal, orthogonal pedestal, flankers only, and rotated flanker targets.

We employed two randomly interleaved Go/No-Go tasks: contrast discrimination of the central patch and rotation detection of the cued flanker pair. In the contrast discrimination task, targets and pedestals were well above threshold. This was done to improve the signal-to-noise ratio for the recorded ERPs, which are often weak with the threshold level stimuli typically used in psychophysical contrast detection paradigms (e.g., Freeman et al., 2001). In addition, such a detection task should produce shorter response time latencies compared to discrimination and thus minimize the overlap between the ERP elicited for the response and the ERP evoked by the subsequent trial. For the secondary task, we used an orientation rotation detection to direct attention to the appropriate flankers, instead of Freeman et al.'s (2001) original two alternative forced choice (2AFC) Vernier offset judgment. Similar to the original Vernier offset judgment, subjects still had to attend to the global virtual contour formed between the flankers to perform the task. Subjects were instructed to respond with a button press whenever they detected the higher contrast central target and a separate button press to flanker-only displays in which there was a rotation of the flanker elements for the attended axis.

Subjects were informed that flanker rotations and target contrast increments would never occur for the same trial.

A 'hit' in the central target task corresponded with a response to a high contrast central target. A 'false alarm' for the central target task corresponded with a response to the lower contrast pedestal. A 'hit' in the secondary flanker task corresponded with a response to trials with rotated flanker elements. A 'false alarm' in the secondary task corresponded to a response for the flanker-only stimuli. After each block, subjects were informed of their hit and false alarm rates for both tasks. Achieving accuracy of responses (i.e., high hit and low false alarm rates) was stressed to the subjects, however, they were discouraged to take longer than 1000 ms for each response. The contrast of the target was adjusted in practice trials to obtain a value of d' less than 2.0 for each subject. For the flanker-rotation discrimination task, subjects practiced until d' values were between 2.0 and 3.0.

After four practice blocks, subjects in Experiment 1 ran in four blocks of each attended-axis condition for a total of eight blocks. In Experiment 2, eight blocks instead of four were run for each stimulus configuration. The order of blocks was counter-balanced between subjects.

4.4. Electrophysiological recordings

Scalp potentials were recorded from 64 evenly distributed tin electrodes mounted in a custom cap (Electro-Cap International). Electrodes in the 64-channel cap are labeled in reference to the 10–20 electrode location system. The single italicized letter following each electrode name describes whether it is slightly superior, inferior, anterior, or posterior to the closest electrode as described by the 10–20 system. Scalp and mastoid electrode impedances were maintained below 5 K Ω and 2 K Ω , respectively. The scalp recordings were referenced to the right mastoid during recording. Vertical eye movements were recorded by placing an electrode above the right and left eye referenced to electrodes FP1 and FP2 respectively. Horizontal eye movements were recorded by placing an electrode over the right outer canthus referenced to the left outer canthus. The left outer canthus electrode was referenced to the right mastoid. Consequently, vertical and horizontal eye movements were recorded as bi-polar channels during the experiment. Offline, eye channels were algebraically re-referenced to the right mastoid. All electroencephalographic (EEG) and electrooculographic (EOG) activities were amplified at an A.C. band-pass of 0.05–100 Hz, digitized at a 500 Hz sampling rate and a gain of 1000.

Subsequently, all ERPs were algebraically re-referenced to the left and right mastoid signal and filtered with a 9-point moving average filter to attenuate signals at and above 56 Hz at our sampling rate of 500 Hz.

4.5. Data analysis

For each subject, ERPs were averaged 1500 ms pre-stimulus and 1500 ms post-stimulus onset. Consequently, each epoch overlapped with the previous epoch. However, the randomized trial sequence ensured that the overlap from the responses to adjacent events in the sequence did not consistently differ between conditions. On average, therefore, the overlap for all event types would be roughly the same and would thus be eliminated during the subtractions (Woldorff,

1993). Offline, automated artifact rejection was used to reject trials that contained large eye movements ($>1^\circ$), blinks, muscle potentials, or amplifier blocking. To rule out any effects of small residual eye movements, the EOG was averaged and quantified in the interval 0–800 ms with respect to the onset of the pedestals, targets, and flankers. The averaged EOG were less than 2 μ V, corresponding to an ocular deviation of $<0.2^\circ$ (Luck and Hillyard, 1994). In addition, eye movements were monitored on-line with an infrared eye tracker (Applied Science Laboratories Model 504). When the subject's gaze deviated from fixation, the experiment was stopped and the subject was reminded to fixate on the fixation cross. These measures ruled out eye movement contamination as a source of the contextual attention effects discussed below.

The ERP amplitudes for the visual evoked potentials were quantified using a mean amplitude measure over a specified time window for the correctly rejected pedestal trials, with latency ranges bracketing the characteristic earlier components of the ERP grand-averaged over all relevant conditions. For the difference waves for midline electrodes (i.e., attend-collinear minus attend-orthogonal conditions), a time window of 190–230 ms and a pre-stimulus baseline of 100 ms duration were used to calculate the mean amplitudes. At lateral electrode sites, a time window of 190–280 ms was used to calculate the mean amplitudes with a pre-stimulus baseline of 100 ms. The data were analyzed in a repeated measures ANOVA, including the following factors: attention (to collinear flankers vs. orthogonal flankers), axis (left-oblique vs. right-oblique), electrode (Pzs vs. Pzi vs. Ozi), and subject. For lateral electrodes, an extra factor of hemisphere was included (left vs. right) in the ANOVA. ANOVA degrees of freedom were adjusted for heterogeneity of variance and covariance by the Greenhouse–Geisser epsilon coefficient. In addition, a sliding time window analysis with multiple ANOVAs was conducted using 20 ms windows (i.e., 0–20 ms, 10–30 ms, 20–40 ms, etc.) to specify the latency at which the ERP differences became statistically different.

4.6. Scalp distribution comparisons

A comparison between the scalp voltage topographies for the C1 component and attentional difference waves was conducted. A procedure similar to the one described by McCarthy and Wood (1985) was used to scale the amplitudes for the scalp distribution analysis. For each condition, the amplitudes were converted into z scores by subtracting the global scalp mean from each scalp amplitude value and dividing by the standard deviation. Scaling the amplitudes in this way ensures that group differences are eliminated while allowing interactions between scalp distributions to be tested.

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