Electrophysiological correlates of lateral interactions in human visual cortex

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Abstract

Detection thresholds for visually presented targets can be influenced by the nature of information in adjacent regions of the visual field. For example, detection thresholds for low-contrast Gabor patches decrease when flanked by patches that are oriented collinearly rather than orthogonally with the target. Such results are consistent with the known microanatomy of primary visual cortex, where long-range horizontal connections link cortical columns with common orientation preferences. To investigate the neural bases of collinearity effects, we recorded event-related brain potentials (ERPs) together with psychophysical measures for targets flanked by collinear vs. orthogonal gratings. Human volunteers performed a contrast discrimination task on a target grating presented at a perifoveal location. For targets flanked by collinear stimuli, we observed an increased positive polarity voltage deflection in the occipital scalp-recorded ERPs between 80 to 140 ms after stimulus onset. Such a midline occipital scalp voltage distribution of this ERP collinearity effect is consistent with a generator in primary visual cortex. Two later negative voltage ERP deflections (latencies of 245–295 and 300–350 ms) were focused at lateral occipital scalp sites, a pattern consistent with activity in extrastriate visual cortex. These ERP effects were correlated with improved contrast discrimination for central targets presented with collinear flanks. These results demonstrate that the integration of local flanking elements with a central stimulus can occur as early as 80 ms in human visual cortex, but this includes processes occurring at longer latencies and appears to involve both striate and extrastriate visual areas.
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1. Introduction

A critical function performed by early visual processing is to integrate information from local feature detectors with surrounding contextual information to form unified percepts. Several lines of research have now established that the response of visual cortical neurons to a stimulus presented inside the classically-defined receptive field (RF) can be modulated by stimuli located outside the RF in adjacent regions of visual space (see Albright & Stoner, 2002, for review). Typically, the geometric relationship between stimuli inside and outside the RF is important in determining the strength of these so-called "contextual influences" (e.g., Kapadia, Ito, Gilbert, & Westheimer, 1995). This contextual-integration may play an important role in feature completion (Allman, Miezin, & McGuinness, 1985; Marr, 1982; Mitchison & Crick, 1982) and the extraction of global object properties (Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003).

Psychophysical studies have revealed analogous behavioral effects of context on target detectability. For example, in the *lateral interaction* paradigm (Polat & Sagi, 1993, 1994), the perception of a low contrast grating stimulus is strongly influenced by the presence and orientation of flanking stimuli in the visual field. Detection of a low contrast central target (a Gabor

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patch composed of a sinusoidal contrast modulation convolved with a Gaussian envelope) was found to be dependent on the relative orientation of a pair of high contrast Gabor flankers. Thus, when all stimuli had the same orientation and were arranged in a *collinear* configuration (as if forming part of a virtual contour), contrast sensitivity improved compared to an isolated-target baseline, even for relatively large target–flanker separations. When target and flankers had *orthogonal* orientations with respect to one another, no such facilitation was observed.

This configuration-specific phenomenon has been replicated and generalized by a number of authors using Gabor stimuli, which are designed to resemble the receptive field profiles of cells in early visual cortex (Bonneh & Sagi, 1998; Freeman, Sagi, & Driver, 2001; Kovacs & Julesz, 1994; Polat & Sagi, 1993, 1994; Snowden & Hammett, 1998; Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001; Zenger & Sagi, 1996). Results are often discussed in relation to the cortical architecture of early visual areas, in particular the pattern of long-range horizontal connections linking neurons with common orientation tunings (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Chisum, Mooser, & Fitzpatrick, 2003; Fisken, Garey, & Powell, 1975; Gilbert & Wiesel, 1979; Hirsch & Gilbert, 1991; Hubel & Wiesel, 1983; Ts'o, Gilbert, & Wiesel, 1986). There have been numerous studies in non-human primates examining the physiology of long-range horizontal connections, however only a few studies have combined physiology and psychophysics. Studies using both approaches have revealed a close relationship between these different measures of contextual integration (Chen, Kasamatsu, Polat, & Norcia, 2001; Kapadia et al., 1995).

In one particularly relevant human study, Polat and Norcia (1996) recorded steady-state visual evoked potentials (SSVEPs) to collinear and orthogonal Gabor target–flanker configurations, which were repeatedly flashed at a frequency of 4.1 Hz. The SSVEP was acquired by performing a frequency analysis on the electroencephalogram (EEG) that extracted the brain activity driven by the presentation rate of the stimuli of interest. An enhanced SSVEP amplitude was observed for the collinear compared to orthogonal stimuli. Polat and Norcia concluded that the presence of collinear flanks increased the effective contrast of the central stimulus. However, in this study it was not possible to determine either the precise time of onset of stimulus-evoked activity or the time-course of its cascade through the visual system. Moreover, there was limited information about the spatial distribution of activity, as they used only 5 electrodes arranged around the occipital pole. In addition, behavioral data was not collected, and the stimuli used were rather different (in terms of their temporal characteristics and suprathreshold contrast of

the target) than those used in the classical lateral interactions studies.

To characterize the temporal and spatial structure of lateral interactions in humans, we recorded event-related potentials (ERPs) to collinear and orthogonal Gabor stimulus configurations using a dense array of scalp electrodes. In contrast to SSVEPs, the temporal resolution of ERPs is much higher, which makes it possible to quantify the latency of any observed contextual effects in the visually evoked responses. For example, a modulation of the short-latency primary visual cortex C1 component in conjunction with a spatial distribution over midline occipital regions would suggest that integration of the collinear flankers occurred within the intrinsic circuitry of primary visual cortex. In contrast, modulation of longer latency components might instead suggest the involvement of early extrastriate visual cortex or feedback signals from extrastriate areas to primary visual cortex. We also collected psychophysical data concurrently with the ERPs to determine the behavioral correlates of any configuration-specific ERP effects. To our knowledge, this is the first study to attempt such a combined psychophysical and electrophysiological investigation of lateral interactions in humans.

2. Experiment 1—Lateral interactions at perifoveal locations

Before measuring the ERPs to collinear and orthogonal Gabor stimulus configurations, we first replicated the psychophysical paradigm of Polat and Sagi (1993, 1994) under conditions suitable for simultaneous measurement of ERPs in order to confirm that our method could produce a reliable behavioral correlate. Past ERP studies have observed that stimuli presented along the horizontal meridian may stimulate both banks of the calcarine sulcus (Clark & Hillyard, 1996). If the collinearity effect is generated in early visual areas, as suggested by single-unit primate studies (Chen et al., 2001; Kapadia et al., 1995; Polat, Mizobe, Kasamatsu, & Norcia, 1998), then stimulating both banks of the calcarine sulcus may generate dipoles of opposite orientation that cancel one another. However, recent psychophysical studies have found that as collinear stimuli configurations move from the fovea towards the periphery of the visual field, the initial enhancement associated with collinear stimuli configurations reverses to suppression (Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). To achieve a compromise between these two constraints, the stimuli were presented in the perifovea.

Furthermore, we used a contrast discrimination task instead of a contrast detection task to address the concern that the ERPs recorded to faint threshold stimuli in

a detection task would have a low signal-to-noise ratio (S/N). The discrimination task allowed us to record ERPs to higher-contrast stimuli. In the present study, we used a fixed pedestal contrast. Both the pedestal and target contrast were at suprathreshold contrast levels. Hence, the quality of the ERPs to suprathreshold stimuli would have a higher S/N than those recorded for faint near-threshold stimuli. Collinear and orthogonal trials were randomly intermixed within the same experimental block, reducing the likelihood of subjects to differentially distribute their spatial attention as a function of stimulus configuration. Lastly, trials consisting of only flankers were included in the experiment. These trials were important in the ERP design to isolate the effect of context, as explained later in Experiment 2.

2.1. Subjects

Ten right handed, normal adults with corrected-to-normal vision from the Duke University community (7 males and 3 females; age range 19–33, mean = 24 years) served as paid volunteers in the experiment. All subjects were naïve in regards to the experiment.

2.2. Stimuli

Stimuli were displayed as a grey level modulation on a NEC MultiSync E750 color monitor in 8-bit RGB mode using a software look-up table for gamma correction. Background luminance was 37 cd/m^2 and viewing distance was 120 cm in a darkened room. A high-contrast cross (0.09×0.09 deg of visual angle) was

maintained as a fixation point throughout the entire run in the center of the screen. Stimuli consisted of configurations of Gabor patches, defined as a sinusoidal-modulated carrier with a wavelength (λ) of 0.15 deg of visual angle (spatial frequency of 6.7 cycles/deg) convolved with a Gaussian envelope with a distribution (σ) also equal to 0.15 deg. Phase was fixed at zero (even-symmetric). Center-to-center separation between individual patches was 4 λ (as established by Polat and Sagi (1993, 1994)) to produce consistent flanker facilitation. The contrast of the flanking Gabors was 0.5 (Michelson contrast). Pedestal contrast was fixed at 0.1, while the target contrast varied from 0.11–0.4; these contrast values were adapted from Chen and Tyler (2001). The location of the targets and pedestals relative to the fixation cross was 0.50 deg to the right of fixation and 0.45 deg above fixation (i.e., 0.67 deg diagonally from fixation).

A combination of vertically and horizontally-oriented flanking Gabor stimuli composed two stimuli configurations either with or without a central stimulus (see Fig. 1a–d). The central stimulus was always oriented vertically. In one condition, the flankers were presented with the pedestal/target (Fig. 1a and b). When the flankers were oriented vertically, this created a collinear-flanker condition with a global vertical contour (Fig 1a). When the flankers were oriented horizontally, this created an orthogonally flanked condition (Fig. 1b). In the second condition, the flankers were presented alone (Fig. 1c and d). The local orientation of the flankers in this condition were collinear (Fig. 1c) or orthogonal (Fig. 1d).
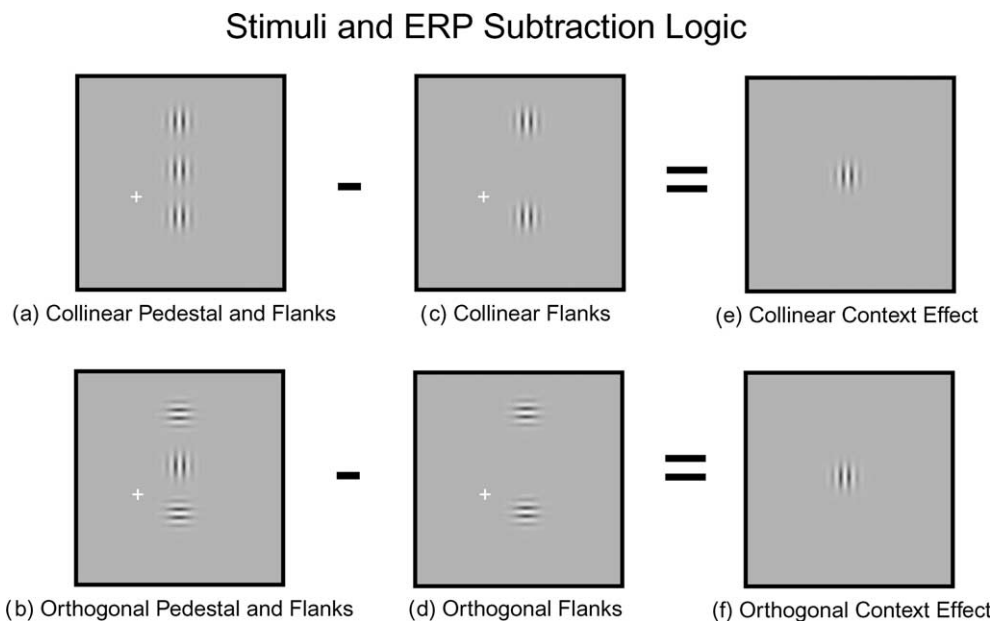
Stimuli and ERP Subtraction Logic

Fig. 1. Stimuli configurations used in Experiments 1 and 2 and ERP subtraction logic. Distance center to center $= 4\lambda$. The parameters of the Gabor stimuli were 6.28 c.p.d, $\lambda = 0.15$ deg, and $\sigma = 0.15$ deg. The contrast of the central patch is enhanced for demonstration purposes. Subtracting stimuli "*c*" from "*a*" and "*d*" from "*b*" results in the identical physical stimulus being isolated.

The above described stimuli configurations were presented in random order. The interstimulus intervals (ISIs) were randomly jittered between 800 and 1200 ms. The presentation duration for each configuration was 83 ms. Each experimental block consisted of 120 trials. Forty of these consisted of flanker-only displays. These 40 trials were divided equally between the collinear and orthogonal flanker-only trials. The remaining 80 trials were divided equally between the collinear and orthogonal pedestal/target and flanker configurations. For the 40 collinear trials, half of the trials consisted of the pedestal and flankers, while the other half consisted of the pedestal plus target with flankers. The 40 orthogonal trials were divided in a similar fashion.

2.3. Procedure

Each subject was tested in one experimental session for approximately 1 h. Subjects were instructed to press a button when they saw a target that was of a higher contrast than the pedestal and to ignore the orientation of the flankers. Otherwise, subjects were instructed to not respond. Accuracy and response time data (RT) were collected for each subject. A correct response within 200–800 ms after stimulus onset to the higher contrast intensity target was scored as a hit. A response to the pedestal was scored as a false alarm. For each subject, d' was calculated from the hits to targets and false alarms to pedestals. False alarms to the flanker-only trials were assessed separately. During preparatory blocks, the target contrast intensity was decreased by the experimenter to achieve a suprathreshold d' of less than 2. After each of these blocks, the subjects were informed of their hit and false alarm rates. Subjects were told that accuracy (i.e., high hit rates and low false alarm rates) was more important than speed of response.

Subsequently, eight experimental blocks were run using the contrast intensities determined in the preparatory blocks, with feedback to the subject given after each block.

An eye-tracker (Applied Science Laboratories Model 504) was used to ensure that subjects kept their eyes on the fixation cross. When subjects appeared to be moving their eyes (by more than ~0.5 deg), the run was paused and the subject was reminded to keep his or her eyes on the fixation cross before continuing.

2.4. Results and discussion

Accuracy data was entered into a one-factor repeated-measures analysis of variance (ANOVA), with the collinear and orthogonal stimulus configurations as the two levels (Table 1). There was a significant difference between the two configurations using a target and pedestal with flankers [$F(1,9) = 7.12$, $p < 0.03$]. Subjects were better at discriminating high contrast targets

Table 1
Subject behavioral performance for Experiments 1–2

Experiment	Stimulus configuration			
	Collinear		Orthogonal	
	d'	RT	d'	RT
1	1.64	522.09	1.41	547.02
2	1.28	508.04	1.09	502.05

from pedestals when presented with collinear rather than orthogonal flankers. False alarms to the flanker-only trials were also analyzed. Subjects had a zero false alarm rate for the collinear flanker-only condition and less than 1% false alarm rate for the orthogonal flanker-only condition. Hence, the false alarm rates to the flanker-only trials would have had a negligible impact on sensitivity estimates for the conditions using a target or pedestals. RTs did not differ significantly between the two stimulus configurations, providing no evidence of a tradeoff between speed and accuracy.

These results differ strikingly from those obtained in previous contrast discrimination studies (e.g., Chen & Tyler, 2001; Williams & Hess, 1998; Xing & Heeger, 2000; Zenger-Landolt & Koch, 2001). Those studies found *suppression* with suprathreshold foveal targets and pedestals in collinearly-flanked configurations. Here, however, we found *facilitation* from collinear flankers under similar contrast conditions. The critical differences between these studies may be the location of the stimulus: the target was presented perifoveally in the present study, but foveally in all previous studies.

3. Experiment 2—ERPs of lateral interactions

ERPs were recorded using the same design as in Experiment 1 to produce reliable collinear facilitation. Analogous to a recent approach used for studying the interactions of attentional context and multisensory processing (Woldorff & Busse, 2002), an ERP "double subtraction" method was used to isolate the effect of collinearity context (see Fig. 1). If we define a pedestal presented within a collinear context as "P^C" and the collinear flankers as "F^C", then the whole pedestal with collinear flankers configuration may be written as $(P^C + F^C)$. Similarly, a pedestal with orthogonal flankers would be defined as $(P^O + F^O)$, with "P^O" as a pedestal in a orthogonal context and "F^O" as the orthogonal flankers. Using the above notation, the following four stimuli combinations can be derived:

$(P^C + F^C)$ = pedestal and collinear flankers

$(P^O + F^O)$ = pedestal and orthogonal flankers

(F^C) = collinear flankers only

(F^O) = orthogonal flankers only

Next, the flanker-only trials can be subtracted from the pedestal and flanker configurations to isolate the ERP to the physical stimulus (see Eqs. (1) and (2) below). Hence, the resulting ERP would be for the identical physical stimulus, differing only in context (Fig. 1e and f). A subsequent subtraction (Eq. (3) below) performed between the collinear and orthogonal context waveforms would isolate the effect of context. The subtractions outlined above can be written as follows:

$$(P^C + F^C) - (F^C) = P^C \qquad (1)$$

$$(P^O + F^O) - (F^O) = P^O \qquad (2)$$

$$(P^C) - (P^O) = \text{effect of context} \qquad (3)$$

Since volume-conducted voltage fields sum linearly (Nunez, 1981), the subtractions outlined above can be used to identify the physiological signature of lateral interactions. The initial subtraction of the flanker-only ERPs from the pedestal and flanker ERPs removes the simple linear contribution of the flankers (Eqs. (1) and (2)), therefore yielding the activity elicited by the pedestal alone, plus the effect of context. However, the neuronal mechanism underlying contextual interactions may not be linear. Increased sensitivity to stimuli may arise from several possible non-linear interactions, such as a multiplicative increase in firing rate, an increase in the effective contrast of the stimulus (cf. Reynolds, Pasterniak, & Desimone, 2000), or a normalization mechanism that is contingent upon the relative contrast of the flankers and target (Cavanaugh, Bair, & Movshon, 2002; Sceniak, Hawken, & Shapley, 2001). The present study does not attempt to distinguish between these alternative mechanisms; however, any non-linearities should not make a difference to the critical outcome of the second subtraction (from Eq. (3)), as any context effect of collinear vs. orthogonal flankers should still be revealed in the resulting ERP difference waves.

3.1. Subjects

Nineteen normal adults from the Duke University community with corrected-to-normal vision (10 males and 9 females; age range 18–32, mean = 22 years) served as paid volunteers in the experiment. Two of the subjects were laboratory personnel familiar with the experiment, and 17 were naïve volunteers.

3.2. Stimuli and procedure

Stimulus parameters and experimental procedure were similar to Experiment 1, with the exception that subjects were run in 14 experimental blocks.

3.3. Electrophysiological recordings

Scalp potentials were recorded from 64 tin electrodes mounted in a custom cap (Electro-Cap International) that were evenly distributed across the scalp. Electrodes in the 64 channel cap are described in reference to the 10–20 electrode location system. The single italicized letter following each electrode name describes the closet location of the electrode relative to the 10–20 electrode coordinate system: *superior*, *inferior*, *anterior*, or *posterior*. Scalp and mastoid electrode impendence was maintained below 5 and 2 kΩ respectively. All scalp channels were referenced to the right mastoid. Vertical eye movements were recorded by placing an electrode above the right and left eye referenced to electrodes *FP*1 and *FP*2, respectively. Horizontal eye-movements were recorded by placing an electrode over the right outer canthus that was 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 bipolar channels during the experiment. Offline, eye channels were algebraically re-referenced to the right mastoid. All electroencephalographic (EEG) and electrooculographic (EOG) activity was digitized at 500 Hz with an amplifier AC bandpass of 0.05–100 Hz, had a gain of 10 000, and was stored for off-line averaging. Subsequently, all ERPs were algebraically re-referenced to the left and right mastoid signal and filtered with a nine-point moving average filter to attenuate signals at and above 57 Hz at our sampling rate of 500 Hz.

3.4. Data analysis

Behavioral accuracy and RT data were recorded for each subject. For each subject, d' was calculated from the hits and false alarms to targets and pedestals-alone for each stimulus configuration. Trials included in the ERP analyses were sorted on the basis of the subject's behavior. For example, only trials with "correctly rejected" pedestals and "hits" to targets were included in the ERP analysis.

ERPs were averaged separately for the two pedestal-flanker configurations, and each electrode site. For each subject, ERPs were averaged from 1500 ms pre-stimulus onset to 1500 ms post-stimulus onset. Consequently, each epoch overlapped with the previous epoch. However, the temporally jittered ISI "smeared out" most of the overlap from the adjacent events in the sequence (Woldorff, 1993). In addition, since the sequence of the trial types was randomized, any residual overlap should be approximately equivalent on average for the different trial types, which may then be eliminated in the subsequent subtraction analyses.

Offline, automated artifact rejection was used to reject trials that contained large eye-movements (>1 deg),

blinks, muscle potentials, or amplifier blocking. Next, EOG's were averaged and time-locked to pedestals, targets, and flankers in order to screen the subjects for any systematic drifts in eye-position from fixation (<1 deg). As a result of this analysis, large eye-movement artifacts can be reliably ruled out as the source of the contextual effects discussed below. In addition, a strict criterion was used to choose which subject ERP data to include for analysis. An independent expert rater, blind to the details and purpose of the experiment (e.g., all stimuli were collapsed into one waveform), rank-ordered the subjects on the basis of the S/N (i.e., amplitude of the residual activity in the pre-stimulus baseline vs. the post-stimulus evoked potential), latency, polarity, and scalp distribution of the visual ERPs (i.e., C1, P1 and N1 occipital visual components). Nine subjects were rejected from further analysis due to low S/N or excessive eye movement (see above). This lower S/N was most likely due in part to the relative faintness of the stimuli. The resulting ERPs were grand-averaged for the resulting waveforms discussed below.

ERP amplitudes were quantified in terms of peak amplitude (maximum or minimum deflection within a specified time window) or mean amplitude measures over a specified time window. Both were referenced to a baseline of 100 ms pre-stimulus onset. These measures were taken from the average waveform. "Difference waves" were calculated by subtracting point by point the ERPs recorded for the collinear and orthogonal stimulus configurations (Eqs. (1)–(3)) and entered into an ANOVA.

To quantify the onset of the difference waves, a fractional local peak latency analysis was performed. This analysis finds an extremum in a pre-defined search window and calculates a "fractional amplitude", in this case 0.2 of the value found at the extremum. Data points at successively smaller latencies are compared to this fractional amplitude. The point at which the amplitude falls below the fractional amplitude approximates the onset of the effect. A baseline of 100 ms pre-stimulus and 40 ms post-stimulus was used for this analysis. Ten ms windows were used to search backwards in time from the local extremum until the values fell below the criterion value set by the fractional amplitude.

Scalp voltage topographies for the early visual evoked potentials (VEP) components and double-difference context effect were constructed with 10 ms time windows. The topographies of the early collinearity difference and the C1 were entered into an ANOVA, with component (short-latency difference vs. C1) and electrode location as factors to infer whether common neural generators may be contributing to the effect of interest. As well, the ANOVA was performed with a normalization procedure (McCarthy & Wood, 1985). The ANOVA model assumes that ERP source strength is additive, but source effects are multiplicative and

differences in multiplicative source strength across experimental conditions may lead to erroneous significant condition×location interactions. To circumvent this problem, a re-scaling of the data was performed to remove differences in mean and variance between different experimental conditions. A z-score normalization was used in the present experiment (Kounios & Holcomb, 1994); mean amplitudes for each component were converted into z-scores across the levels of scalp electrodes and, following the transformations, the z-scores were entered into an ANOVA.

3.5. Behavior

During the experiment, discrimination accuracy tended to improve due to practice such that the initial contrast intensity was no longer appropriate for some subjects by the end of the experiment. In contrast to the first experiment, this experiment ran 14 rather than 8 experimental blocks. Examining the data from the last two experimental blocks confirmed that overall d' averaged across the two stimulus configurations was greater than 2. Consequently, data from the last two experimental blocks was not included in the behavior and ERP analysis, even though including the last two blocks resulted in greater overall performance in the collinear configuration condition relative to the orthogonal condition. A repeated-measures ANOVA performed on the remaining 12 experimental blocks showed significantly higher contrast discriminability for collinear compared to orthogonal configurations [$F(1,9) = 7.60$, $p < 0.022$] (Table 1).

3.6. ERP waveforms

The visual ERPs to the pedestals alone (correctly rejected) and targets (hits) were characterized by a series of early VEP including the early C1, P1 and N1 components (Fig. 2). Latencies for each component were determined from the grand average waveforms. At midline occipital-parietal electrode sites (Pzi, Ozs and Ozi), an initial negative deflection at 82 ms (C1) was followed by positive and negative deflections at 153 ms (P1) and 200 ms (N1), respectively. Similarly, at lateral occipital sites (O1s, O2s, PO1, PO2, P1s and P2s), a negative deflection at 80 ms (C1) was followed by positive and negative deflections at 151 ms (P1) and 196 ms (N1), respectively.

3.7. Short-latency interactions

The waveforms for the collinear flankers-only stimuli elicited a larger negativity relative to the collinear pedestal with flankers stimuli, starting at approximately 80 ms and ending at 140 ms (Fig. 2). No such differences were observed in the orthogonal condition. To clearly
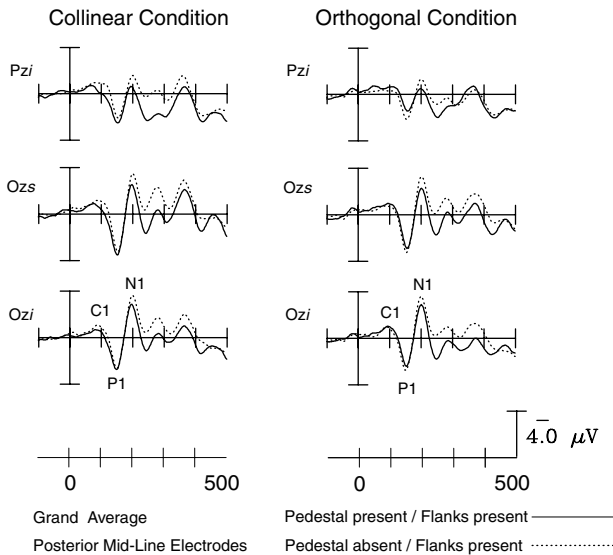
Fig. 2. Event-related potentials (ERPs) from Experiment 3 recorded from occipital mid-line electrodes re-referenced to the average mastoid. ERPs recorded from the collinear and orthogonal stimuli conditions for the flanker and pedestals, and the flanker only conditions. The ERPs contain C1, P1 and N1 components.
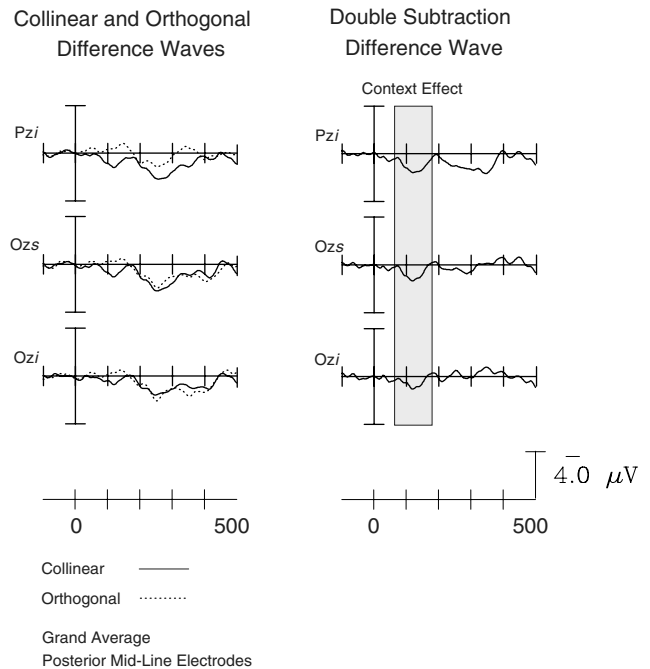

Fig. 3. The product of the subtractions from Experiment 3 from occipital mid-line electrodes re-referenced to the average mastoid. The left column contains the initial subtraction of subtracting the flankers from the collinear and orthogonal stimulus configurations to isolate the identical physical stimulus. The right column contains the subtraction of the waveforms from the left column (i.e., collinear context–orthogonal context) to segregate the effect of context. The grey shaded box indicates the portion of the waveform where the effect of context was statistically significant.

see the variance between the two stimuli configurations, difference waves to the two flanker orientation conditions were computed by subtracting the ERPs for the flanker-only stimuli from the ERPs for the pedestal with flanker stimuli for each of the collinear and orthogonal stimulus configurations (Eqs. (1) and (2)). The resultant waveforms represent the neuronal response for the physically identical pedestal only, as the ERPs from the flankers have been removed (Fig. 3).

The difference wave for the collinear condition elicited a larger positivity, starting at approximately 80 ms and ending at 140 ms, compared to the orthogonal condition difference wave. Subsequently, subtracting the two difference waves from each other cancels the activity elicited by the pedestal stimuli (Eq. (3)). Thus, the residual ERP after the second subtraction is the ERP correlate of the collinear vs. orthogonal context effect (Fig. 3). The resulting wave contained an early peak starting at approximately 80 ms that extended to 140 ms.

Previous ERP research suggested that midline occipital electrodes are optimally located to record potentials originating from striate cortex (Clark & Hillyard, 1996; Gomez Gonazalez, Clark, Fan, Luck, & Hillyard, 1994; Jeffreys & Axford, 1972). For midline occipital electrode sites (Pzi, Ozs and Ozi), the difference waves from the initial subtraction were entered into an ANOVA with the following factors: stimulus configuration (collinear vs. orthogonal), stimulus (pedestal alone vs. target), and electrode location. A time window of 80–140 ms and pre-stimulus baseline of 100 ms was used to measure the mean amplitude. A main effect of

collinearity was significant [$F(1,9) = 10.62$, $p < 0.01$], with the collinear context eliciting a larger positivity than the orthogonal context. There were no other significant main effects or interactions. In addition, multiple ANOVAs were performed using a sliding time window of 20 ms from 0–180 ms (i.e., 0–20 ms, 10–30 ms, 20–40 ms, etc.) to provide a finer temporal analysis of the collinearity effect (Table 2). Starting at time zero, the first window to show a significant difference was at 100–120 ms [$F(1,9) = 9.93$, $p < 0.014$], although the trend of increasing F-values appeared to begin at 80 ms. Analysis of the fractional peak latency analysis revealed the onset of this effect began at approximately 80 ms at midline electrode sites. A significant contextual difference was sustained for the subsequent windows to 130–150 ms [$F(1,9) = 6.69$, $p < 0.03$].

Lateral occipital electrode pairs (O1s/O2s, PO1/PO2, and P1s/P2s) were also entered into an ANOVA with the following factors: hemisphere (left vs. right), stimulus configuration (collinear vs. orthogonal), stimulus (pedestal alone vs. target), and electrode. A time window of 90–140 ms and pre-stimulus baseline of 100 ms was used to measure the mean amplitude. Similar to the results with midline electrodes, the main effect of collinearity was significant [$F(1,9) = 5.31$, $p < 0.05$]. No other

Table 2
Experiment 2: Onset of collinearity difference for midline and lateral occipital electrodes

Window (ms)	Midline			Lateral		
	F-value	*p*-value	Difference (μV)	*F*-value	*p*-value	Difference (μV)
0–20	<1	–	0.09	<1	–	−0.028
10–30	<1	–	0.16	<1	–	−0.022
20–40	<1	–	0.18	<1	–	−0.037
30–50	1.41	0.26	0.33	<1	–	0.071
40–60	3.37	0.099	0.42	<1	–	0.15
50–70	2.59	0.14	0.33	<1	–	0.1
60–80	1.02	0.34	0.25	<1	–	0.061
70–90	1.02	0.34	0.36	<1	–	0.16
80–100	1.80	0.21	0.65	<1	–	0.36
90–110	3.40	0.098	0.88	1.60	0.24	0.55
100–120	9.33	0.014*	1.09	4.48	0.063	0.76
110–130	17.75	0.0023*	1.23	7.08	0.03*	0.87
120–140	11.34	0.0083*	1.19	5.05	0.05*	0.75
130–150	6.69	0.029*	1.07	3.14	0.11	0.56
140–160	2.67	0.14	0.84	1.43	0.026	0.39
150–170	<1	–	0.48	<1	–	0.13
160–180	<1	–	0.17	<1	–	−0.11

*Indicates significance.

effects were significant. As well, a sliding time window analysis with 20 ms bins was performed (Table 2). The first time window to exhibit a significant difference was at 110–130 ms [$F(1,9) = 7.08$, $p < 0.03$]. In contrast to results with the midline electrode sites, the significant difference was of a shorter duration, continuing only to the next subsequent window at 120–140 ms [$F(1,9) = 5.05$, $p < 0.05$].

3.8. Longer latency interactions

In addition to the short-latency context differences, longer latency differences were observed in the difference waveforms. Between 245 and 350 ms, two negativities were observed at lateral occipital electrode sites, which appeared to have some temporal separation. For the first negativity between 245 and 295 ms, lateral occipital electrode pairs (O1*i*/O2*i*, TO1/TO2 and P3*i*/P4*i*) were entered in to an ANOVA. The factors entered into the ANOVA were hemisphere (left vs. right), stimulus configuration (collinear vs. orthogonal), stimulus (pedestal alone vs. target), and electrode site. The main effect of stimulus configuration was significant [$F(1,9) = 5.18$, $p < 0.05$], with collinear stimulus configuration eliciting a larger negativity vs. the orthogonal stimulus configurations. Other significant main effects were stimulus [$F(1,9) = 5.81$, $p < 0.039$] and electrode site [$F(2,18) = 4$, $p < 0.037$]. The stimulus x electrode site interaction was also significant [$F(2,18) = 10.64$, $p < 0.001$]. The second negativity between 300 and 350 ms was entered into a similar ANOVA, except the electrode site factor included an additional pair of electrodes (O1/O2). The main effect of stimulus configuration was significant [$F(1,9) = 7.64$, $p < 0.02$]. Again, collinear stimulus

configurations elicited a larger negativity relative to orthogonal configurations. Other significant effects include the main effect of electrode site [$F(3,27) = 5.34$, $p < 0.005$], hemisphere x stimulus interaction [$F(3,27) = 5.74$, $p < 0.04$], and stimulus x electrode site interaction [$F(3,27) = 12.32$, $p < 0.001$].

At contra-lateral electrode sites (O1*s*, O1*i* and P3*i*), the visual evoked responses for pedestals (correctly-rejected) and targets (hits) for the two flanker conditions were entered into an ANOVA. The factors entered into the ANOVA were stimulus configuration (collinear vs. orthogonal), stimulus (pedestal alone vs. target) and electrode site in the N2 time range at 260–300 ms. An interactions between stimulus configuration and stimulus was highly significant ($F(3,27) = 8.58$, $p < 0.017$). The *N2* for targets in the collinear condition was larger than for the pedestals. In contrast, there was no difference in the *N2* component for targets and pedestals in the orthogonal conditions.

3.9. Scalp voltage topographies

Past ERP studies have reported that the scalp topography of the C1 is typically focused at midline occipital electrode sites, whereas the P1 and N1 is maximal at lateral electrode sites. Dipole modeling, retinotopic mapping, and multi-channel scalp-recording techniques have suggested the C1 is generated in primary visual cortex, whereas the P1 and N1 are generated in extrastriate visual areas (Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Heinze et al., 1994; Jeffreys & Axford, 1972; Mangun, 1995; Woldorff et al., 1997). Consistent with past ERP literature, the C1 component in the present

study was focused at midline occipital electrode sites, while the P1 and N1 components were focused at lateral occipital sites.

Inspection of the scalp topographies of the short-latency double subtraction context effect revealed a sharp focus at midline occipital electrode sites beginning at 60–70 ms and ending at 140–150 ms (Fig. 4). Qualitatively, the topography of the short-latency difference was similar to the C1 topography, with a maximum at midline occipital electrode sites, which is consistent with a generator in primary visual cortex. In other words, the topography of the difference wave overlapped with the C1 midline maximum and not the P1 lateral maximum (Fig. 5). In addition, the scalp voltage topographies of the longer latency effects at 245–295 ms and 300–350 ms revealed a sharp focus at lateral occipital sites, which is consistent with a generator in extrastriate cortex. The topography and polarity of these longer-latency effects were similar to the N1 component (Fig. 6).

ANOVAs were performed for four groups of electrode sites (Tables 3 and 4). For the short-latency difference, a time window of 100–150 ms was used to compute the mean amplitude. For the C1 component, a time window of 55–105 ms was used to compute the mean amplitude. A baseline between 100 pre-stimulus to time zero was used. The four groups included a column of electrodes from occipital midline sites (Pzs, Pzi, Ozs, Ozi) and rows of electrodes from different regions of the occipital region (group 1: P1, Pzi, P2; group 2: PO1, Ozs, PO2; group 3: O1, Ozi, O2). The results of the ANOVA are presented in Table 3. Without the normalization procedure, a main effect of component was highly significant for all electrode sites. However, only one component x electrode interaction reached significance [$F(1, 9) = 3.87$, $p < 0.04$] at electrode sites P1, Pzi and P2. After the normalization procedure was employed, the main effect of components was not significant. Furthermore, the component x electrode interaction found in the first analysis was not significant after the z-score correction [$F(1, 9) = 3.02$, $p < 0.074$]. The lack of a significant interaction between components x electrode sites suggests that the short-latency collinearity effect shares a common neural generator with the C1 component, possibly primary visual cortex. An additional ANOVA between the C1 and P1 components was conducted to rule out that extrastriate activity contributed to the C1. An ANOVA was performed with a column of electrodes from occipital midline sites (Pzs, Pzi, Ozs, Ozi).

Scalp Voltage Topographies for Context Difference
0–200 ms, 10 ms Intervals
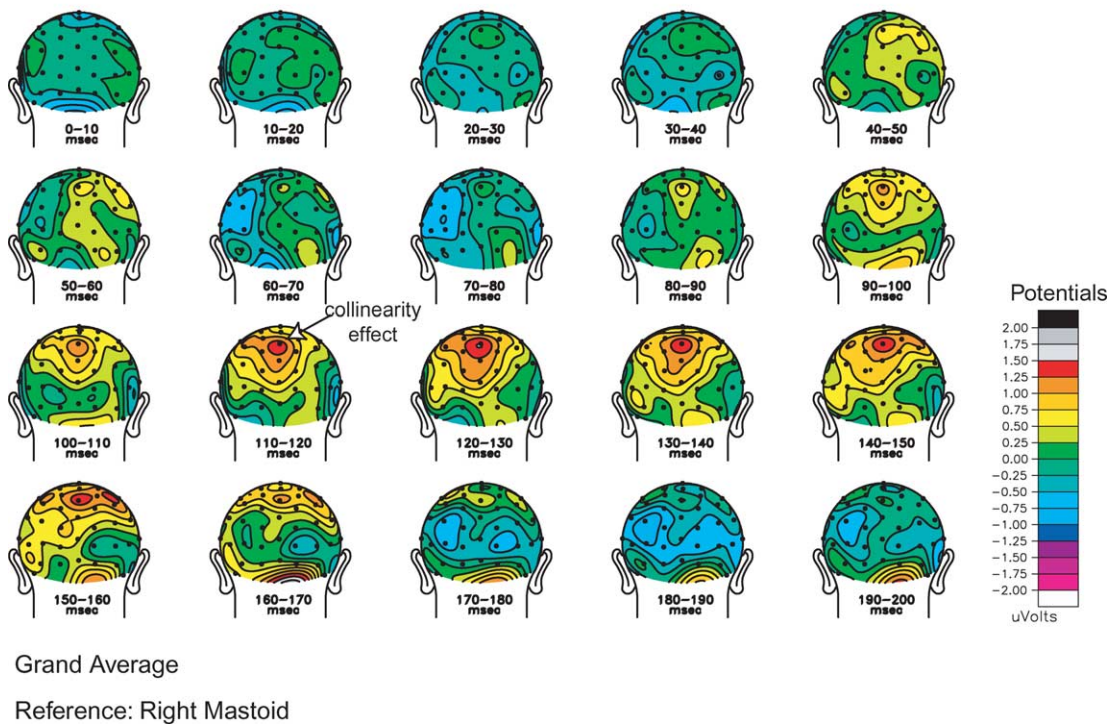
Grand Average

Reference: Right Mastoid

Fig. 4. Scalp topographic voltage maps of the context double subtraction difference wave for the latency range of 0–200 ms in 10 ms intervals, in the rear view of the head, referenced to the right mastoid with the voltage scale at the bottom right of the figure. At 80–90 ms, within the time range of the measured N82 component, an effect of context is found over occipital mid-line sites. The occipital mid-line topography suggests that the early effect of context is consistent with a generator in primary visual cortex.
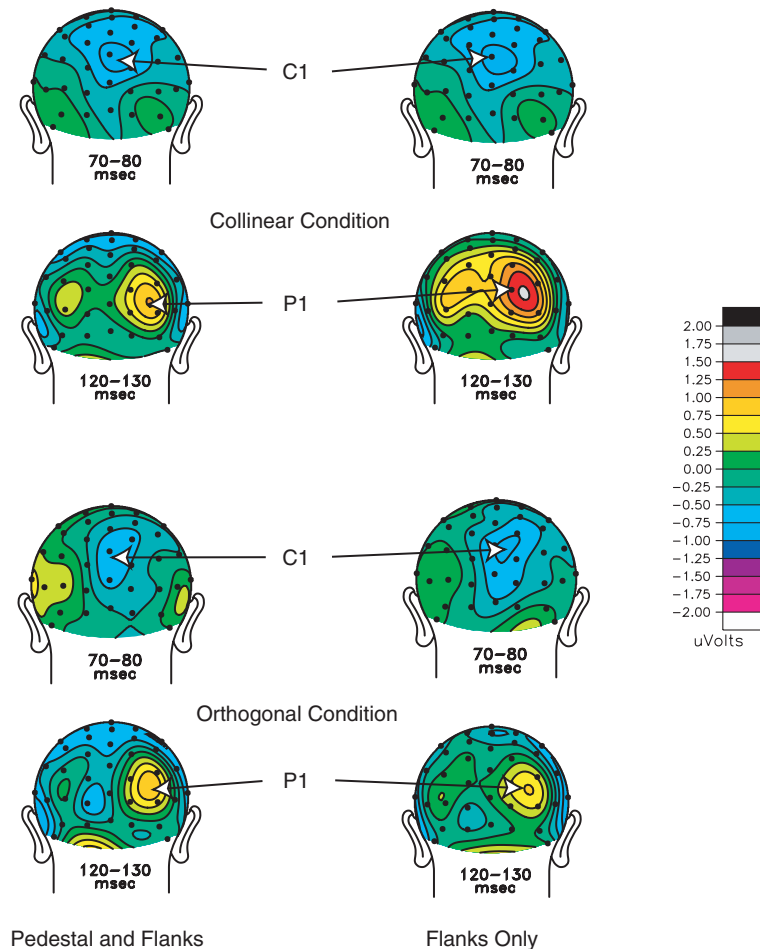
Fig. 5. Scalp topographic voltage maps of the C1 and P1 components for the collinear and orthogonal stimulus configurations, in the rear view of the head, referenced to the right mastoid with the voltage scale to the right of the figure.

A component by electrode interaction was significant ($F(1,9) = 3.97$, $p < 0.03$).

3.10. Discussion

The ERP and the corresponding behavioral data suggest that targets embedded in a collinear surround were processed differently than those in a orthogonal surround. The scalp topographies revealed that the difference in processing was focused at occipital midline electrode sites. A sliding time window analysis revealed the ERP for the short-latency context-dependent effect reached significance between 100 and 150 ms. Closer inspection of the multiple F-values revealed that they began to increase at 80 ms for the six subsequent time windows, suggesting the effect may begin as early as 80 ms. The fractional local peak latency analysis revealed the onset to be at approximately 80 ms. Both of these analysis techniques are, however, rather conservative and tend to overestimate the onset of the difference, quantifying only the point at which differences significantly achieve statistical significance. Past studies (Gir-

ard, Hupe, & Bullier, 2001; Nowak, Munk, Girard, & Bullier, 1995; Schmolesky et al., 1998) have found that some neurons in higher cortical areas in the visual hierarchy may be activated *before* neurons in striate cortex, suggesting that the activity seen in our study may be due to short-latency activity in extrastriate cortex. However, even though the difference wave does not seem to completely overlap with the C1 time course, it has a similar spatial topography with the C1. Taking this together with its relatively early onset, our results are still consistent with the idea that both components share similar neural generators in primary visual cortex. The short-latency effects were followed by a series of longer-latency context negativities at 245–295 and 300–350 ms at lateral occipital electrode sites. Corresponding to the short and longer-latency ERP differences, subject performance was facilitated for target stimuli presented within a collinear context relative to an orthogonal context.

It might be noted that there was no configuration by stimulus interaction at the shorter latency effects (i.e., no differential effect of collinearity for the targets vs. the
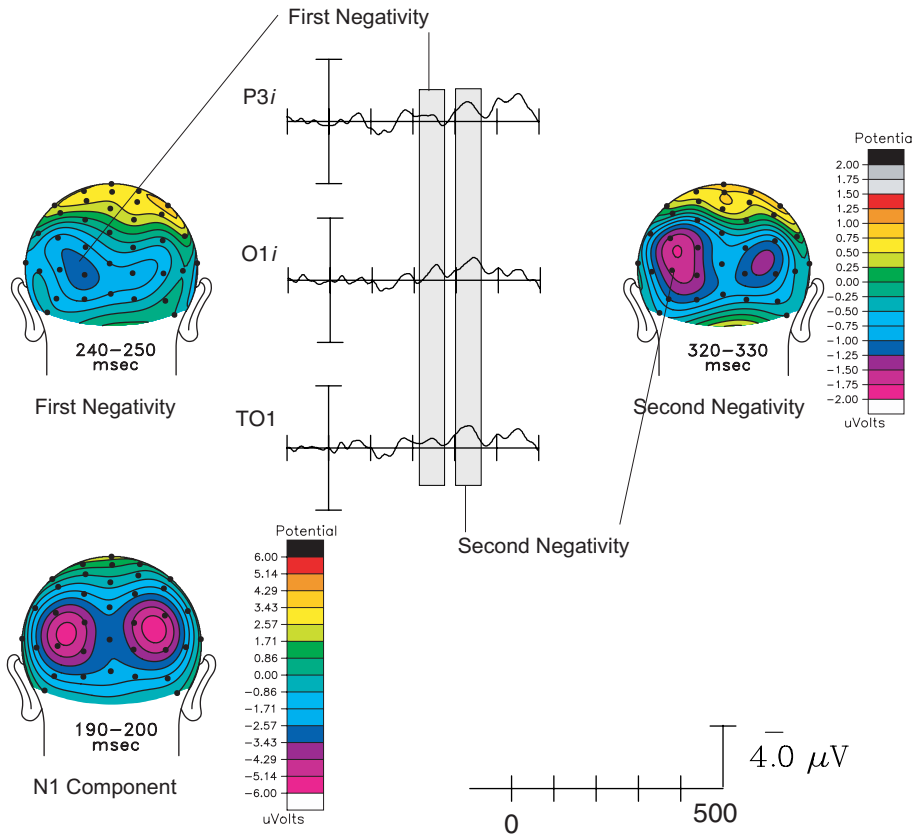
Fig. 6. Scalp topographic voltage maps of the context double subtraction difference wave for the latency range of 200–400 ms in 10 ms intervals, in the rear view of the head, referenced to the right mastoid with the voltage scale at the bottom right of the figure. At 240–290 and 300–350 ms there is an effect of context over lateral occipital sites. The topography of these effects is similar to the N1 component shown at the lower right hand corner of the figure to collinear stimulus configurations.

Table 3
Experiment 2: ANOVA F-values and associated probabilities for scalp voltage topographies without z-score correction procedure

Electrode group	ANOVA factor	F-value	p-value
Pzs, Pzi, Ozs, Ozi	Component	16.76	0.003*
	Electrode	<1	–
	Component × electrode	2.38	0.09
PO1, Ozs, PO2	Component	18.6	0.002*
	Electrode	<1	–
	Component × electrode	1.25	0.3
P1, Pzi, P2	Component	15.61	0.0033*
	Electrode	<1	–
	Component × electrode	3.87	0.04*
O1, Ozi, O2	Component	14.61	0.004*
	Electrode	<1	–
	Component × electrode	<1	–

*Indicates significance.

pedestals), despite there being significant behavioral differences in the target-pedestal discrimination in the two stimulus configurations. A likely explanation is that the physiological correlates of any difference in this early-latency collinearity modulation for the targets vs. the pedestals either did not occur or was not strong enough to be detected in the present experimental de-sign. A difference might have occurred if the collinear flanks simply multiplied the responses to the target or pedestal by a constant gain factor; thus, within limits, the higher contrast targets might have been influenced by context at these early latencies more than the lower contrast pedestals. However, the present experiment was not aimed at detecting subtle differences between the

Table 4
Experiment 2: ANOVA F-values and associated probabilities for scalp voltage topographies with z-score correction procedure

Electrode group	ANOVA factor	F-value	p-value
Pzs, Pzi, Ozs, Ozi	Component	<1	–
	Electrode	<1	–
	Component × electrode	2.76	0.06
PO1, Ozs, PO2	Component	<1	–
	Electrode	<1	–
	Component × electrode	1.25	0.18
P1, Pzi, P2	Component	<1	–
	Electrode	<1	–
	Component × electrode	3.02	0.07
O1, Ozi, O2	Component	<1	–
	Electrode	1.11	0.4
	Component × electrode	< 1	–

*Indicates significance.

targets and pedestals in various configurations. Instead, our experiment was concerned with measuring the main effects of flanker configurations on all the suprathreshold pedestals (both targets and pedestals). Lastly, it is not the case that the ERPs did not discriminate at all between the target and pedestals, as there was a significant interaction between stimulus type and configuration at longer latencies, namely for the N2 components at around 250 ms. The difference between targets and pedestals was larger in the collinear configuration than in the orthogonal case for this later ERP component.

4. General discussion

4.1. Modulatory effects from outside the CRF

In the present study, ERPs and behavior were recorded simultaneously from humans in a stimulus discrimination task performed under different contextual conditions (cf., Polat & Sagi, 1993, 1994). Both behavioral and physiological measures showed that visibility of a target improved in the context of collinear vs. orthogonal flankers. While previous studies found only suppression for suprathreshold contrast discrimination (Chen & Tyler, 2001; Zenger-Landolt & Koch, 2001), both in fovea and periphery (4 deg eccentricity), we have obtained the first evidence of facilitation with suprathreshold target and pedestal stimuli presented perifoveally (0.67 deg from fixation). Furthermore, the present study is the first to measure the ERP correlate of this behavioral collinearity effect, with much higher temporal and spatial resolution than was possible in the only previous electrophysiological study of SSVEPs (Polat & Norcia, 1996).

We observed a short-latency ERP difference between 90 and 140 ms for central targets as a function of collinear vs. orthogonal flanker configurations, sharply focused over occipital midline sites. Following the early difference, longer-latency differences between 245 and 295 ms and 300 and 350 ms were observed at lateral occipital sites. The present results are consistent with single-unit neurophysiology (Chen et al., 2001; Polat et al., 1998), where the neuronal response in V1 to a central stimulus has been found to be enhanced by the presence of collinear flankers positioned far outside the cell's classical receptive field.

4.2. Contributions of lateral connections to the collinear enhancement effect

The collinearity-dependent ERP effects are consistent with the known anatomy and physiology of long-range connections in striate cortex. For example, anatomical studies (Bosking et al., 1997; Fitzpatrick, Lund, & Blasdel, 1985; Gilbert & Wiesel, 1983; Hubel & Wiesel, 1983; Kapadia et al., 1995; Rockland & Lund, 1983; Weliky, Kandler, Fitzpatrick, & Katz, 1995) have uncovered a network of long-range horizontal connections between cortical pyramidal cells in striate cortex. Furthermore, Gilbert and his colleagues (Gilbert & Wiesel, 1989; Hirsch & Gilbert, 1991; Ts'o et al., 1986) have found that these long-range horizontal connections tend to interconnect cells having similar orientation preferences, along lines running parallel to their orientation preference. More recent single-cell studies (Chen et al., 2001; Polat et al., 1998) have confirmed that such an architecture is especially sensitive to elements of similar orientation configurations in a collinear arrangement, showing that neuronal responses of a cell to a central Gabor were enhanced in the presence of collinear vs. orthogonal flankers presented outside the cell's classical receptive field.

The double-subtraction ERP waveforms from this study may reflect such a context-specific modulation of

the neuronal response to the central pedestal/target, via horizontal connections. However, ERPs are only sensitive to neuronal configurations that are oriented perpendicular to the surface of the cortex (Vaughan & Arezzo, 1988). The ERPs we recorded at the scalp therefore most likely reflect activity of the pyramidal cells rather than the horizontal connections themselves. The double-subtraction waveforms we observed should not reflect simple flanker-triggered activity, since that would have been subtracted away, but rather the modulated activity of the pyramidal cells responding to the pedestal, modulated by the flankers via long-range horizontal connections.

Although intrinsic connections between columns in striate cortex may underlie the contextual observations observed, feedback connections from higher visual cortical areas may also contribute to lateral interactions (Budd, 1998; Grossberg & Raizada, 2000; Hupé et al., 1998; Lamme & Roelfsema, 2000; Zipser, Lamme, & Schiller, 1996). For example, DeYoe and Van Essen (1985) found that V2 neurons in anesthetized primates exhibit similar context-sensitivity to V1 cells. They proposed that feedback connections from V2 to V1 generate surround effects that are passed to V1 recurrently. A feedback model is also consistent with the temporal delay of approximately 80 ms seen in single-unit studies of contextual modulation (Zipser et al., 1996). Furthermore, deactivating feedback projections from V2 to V1 can affect figure-ground discrimination (Hupé et al., 1998). In the present study, the collinear enhancement effect began at approximately 80–90 ms. However, significant differences appeared at later latencies (i.e., 100–120 ms) compared to latencies associated with the C1 striate component in the present data and in classical studies. Contextual modulation was not evident at the leading edge of the C1 component, but rather during the descending edge of the C1, which further increased during the time range of 130 to 150 ms. Still, the spatial distribution of the double-subtraction difference wave was similar to the distribution of the C1 component. While this pattern could be consistent with an account based on recurrent feedback, it is also possible that the 50 ms latency lag reflects slow feed-forward modulation of the stimulus response via long-range connections (Knierim & Van Essen, 1992).

The possible role of a feedback mechanism in the 50 ms delayed striate activity enhancements for collinear configurations implies that top-down attentional influences might modulate lateral interaction effects in striate cortex. Such a hypothesis would be consistent with the recent suggestion that selective attention and contextual effects may rely on common neural mechanisms based on both intrinsic horizontal connections in V1 and V2 and feedback projections from V2 to V1 (Grossberg & Raizada, 2000). In support of this, attentional modulation of lateral interactions has indeed been observed in a psychophysical study (Freeman et al., 2001). Identifying the electrophysiological correlate of such a modulation would be a worthwhile goal for future research.

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