Visual Processing of Contour Patterns under Conditions of Inattentional Blindness

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Abstract

■ An inattentional blindness paradigm was adapted to measure ERPs elicited by visual contour patterns that were or were not consciously perceived. In the first phase of the experiment, subjects performed an attentionally demanding task while task-irrelevant line segments formed square-shaped patterns or random configurations. After the square patterns had been presented 240 times, subjects' awareness of these patterns was assessed. More than half of all subjects, when queried, failed to notice the square patterns and were thus considered inattentionally blind during this first phase. In the second phase of the experiment, the task and stimuli were the same, but following this phase, all of the subjects reported having seen the patterns. ERPs recorded over the occipital pole differed in amplitude from 220 to 260 msec for the pattern stimuli compared with the random arrays regardless of whether subjects were aware of the patterns. At subsequent latencies (300–340 msec) however, ERPs over bilateral occipital-parietal areas differed between patterns and random arrays only when subjects were aware of the patterns. Finally, in a third phase of the experiment, subjects viewed the same stimuli, but the task was altered so that the patterns became task relevant. Here, the same two difference components were evident but were followed by a series of additional components that were absent in the first two phases of the experiment. We hypothesize that the ERP difference at 220–260 msec reflects neural activity associated with automatic contour integration whereas the difference at 300–340 msec reflects visual awareness, both of which are dissociable from task-related postperceptual processing. ■

INTRODUCTION

A longstanding but elusive goal of cognitive neuroscience has been to identify the neural basis of conscious perception. Research in this area has primarily focused on identifying the neural correlates of conscious access; that is, what neural processes lead to perceptual awareness of a stimulus so that a subject can explicitly report its presence or properties (Dehaene & Changeux, 2004)? Recent brain imaging and electrophysiological studies have identified different classes of neural events linked with perceptual awareness. Some evidence has pointed toward an early or intermediate stage of perceptual processing (Haynes, 2009; Lamme, 2006; Pins & ffytche, 2003), whereas other results suggest that activity in more wide-spread frontal-parietal networks is necessary for awareness (Dehaene & Changeux, 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Rees, 2001). Critical to resolving this issue is an experimental paradigm that allows a straightforward comparison between conditions in which subjects are aware versus unaware of physically identical stimuli.

More than 10 years ago, Simons and Chabris (1999) famously demonstrated that a salient yet unexpected visual object (woman dressed in a gorilla costume) can go completely unnoticed when attention is otherwise engaged. This phenomenon, dubbed as "inattentional blindness," has been well documented in a variety of behavioral studies using various stimuli and tasks (Richards, Hannon, & Derakshan, 2010; Devue, Laloyaux, Feyers, Theeuwes, & Bredart, 2009; Simons & Jensen, 2009; Bressan & Pizzighello, 2008; Koivisto & Revonsuo, 2008b; Lo & Yeh, 2008; Pizzighello & Bressan, 2008; Fougnie & Marois, 2007; Jingling & Yeh, 2007; Sinnett, Costa, & Soto-Faraco, 2006; Most, Scholl, Clifford, & Simons, 2005; Mack, 2003; Mack & Rock, 1998; Mack, Tang, Tuma, Kahn, & Rock, 1992; Neisser & Becklen, 1975). To date however, little is known about how the brain processes information during inattentional blindness and how processing differs when a previously unseen object is later seen (Scholte, Witteveen, Spekreijse, & Lamme, 2006; Rees, Russell, Frith, & Driver, 1999). For example, to what extent (if at all) was the "invisible gorilla" encoded by the visual system, and how did neural activity differ when subjects later became aware of the gorilla? The current study used a modified version of the inattentional blindness paradigm while recording electrophysiological brain activity to assess the extent to which information is processed without awareness and to identify stages of processing specifically associated with conscious perception.

To adapt the inattention paradigm for use in an ERP experiment, several methodological considerations were

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required. In typical behavioral designs (e.g., Mack & Rock, 1998), subjects perform a distracter task for a few trials, then on a "critical" trial, an additional unexpected object appears. Subjects are immediately queried as to whether they noticed the object and are then instructed to perform the same task again. The intervening questions serve as cues biasing perception, and most subjects who fail to notice the object on the critical trial easily recognize it on subsequent trials. With this type of design, the inattentional blindness condition consists of only a single trial because, once subjects are queried, the unexpected stimuli become expected. To record ERPs with adequate signal–noise ratios, however, stimuli must be presented many times (e.g., 100+). Thus, to measure ERPs during inattentional blindness, stimuli that can completely evade conscious detection for more than 100 trials are required. Also, to permit controlled comparisons between seen and unseen conditions, the stimuli must remain task irrelevant but be easily noticeable on subsequent trials.

In the present study, stimuli consisted of grids of line elements that were either randomly oriented or arranged to form salient contour patterns. Similar stimuli have been used previously to investigate processes of contour integration and texture segregation as well as perceptual salience and awareness; these processes were generally associated with negative shifts in ERP amplitude from 100 to 300 msec poststimulus onset over occipital and parietal scalp regions (Straube, Grimsen, & Fahle, 2010; Casco, Campana, Han, & Guzzon, 2009; Fahrenfort, Scholte, & Lamme, 2008; Scholte, Jolij, Fahrenfort, & Lamme, 2008; Heinrich, Andres, & Bach, 2007; Mathes & Fahle, 2007b; Wilenius & Revonsuo, 2007; Sehatpour, Molholm, Javitt, & Foxe, 2006; Casco, Grieco, Campana, Corvino, & Caputo, 2005; Doniger et al., 2001; Bach, Schmitt, Quenzer, Meigen, & Fahle, 2000). In the present design, ERPs elicited by contour-patterned stimuli were compared with ERPs elicited by contour-absent stimuli during inattentional blindness, thereby assessing the extent to which visual pattern processing proceeds in the absence of awareness. Moreover, the inattentional blindness paradigm allowed comparisons between ERPs to patterned stimuli of which the subjects were perceptually aware versus unaware, while the stimuli remained irrelevant to the ongoing task. This made it possible to dissociate the neural correlates of perceptual awareness from those of task-related postperceptual processes.

METHODS

Participants

Thirty-eight healthy adults participated in the experiment. Data from six participants were later excluded because of excessive artifact in their EEG recordings (e.g., due to blinks, muscle, movement). The final group consisted of 32 participants (mean age = 21 years; 19 women). All were recruited as volunteers and gave informed consent before the beginning of each experiment. The experimental procedures were approved by the University of California-San Diego institutional review board in compliance with the Declaration of Helsinki.

Stimuli

Stimuli consisted of a central 20 × 20 grid (visual angle = 6.2° × 6.2°) composed of small (0.34°) white line segments. This grid was surrounded by a large ring (9.8°) made up of eight evenly spaced red discs (each at 1.0°; see Figure 1). A central fixation cross (0.5°) was present at all times. All stimuli were presented on a dark background (0.07 cd/m^2) on an LCD monitor (refresh rate = 60 Hz) and were viewed from a distance of 120 cm. Stimuli were created and displayed using Presentation software (Neurobehavioral Systems, Albany, CA).

Across trials, the orientations of the line segments alternated between a baseline random configuration (duration = 600–800 msec) and one of three possible configurations (duration = 300 msec): a square pattern (formed by 12 × 12 vertically and horizontally aligned segments; 3.5° × 3.5°), a diamond pattern (formed by 8 × 8 diagonally aligned segments; 3.2° × 3.2°), or another random configuration (different on each trial). These three stimulus types were presented in random order. Throughout the experiment, square patterns were presented on 40% of trials, diamond patterns on 10%, and random configurations on 50%. The orientation of each line segment in the random configurations was determined by selecting a random angle from 0 to 180° in 15° steps, with logical rules preventing adjacent line segments from having the same orientation. Each stimulus array was drawn separately and was never repeated. To subjects, the changes in line orientations appeared as brief rotations or "twitches."

The ring of discs surrounding the line segments alternated between a standard position (duration = 600–800 msec) and one of two rotated positions (duration = 300 msec). The changes in disc position occurred simultaneously with the changes in line segment orientation. The alternate disc positions were formed by rotating the entire ring of discs unpredictably by 15° in either a clockwise or counterclockwise direction. Target stimuli for experimental Phases 1 and 2 consisted of one slightly dimmed disc (38% luminance decrement) that appeared randomly at one of the eight disc positions on 10% of the trials. Target stimuli for Phase 3, when the line segments became task relevant, were the diamond patterns that appeared on 10% of trials. Sample stimuli are shown in Figure 1, and an sample block of trials can be viewed as an on-line video at www.youtube.com/watch?v=8-9NAFUn_CI.

Procedure

The experiment was divided into three phases following an initial practice phase. During the practice phase and

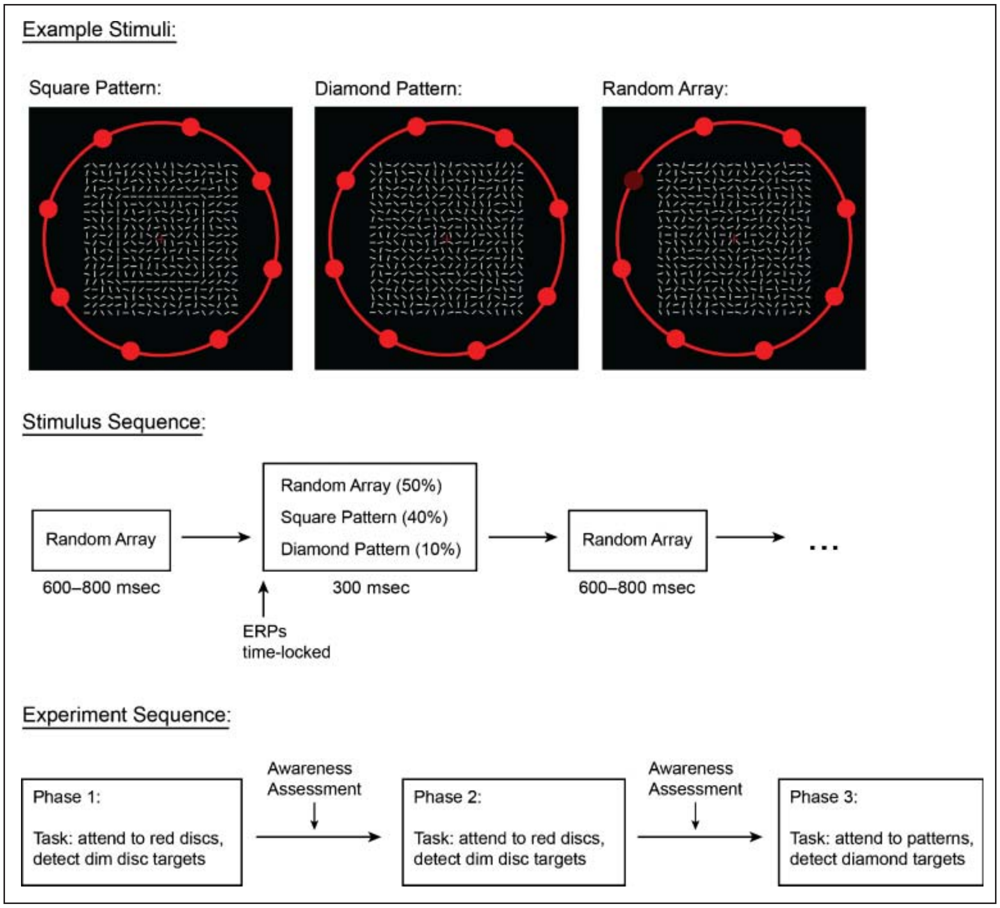


Figure 1. Sample stimuli, stimulus presentation sequence, and experiment sequence. Line segment orientations alternated between random configurations and one of three stimulus types: a square pattern, a diamond pattern, or another random array. At the same time, the red ring of discs alternated between a standard position and two alternative positions that appeared as small clockwise or counterclockwise rotations. In Phases 1 and 2, the subjects' task was to detect infrequent (10%) dim-disc targets (e.g., as shown here on the random array sample) that could appear at any one of the eight disc locations. In Phase 3, the subjects' task was to detect the infrequent diamond patterns (10%). After Phases 1 and 2, observers were queried about their awareness of the square patterns (see Appendix).

Phases 1 and 2 of the experiment, subjects were instructed to maintain fixation on the central cross while paying attention to the ring of discs to detect the occasional dim target discs, pressing a key whenever they detected a target. The practice phase consisted of five 1-min runs, in which the line segments always formed random configurations.

During Phase 1 of the experiment, the critical stimulus (square pattern formed by collinear line segments) first appeared and was presented 240 times. Immediately following Phase 1, subjects were asked a series of questions to assess their awareness of the square pattern. The complete questionnaire is provided in the Appendix. Briefly, subjects were first asked if they had noticed any patterns within the line segment array and, if so, describe what they saw in detail. Then, regardless of whether they reported seeing any patterns, six sample patterns were presented, including the square and diamond patterns, along with four foil patterns that were never shown (see Appendix). Subjects were asked to rate their confidence in seeing each pattern during the experiment on a 5-point scale (confidence ratings) and, for any patterns they saw, estimate how often they saw it on a separate 5-point scale (frequency ratings). After completing the questionnaire, subjects were instructed to continue performing the dim-disc detection task during Phase 2 of the experiment. Following Phase 2, the same questionnaire was given again. Finally, in Phase 3, observers were instructed to ignore the ring of discs and attend to the line segments to detect the diamond pattern targets. For all phases of the experiment, the stimuli were physically identical. Each phase consisted of ten 1-min runs. A total of 600 stimuli were presented during each phase. Observers took self-paced breaks after each run, with a mandatory extended break after every 5 runs.

EEG/ERP Methods

Brain electrical activity was recorded noninvasively from the scalp using commercially available electrode caps (Electro-Cap International) with 64 electrode placements. Electrode impedances were kept below 5 kΩ. Scalp signals were amplified by a battery-powered amplifier (SA Instrumentation, San Diego, CA) with a gain of 10,000 and band-pass filtered from 0.1 to 250 Hz. Signals were digitized to disk at 500 Hz. During task performance, eye position and eye movements were monitored by means of vertical and horizontal EOG recordings. A right mastoid electrode served as the reference for all scalp channels and vertical EOG. Left and right horizontal EOG channels were recorded as a bipolar pair. Each recording session lasted for 120–150 min, including setup and cap/electrode preparation.

ERPs were time-locked to the line segment orientation changes (and coincident ring rotations), baseline corrected from −100 to 0 msec, and low-pass filtered at 30 Hz. Trials were discarded if they contained an eye blink or eye movement artifact or if any electrode channel exceeded signal amplitudes of 50 μV. On average, 12% of trials per individual were rejected because of these artifacts. Before analysis ERPs were re-referenced to the average of the left and right mastoid channels. Comparisons of interest were between ERPs elicited by the square patterns versus the random arrays; ERPs were sorted according to whether participants were inattentionally blind or aware of the square patterns (Groups 1 and 2, respectively). Trials that included a dim-disc or diamond pattern were excluded from the ERP analyses.

To assess the neural correlates of perceptual awareness, we focused on two main components in the statistical analyses of ERPs recorded during Phases 1 and 2. Time windows and electrode locations for component measurement were chosen based on the peak amplitudes and scalp distributions of the main experimental effects (square pattern–random array) in the grand averaged waveforms. The first difference (Nd1) was assessed by comparing mean amplitudes from 220 to 260 msec in occipital channels POz, Oz, Iz, SIz, O1, and O2. The second difference (Nd2) was assessed by mean amplitude comparisons from 300 to 340 msec in left (P5, P7, PO3, PO7, O1, I3, SI3) and right (P6, P8, PO4, PO8, O2, I4, SI4) occipital-parietal channels. Two separate ANOVAs with the within-subject factors stimulus type (square pattern, random array), phase of experiment (1, 2), and electrode location (see above) and the between-subject factor group (1, 2) were used to test mean amplitude differences during the aforementioned time windows of interest (220–260 and 300–340 msec).

To assess neural events associated with task-related processing and to distinguish these from activity associated with visual awareness, additional analyses incorporating the ERPs recorded in Phase 3 were conducted. In this phase, two difference components with scalp distributions very similar to the Nd1 and Nd2 (tested by comparisons of amplitude-normalized difference wave topographies across Phases 2 and 3) were apparent but appeared at earlier latencies in Phase 3 (180–220 and 220–260 msec, respectively). In addition, a selection negativity (SN; 260–300 msec) and two positive difference components (Pd1: 340–380 msec; Pd2: 420–460 msec) were evident in Phase 3 and were assessed at bilateral occipital, central occipital, and vertex-centered channel groups, respectively. Subsequent planned pairwise comparisons of difference amplitudes between groups and across phases were employed to further explore the main effects and interactions revealed by ANOVA.

Source Analyses

To obtain preliminary estimates of the source locations of the grand-averaged ERP difference components (formed by subtracting ERPs associated with the random arrays from those associated with the square pattern), neural generators were modeled using a minimum-norm linear inverse solution approach that involves local autoregressive averaging (LAURA; Grave de Peralta Menendez, Murray, Michel, Martuzzi, & Gonzalez Andino, 2004). The current distributions were computed in a grid of 3005 solution points that were regularly distributed within the gray matter of the cerebral cortex and limbic structures of the average brain provided by the Montreal Neurological Institute (MNI 152). No a priori assumptions were made regarding the number or location of active sources. Time windows for estimating the sources of each component were the same as in the ERP statistical analyses. LAURA solutions were visualized using Cartool software (brainmapping.unige.ch/Cartool.php).

RESULTS

Behavioral Results

Participants were divided into two groups based on the questionnaire data obtained after Phase 1. If a participant reported not seeing any patterns and rated their confidence in seeing the square pattern (once shown the sample) as a 3 or less (1 = *least confident*, 5 = m*ost confident*), she or he was placed in Group 1 and was considered to be inattentionally blind to the square patterns in Phase 1. Those participants who reported seeing the square *or* rated their confidence in seeing the square as a 4 or 5 were placed in Group 2 and were considered to be aware of the square patterns. Only two subjects reported not seeing any patterns while rating their confidence in seeing the square as a 4 or 5 (upon seeing the sample square pattern). No subjects who reported seeing the square rated their confidence less than 4. On the basis of these criteria, of the original 38 subjects, 20 were inattentionally blind to the squares during Phase 1 (53%). Because six subjects were rejected due to excessive artifact in their EEG recordings, the final groups consisted of 16 subjects each (see Table 1).

After Phase 2, all subjects reported seeing the square patterns and were confident (rating ≥ 4) that they had seen these patterns. This result confirmed that the questioning following Phase 1 had provoked the subjects who initially did not notice the patterns to look for them in Phase 2. Many participants who were inattentionally blind during Phase 1 voluntarily self-reported their change in awareness halfway through the second phase, for example, "I didn't notice before, but since you asked, now I can't stop seeing the square!" Table 1 summarizes the results from the questionnaires.

Behavioral performance on the dim-disc detection task was evaluated in separate ANOVA for RTs, accuracy, and *d′*. Each ANOVA assessed the within-subject factor phase (1, 2) and the between-subject factor group (1, 2). The only significant difference was a main effect of Phase on RTs because of faster responses in Phase 2 compared with Phase 1 (614 msec vs. 601 msec, respectively). Importantly, there were no differences in task performance according to whether subjects noticed the contour patterns or not (all Phase × Group interactions were not significant). The task performance results are provided in Table 2.

Table 1. Questionnaire Results

	Number of Observers		*Mean Confidence Ratings*						*Mean Frequency Ratings*					
	Reported Square	*Reported Diamond*	*Square*	*Diamond*	*X Pattern*	*Horizontal Rectangle*	*Vertical Rectangle*	*Four Squares*	*Square*	*Diamond*	*X Pattern*	*Horizontal Rectangle*	*Vertical Rectangle*	*Four Squares*
Phase 1														
Group 1	0	0	1.8 (0.8)	2.3 (1.3)	2.8 (1.3)	1.4 (0.8)	1.6 (0.7)	1.3 (0.6)	1.6 (0.8)	1.9 (1.0)	2.4 (1.4)	1.3 (0.6)	1.3 (0.4)	1.2 (0.4)
Group 2	16	1	4.8 (0.4)	3.0 (1.1)	2.5 (0.9)	1.5 (0.6)	2.1 (1.0)	1.8 (0.8)	3.8 (0.9)	2.1 (0.9)	1.6 (0.5)	1.2 (0.4)	1.5 (0.6)	1.4 (0.6)
Phase 2														
Group 1	14	5	4.9 (0.3)	3.1 (1.7)	1.9 (1.1)	1.9 (1.2)	1.9 (1.2)	1.4 (0.7)	4.2 (0.9)	2.3 (1.3)	1.7 (0.9)	1.5 (0.7)	1.4 (0.5)	1.1 (0.5)
Group 2	16	11	5.0 (0.0)	3.8 (1.7)	2.3 (1.4)	1.8 (1.0)	1.9 (1.3)	1.6 (0.7)	4.1 (0.7)	2.8 (1.2)	1.8 (1.3)	1.3 (0.6)	1.6 (1.1)	1.2 (0.4)

Mean rating scores are based on 5-point scales ranging from 1 (*least confident*) to 5 (*most confident*) and 1 (*least frequent*) to 5 (*most frequent*).

Standard deviations (in parentheses) are provided after each mean value.

ERP Results

To assess the neural correlates of perceptual awareness, the comparisons of interest were between ERPs elicited by the square patterns and random arrays: (1) within the group of subjects who were initially unaware and later became aware of the patterns (Phase 1 vs. Phase 2) and (2) between the two groups of subjects who differed in awareness in Phase 1 (Group 1 vs. Group 2). ERPs elicited by the square patterns were more negative than ERPs elicited by random arrays from 220 to 260 msec (during the P2 latency range) over the occipital pole, regardless of whether observers were aware of the square patterns. For simplicity, we, hereafter, refer to this first negative difference as the "Nd1." Conversely, from 300 to 340 msec (during the N2 latency range), ERPs to the square patterns, over bilateral occipital-parietal regions, were more negative than ERPs to the random arrays only in conditions in which observers reported awareness of the square patterns. We subsequently refer to this negative difference as the "Nd2." Grand averaged ERPs from representative electrodes as well as difference topographies are shown in Figures 2 and 3.

Table 2. Task Performance

	Accuracy (%)	*d′*	*Reaction Times (msec)*
Phase 1			
Group 1	67 (25)	3.01 (0.99)	609 (49)
Group 2	70 (14)	2.96 (0.62)	618 (56)
Phase 2			
Group 1	68 (24)	3.05 (1.09)	588 (62)
Group 2	71 (15)	3.18 (0.67)	615 (60)
Phase 3			
Group 1	78 (10)	3.50 (0.56)	606 (50)
Group 2	85 (7)	3.77 (0.46)	602 (51)

The task for Phases 1 and 2 was to detect dim-disc targets.

The task for Phase 3 was to detect diamond patterns.

Standard deviations (in parentheses) are provided after each mean value.

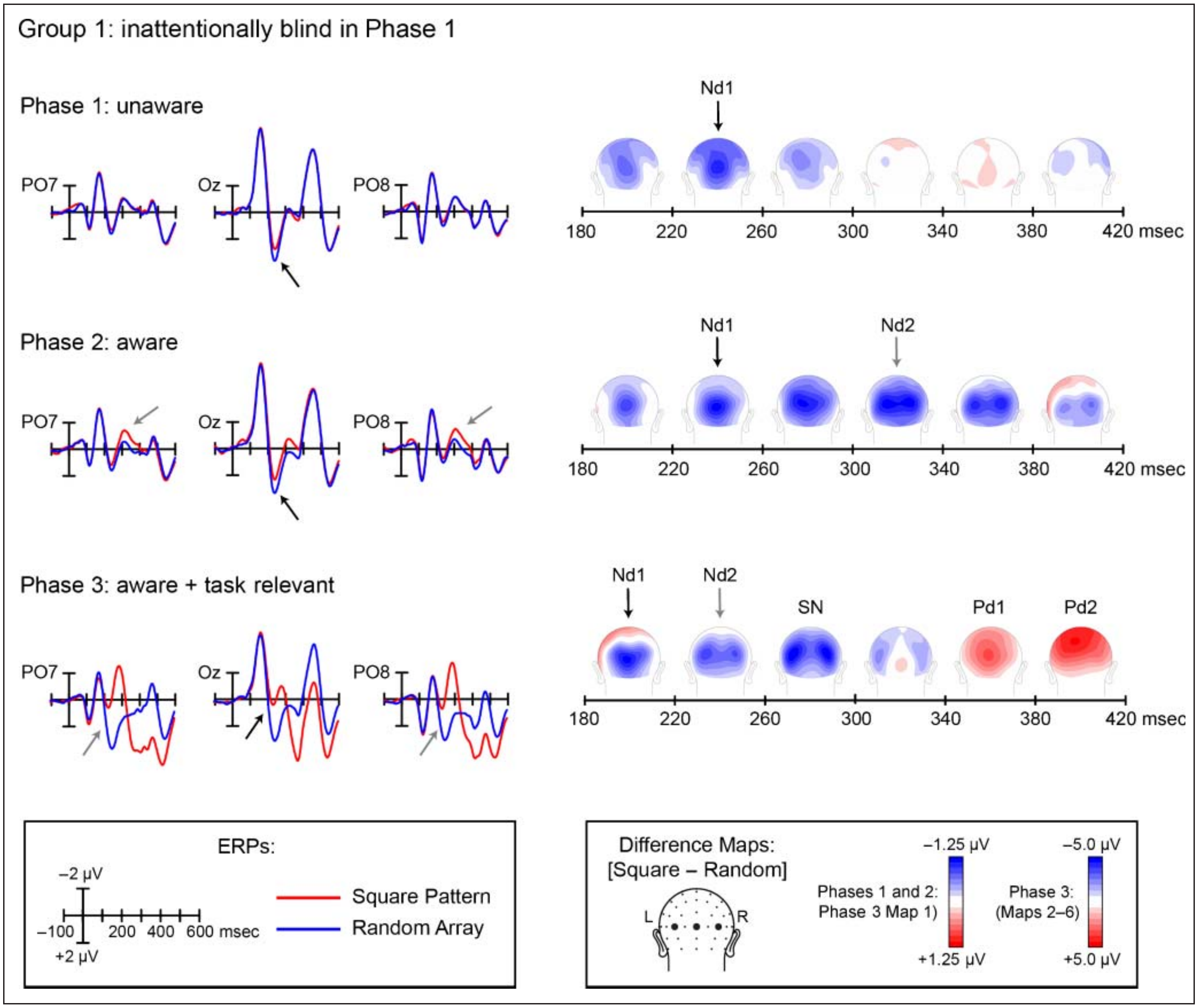


Figure 2. Grand averaged ERPs and difference topographies (square pattern–random array) for Group 1 (subjects who were deemed inattentionally blind in Phase 1). Negative voltage is plotted up. The subjects' task during Phases 1 and 2 was to attend to the red ring surrounding the line element array to detect infrequent dim-disc targets. During the first time window of interest (220–260 msec), ERPs elicited by the square patterns were more negative than those elicited by the random arrays, regardless of whether observers were aware of the patterns (black arrow). This difference (Nd1) was distributed over the occipital pole. During a second time window (300–340 msec), bilateral occipital-parietal differences (Nd2) were evident, but only for conditions in which observers were aware of the square patterns (gray arrow). In Phase 3, observers attended to the patterns to detect infrequent diamond shapes. The Nd1 appeared earlier in this condition (180–220 msec), compared with Phases 1 and 2, but was not larger in amplitude. The Nd2 (220–260 msec) also appeared earlier and its amplitude was significantly enhanced in Phase 3. At subsequent time intervals, an SN (260–300 msec) and two positive components were also evident (Pd1: 340–380 msec; Pd2: 420–460 msec). No SN or late positive components were elicited in Phases 1 and 2 when the patterns were task irrelevant.

Analysis of the Nd1 revealed a main effect of Stimulus Type (square pattern vs. random array), $F(1, 30) = 30.48$, $p = .000005$, a main effect of Phase (1 vs. 2), $F(1, 30) = 21.02$, $p = .008$, and no interactions. The main effect of Phase with a lack of Stimulus Type × Phase interaction was because of smaller ERP amplitudes to all stimuli during the second phase (see Table 3). Follow-up comparisons confirmed that ERPs elicited by the square patterns were significantly more negative than those elicited by the random arrays (220–260 msec) for each group during each phase separately. Most importantly, the amplitude of the Nd1 and its central-occipital distribution did not differ between the aware and unaware groups in Phase 1, $F(1, 30) = 0.09$, $p = .76$, or between phases (1 vs. 2) within the group of subjects whose awareness changed, $F(1, 15) = 0.24$, $p = .63$.

For the Nd2, a main effect of Stimulus Type, $F(1, 30) = 22.78$, $p = .00004$, and an interaction between Stimulus Type × Phase × Group, $F(1, 30) = 5.10$, $p = .031$, was evident. To further assess this interaction, one-way

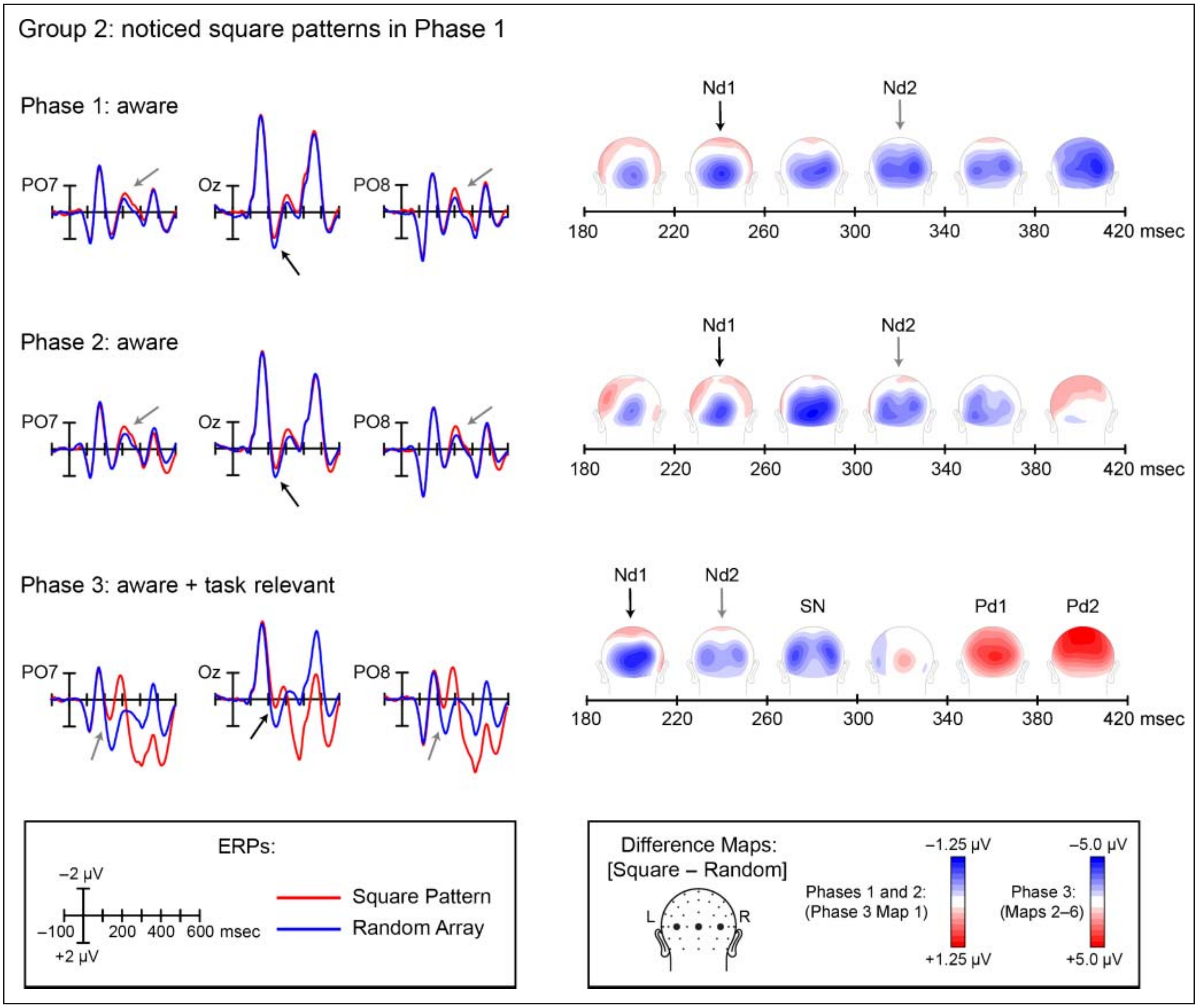


Figure 3. Grand averaged ERPs and difference topographies (square pattern–random array) for Group 2 (subjects who noticed the square pattern in Phase 1). Results were similar to those of Group 1, with the exception of the Nd2 being elicited in this group of subjects in Phase 1 (the Nd2 was absent in Group 1, Phase 1; see Figure 2).

Table 3. ERP Amplitudes

	220–260 msec			*300–340 msec*		
	Square Pattern	*No Pattern*	*Difference*	*Square Pattern*	*No Pattern*	*Difference*
Phase 1						
Group 1	1.80	2.44	−0.64**	−0.56	−0.53	−0.03
Group 2	1.37	1.91	−0.54**	−0.93	−0.24	−0.69**
Phase 2						
Group 1	1.46	2.22	−0.76**	−0.97	−0.54	−0.43**
Group 2	1.04	1.50	−0.46**	−1.10	−0.77	−0.33*

Amplitudes are mean voltages (μV) at electrode locations described in the text.

*$p < .10$

**$p < .05$

ANOVAs were conducted for each group and each phase separately. These analyses revealed significant main effects of Stimulus Type for all conditions in which subjects were aware of the patterns: for Group 1, Phase 2, $F(1, 15) = 18.52, p = .0006$; Group 2, Phase 1, $F(1, 15) = 9.07, p = .009$; and marginally significant effects for Group 2, Phase 2, $F(1, 15) = 3.72, p = .07$. Conversely, in the inattentionally blind condition (Group 1, Phase 1), no main effect of Stimulus Type, that is, no Nd2, was evident, $F(1, 15) = 0.02, p = .88$. Thus, the Nd2, with a bilateral occipito-parietal distribution, was only elicited in conditions when subjects reported awareness of the patterns and appeared, although these patterns were not task relevant. Mean ERP and difference amplitudes for each stimulus, phase, and group are provided in Table 3. It is worth noting that these measurements of Nd2 amplitudes are highly conservative because of the necessity of waiting until after each phase to inquire subjects about their awareness. In other words, it is likely that subjects who reported awareness of the squares in the postphase questionnaires noticed the squares on only a fraction of the 240 trials. This was evident in the frequency ratings, as only 7 of 32 subjects estimated having seen the squares more than 100 times.

To assess the influence of task relevance on the processing of these same stimuli, ERPs elicited by the square patterns and random arrays during Phase 3 were compared. In this phase, the square patterns were nontargets but were task relevant, as the subjects' task was to discriminate and respond to the diamond patterns. Here, the first difference component (Nd1) appeared slightly earlier in time (180–220 msec) than in Phases 1 and 2 and was immediately followed by a second difference component (Nd2) from 220 to 260 msec (see Figures 2 and 3). Both were significant: $F(1, 30) = 10.51, p = .003$ and $F(1, 30) = 31.36, p < .00001$. To test whether these difference components in Phase 3 had the same scalp distributions as those in Phase 2, amplitudes were normalized (McCarthy & Wood, 1985) and divided into 12 clusters of three electrodes each (covering central, parietal, temporal, and occipital scalp regions) and compared via ANOVA with the factors Phase (2, 3) and Cluster Location (1–12). These tests showed no interactions between Phase and Cluster Location, suggesting that the distributions of the Nd1 and Nd2 in Phase 3 did not differ from those in Phase 2. Mean difference amplitudes were then compared between Phase 2 and Phase 3 for each component separately. Amplitudes of the Nd1 did not differ between Phases 2 and 3, $F(1, 30) = 0.71, p = .40$, whereas amplitudes of the Nd2 were significantly enhanced in Phase 3, $F(1, 30) = 20.75, p = .00008$.

Following the Nd1 and Nd2, subsequent differences were observed in the ERPs to the square patterns versus the random arrays in Phase 3 that were not present in Phases 1 or 2. From 260–300 msec a later negativity was evident, which had a different topography from the Nd2. This distinction between voltage distributions was confirmed with ANOVA comparing amplitude-normalized scalp distributions, $F(11, 341) = 9.35, p < .0001$. This later negativity appears equivalent to the SN that is typically observed for task-relevant, attended, nontarget stimuli (here, the square patterns) that share features with the targets (the diamond patterns; Hillyard & Anllo-Vento, 1998; Harter & Aine, 1984). This difference (SN; 260–300 msec) between the square patterns and the random arrays was significant, $F(1, 30) = 64.61, p < .00001$. Following the SN, two positive difference components were evident in the ERPs to the square patterns versus the random arrays: the first with a distribution centered at the occipital pole (340–380 msec) and the second with a vertex-centered topography (420–460 msec). These components, referred to here as "Pd1" and "Pd2" for simplicity, were both significant, $F(1, 30) = 63.44, p < .00001$, and $F(1, 30) = 104.83, p < .00001$, respectively.

To obtain preliminary estimates of the neuroanatomical generators of these ERP components, distributed source inverse solutions (LAURA) were calculated on the grand averages over the same time intervals as in the statistical analyses. Source estimates were obtained for each group and each phase, separately. The results are provided in Figures 4 and 5. For the Nd1, sources within early visual areas (cuneus, lingual gyrus) were evident for both groups in all three phases. For the Nd2, the inverse solutions pointed toward sources within bilateral middle occipital and inferior occipital-temporal cortex, in the vicinity of the lateral occipital complex (LOC). As the forgoing analyses indicate, these LOC sources were only present for the conditions in which subjects reported awareness of the patterns. In Phase 3, sources of the SN component were estimated in both the LOC and early visual areas. Sources of the Pd1 component, which had a distribution similar to the Nd1, were located in similar anatomically early visual areas. The Pd2 component, which had a vertex-centered distribution, was estimated to have generators in more wide-spread brain regions, including anterior temporal cortex, the TPJ, and inferior frontal cortex. Talairach coordinates of maximum source intensity for each component are provided in Table 4.

To further assess the relationship between the first two difference components (Nd1, Nd2) and perceptual awareness, we tested the correlation between difference amplitudes (square pattern–random array) and confidence and frequency ratings obtained in the first questionnaire across all subjects (where the ratings were well distributed across the 5-point scales). Figure 6 shows the results of these correlations. Briefly, Nd1 amplitudes were not significantly correlated with either behavioral measure of perceptual awareness. In contrast, Nd2 amplitudes were significantly correlated with both confidence, $r = -.49, p = .005$, and frequency, $r = -.59, p < .001$ ratings such that subjects with a larger Nd2 had more confidence and estimated seeing the

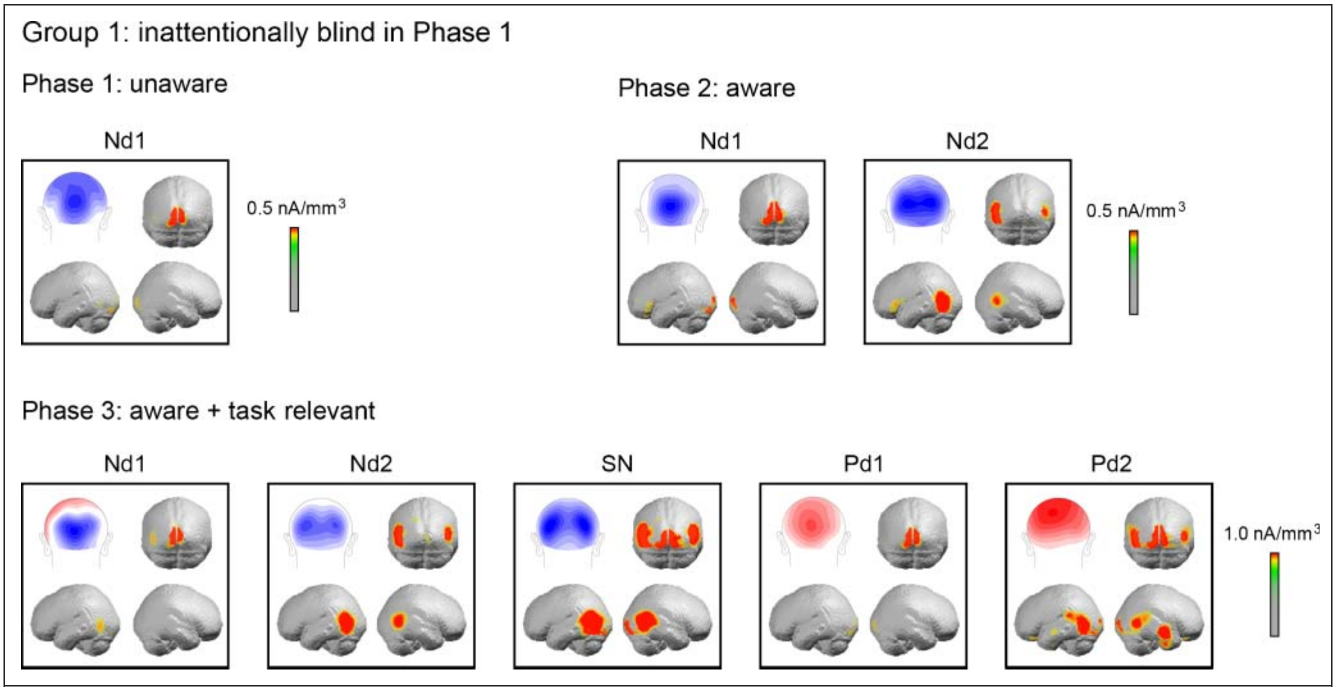


Figure 4. Results of the distributed inverse solution analyses (LAURA) used to estimate the neuroanatomical sources of the ERP differences for Group 1. Sources are displayed on the surface of the Montreal Neurological Institute brain with red representing sources with maximum estimated intensity. In each panel, the top left shows the difference topography from which the model was based (posterior view of the scalp), the top right shows a posterior view of the brain, and the bottom shows left and right hemisphere views.

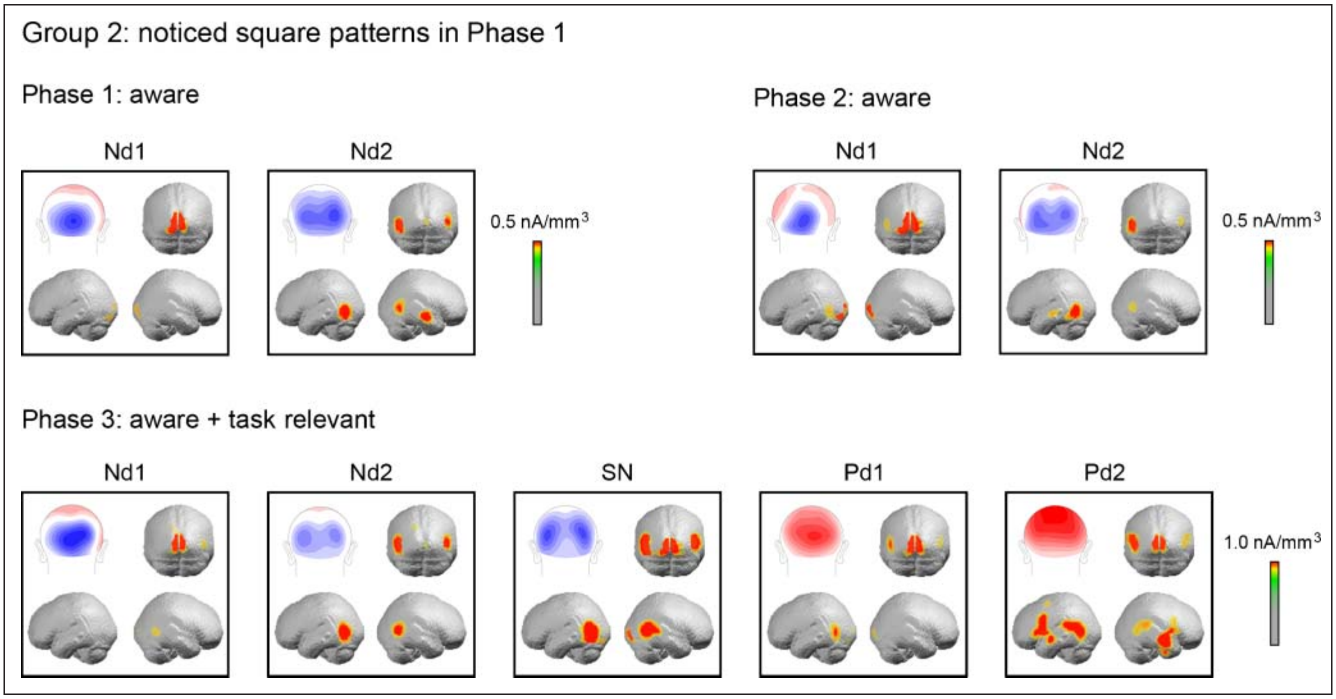


Figure 5. Results of the distributed inverse solution analyses (LAURA) used to estimate the neuroanatomical sources of the ERP differences for Group 2. Results were similar to those of Group 1, with the exception of the Nd2 being elicited by this group in Phase 1.

Table 4. Talairach Coordinates of Source Estimates

	Nd1	*Nd2*	*SN*	*Pd1*	*Pd2*
Phase 1					
Group 1	−3, −82, 7				
Group 2	3, −82, 7	−48, −61, 1			
Phase 2					
Group 1	−3, −82, 7	−49, −67, 6			
Group 2	3, −88, 7	−43, −62, 1			
Phase 3					
Group 1	−3, −82, 7	−48, −61, 6	−49, −73, 1	−3, −76, 7	27, 0, −16
Group 2	−3, −76, 12	−48, −61, 1	−48, −67, 1	3, −88, 7	27, −11, −15

Values represent *x*, *y*, and *z* coordinates of maximal source intensity.

Note that other simultaneously active sources were evident for some components (see Figures 4 and 5).

patterns more frequently than subjects with a smaller (or nonexistent) Nd2.

DISCUSSION

In the present study, the inattentional blindness paradigm was adapted to allow concurrent recordings of ERPs. During the first phase of the experiment, while performing an attentionally demanding task in the visual periphery, more than half of all participants failed to notice square-shaped contour patterns that appeared unexpectedly 240 times. After being questioned about these patterns, participants performed the same task again. Following this second phase, all participants reported seeing the previously unseen patterns. ERP analyses revealed two distinct components associated with successive stages of

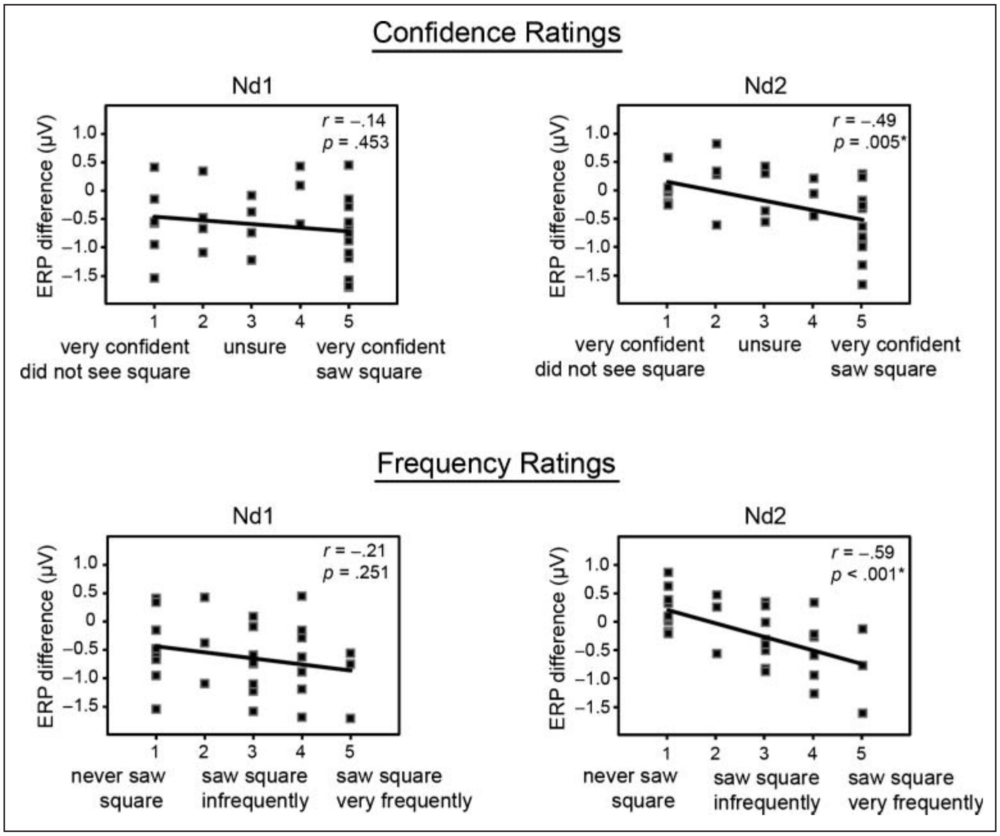


Figure 6. Correlations between ERP difference amplitudes (square pattern–random array) and subjects' confidence and frequency ratings for Phase 1. Amplitudes were averaged across the same electrodes selected for the statistical analyses. Correlations between Nd1 amplitudes and the awareness measures were not significant. Significant correlations were apparent, however, for Nd2 amplitudes and subjects' confidence in seeing the square pattern and estimates of how often they saw the pattern. Subjects who reported more confidence and reported seeing the square pattern more frequently showed a larger Nd2.

visual processing. The first component (Nd1) was evident regardless of whether subjects reported conscious awareness of the patterns. The second component (Nd2), however, was elicited only in conditions when observers were aware of the patterns. We hypothesize that the Nd1 reflects contour integration processes that occur without attention or awareness whereas the Nd2 reflects processes related to conscious perception. Both the Nd1 and the Nd2 were dissociable from additional task-related components reflecting postperceptual processing that appeared only when the patterned stimuli were made task relevant in the third phase of the experiment.

Nonconscious Processing

The present experiment revealed an early stage of visual processing that was evidently carried out in the absence of awareness. We propose that this ERP difference component (Nd1) that was present in all conditions (including inattentional blindness) reflects an early stage of contour integration, a process by which spatially separate collinear elements are integrated to form larger multielement contours. A number of previous studies in monkeys have provided converging evidence suggesting that contour integration is carried out within anatomically early visual cortex (Mandon & Kreiter, 2005; Bauer & Heinze, 2002; Stettler, Das, Bennett, & Gilbert, 2002; Gilbert, Ito, Kapadia, & Westheimer, 2000; Hess & Field, 1999; Kapadia, Ito, Gilbert, & Westheimer, 1995). It has also been proposed that whereas contour integration can be modified by top–down attention under certain conditions (Li, Piech, & Gilbert, 2004, 2006, 2008), highly salient contours may be integrated automatically, for example, when the distance over which the line segments must be integrated is small (Mathes & Fahle, 2007a; Li & Gilbert, 2002). Although behavioral studies in humans initially suggested that multielement grouping requires attention (Mack et al., 1992; Rock, Linnett, Grant, & Mack, 1992), subsequent experiments showed that grouping can occur outside the focus of attention and without awareness (Moore & Egeth, 1997). Results from the current study support this latter view and suggest that the Nd1 (with estimated generators in early visual areas) may be a neural correlate of contour integration (grouping) that occurs during a nonconscious stage of processing.

The timing of the Nd1 (220 msec) suggests that this automatic contour integration process may have been carried out after the initial feed-forward sweep of cortical activity and, therefore, may depend on feedback from higher-level visual areas (Lamme, 2006). If correct, this would suggest that re-entrant (feedback) processing may not be sufficient for visual awareness of the contour information, as the Nd1 was elicited even when subjects were unaware of the pattern stimuli. Alternatively, feed-forward processing of the contour patterns might have been delayed by the need to carry out the primary discrimination task first. Whether the Nd1 reflects re-entrant feedback or delayed feed-forward processing is an important question for future research.

Conscious Processing

Consistent with our finding of a relationship between the Nd2 and visual awareness, previous studies using backward masking techniques have consistently identified a component, the so-called "visual awareness negativity," having the same polarity and similar latencies and scalp distributions as the Nd2 by comparing ERPs elicited by seen (unmasked) stimuli to ERPs elicited by unseen (masked) stimuli (Koivisto & Revonsuo, 2003, 2007, 2010; Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto et al., 2008; Koivisto, Revonsuo, & Lehtonen, 2006). These studies have employed a variety of visual stimuli, for example, line drawings of objects, letters, global shapes, gratings, and in some cases were able to compare seen versus unseen stimuli for identical mask-onset latencies (Koivisto & Revonsuo, 2008a; Wilenius & Revonsuo, 2007; Koivisto, Revonsuo, & Salminen, 2005). Notably, in these backward masking studies, as well as in other experiments that used signal detection or attentional blink paradigms to manipulate awareness, a number of additional ERP components reflecting more wide-spread brain activity were found to be associated with awareness (Lamy, Salti, & Bar-Haim, 2009; Fahrenfort et al., 2008; Del Cul, Baillet, & Dehaene, 2007; Sergent, Baillet, & Dehaene, 2005; Pins & ffytche, 2003). Because the stimuli were task-relevant targets in these studies, it was unclear whether these later components reflected neural events associated with awareness or with other postperceptual processes, although Koivisto et al.'s (2006) results suggested the latter. Consistent with this, in the current study, additional neural processing was found only in Phase 3 (SN, Pd1, Pd2), in which the stimuli became task relevant. In Phase 2, subjects were fully aware of the task-irrelevant patterns, but there was no indication of any additional wide-spread neural activity subsequent to the two initial negative components (Nd1, Nd2). This pattern of results suggests that the neural events reflected in the Nd1–Nd2 sequence may be adequate in themselves to produce visual awareness, whereas more wide-spread activity (indexed here by the SN, Pd1, and Pd2) might be required only when the stimuli need to be processed further to fulfill the goals of the task at hand. This distinction parallels that made by previous theorists (e.g., Block, 2005) between "phenomenal consciousness" (the Nd2) and "access consciousness" (the SN–Pd1–Pd2 sequence).

fMRI and magnetoencephalography studies have suggested that initial grouping of simple contours into more complex shapes is carried out within the LOC (Grill-Spector, 2003; Grill-Spector, Kourtzi, & Kanwisher, 2001) and that activity in this region is correlated with visual awareness of objects (Grill-Spector, Kushnir, Hendler, & Malach, 2000; Vanni, Revonsuo, Saarinen, & Hari, 1996). ERP and source localization experiments have similarly pointed toward a role for the LOC in perceptual closure, figure-ground segregation, and the perception of illusory shapes (Pitts, Martínez, Brewer, & Hillyard, 2011; Grutzner et al., 2010; Jiang et al., 2008; Murray, Imber, Javitt, & Foxe, 2006; Sehatpour et al., 2006; Yoshino et al., 2006; Senkowski, Rottger, Grimm, Foxe, & Herrmann, 2005; Pegna, Khateb, Michel, & Landis, 2004; Murray et al., 2002; Pegna, Khateb, Murray, Landis, & Michel, 2002; Doniger et al., 2001; Kruggel, Herrmann, Wiggins, & von Cramon, 2001). Compared with contour integration, this stage of processing appears to be more strongly influenced by attention (Martinez, Ramanathan, Foxe, Javitt, & Hillyard, 2007; Martinez et al., 2006). It is also interesting to note the similarities between the current results and those found for texture segregation in which an early attention-independent negativity was followed by a subsequent negative component that was reduced or absent when attention was diverted to another task (Heinrich et al., 2007; Scholte et al., 2006). The current results are consistent with these findings in that the Nd2 (localized to the region of the LOC) was correlated with awareness in Phases 1 and 2, and its amplitude was significantly enhanced by focused attention in Phase 3.

The relatively late timing of Nd2 contrasts with a previous study that suggested a correlate of visual awareness as early as 100-msec poststimulus (Pins & ffytche 2003). Pins and ffytche (2003) used a signal detection approach and compared ERPs elicited by threshold level stimuli that were seen versus not seen. With such a design, trial-by-trial variations in noise may determine whether the physically weak signal is detected or not. In other words, stimuli presented at threshold may fail to be perceived because of impoverished low-level sensory input. This was the conclusion reached by Squires, Hillyard, and Lindsay (1973) in a similar ERP study of auditory signal detection. Thus, the P1 modulation (~100 msec) reported by Pins and ffytche (2003) likely reflects a precurser to awareness (e.g., nonconscious sensory processing or the "quantity of signal information" that is available for subsequent processing) as opposed to awareness per se (Squires et al., 1973). Awareness may have been indexed in Pins and ffytche's (2003) study by the reported N2 difference which had a similar latency to the Nd2 reported here (~260–300 msec).

Previous studies that manipulated the visibility of contour patterns reported reductions in P2 amplitudes (at 180–260 msec) associated with higher levels of perceptual salience (Melloni, Schwiedrzik, Muller, Rodriguez, & Singer, 2011; Straube & Fahle, 2010; Straube et al., 2010). These P2 reductions, however, may reflect the activation of additional surface negative neural generators in the same time window as the P2 instead of modulations of the P2 generator itself. In the present study, reductions of P2 amplitudes were apparent for contour-present versus contour-absent stimuli and corresponded with the Nd1 in Phases 1 and 2 and with the Nd2 in Phase 3. These difference components had distinct scalp topographies from the evoked P2, however, and their latencies shifted depending on the task (earlier when pattern discrimination was the primary task). Both of these characteristics suggest additional endogenous activity rather than a modulation of the evoked P2.

Although the present study revealed an ERP component (Nd2) that was generated only in conditions when subjects reported awareness of the patterned stimuli, it is important to remain skeptical of the direct link between this pattern of brain activity and visual awareness. The visual process reflected by this ERP component may be *necessary* for awareness (of these particular stimuli), but not *sufficient*. Other, as yet unidentified, neural mechanisms might require input from this stage of processing to establish visual awareness, and the complex relationship between attention and awareness is not fully understood (Koch & Tsuchiya, 2007; Dehaene et al., 2006; Lamme, 2003). Also, as this study marks one of the first attempts to measure ERPs during inattentional blindness (see also Scholte et al., 2006), it is currently unclear whether this component reflects a general process that is engaged in awareness of various types of stimuli. Although it is possible that the Nd2 observed here and the visual awareness negativity reported in previous studies (Koivisto et al., 2006) may index general awareness-related processes (separate from task relevance), it is also possible that these components instead reflect a stage of processing in which simple features are grouped ("bound") together to form more complex object representations. As Engel and Singer (2001) have suggested, this binding process may be necessary for awareness of visual objects but not sufficient. Additional experiments are necessary before we can claim that this ERP component directly reflects visual awareness. The present study provides a decent starting point.

Conclusion

By using an inattentional blindness paradigm adapted for ERPs, this study isolated neural activity associated with specific stages of visual perception and awareness. The Nd1 component was elicited by contour patterns during inattentional blindness and was, thus, dissociated from components associated with awareness. We propose that the Nd1 reflects an early stage of contour integration that provides input to mechanisms of perceptual awareness but does not in itself produce awareness. The Nd2 component was evident only when subjects were aware of the visual patterns, even when the patterns were task irrelevant. Subsequent components (SN, Pd1, Pd2) were elicited only when the patterns became relevant to the task. The Nd2 component, thus, appeared to reflect awareness per se, separate from task-related processing.

APPENDIX

Awareness questionnaire.

Page 1:

POST-TEST QUESTIONAIRE

Phase: _______

Subject: ____________

Date: ____________

1) During the experiment, did you notice any patterns within the little white lines?

☐ Yes	☐ No

2) If you did see any patterns, please describe (or draw) what you saw in as much detail as possible:

Page 2:

*For the items below, the experimenter will provide examples on the computer screen…

3) Rate how confident you are that you saw each pattern during the experiment.

Please use the following scale:

1 = very confident I *did not* see it
2 = confident I *did not* see it
3 = uncertain
4 = confident I saw it
5 = very confident I saw it

Diamond	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
Horizontal Rectangle	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
X Pattern	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
One Big Square	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
Four Small Squares	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
Vertical Rectangle	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5

4) Estimate how often you saw each pattern.

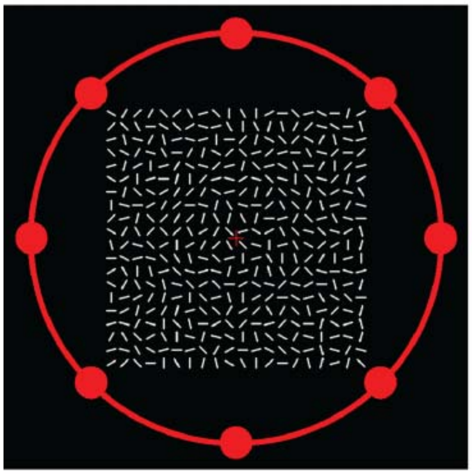
Please use the following scale:

1 = never
2 = rarely / less than 10 times
3 = infrequently / 10–50 times
4 = frequently / 50–100 times
5 = very frequently / more than 100 times

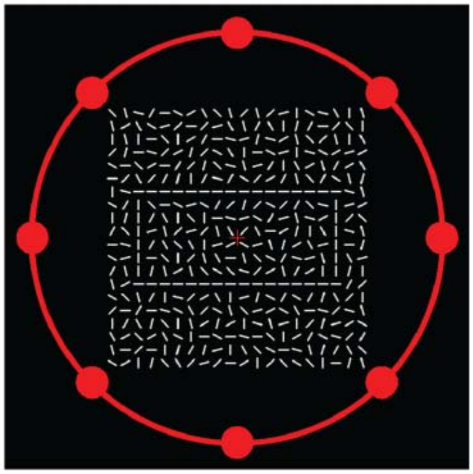
Diamond	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
Horizontal Rectangle	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
X Pattern	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
One Big Square	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
Four Small Squares	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5
Vertical Rectangle	☐ 1	☐ 2	☐ 3	☐ 4	☐ 5

Sample patterns shown during Part 2 of awareness questionnaire. Note that the square and diamond patterns were actually presented during the experiment. The other four patterns served as foils.

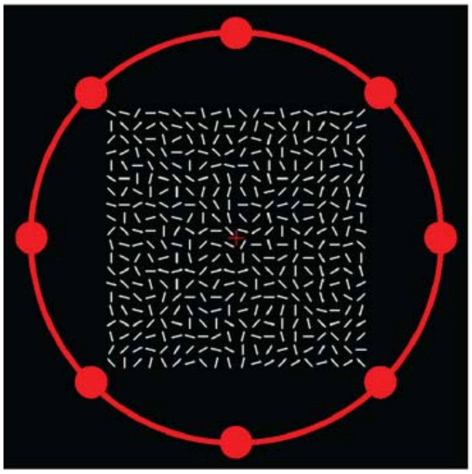
1) Diamond



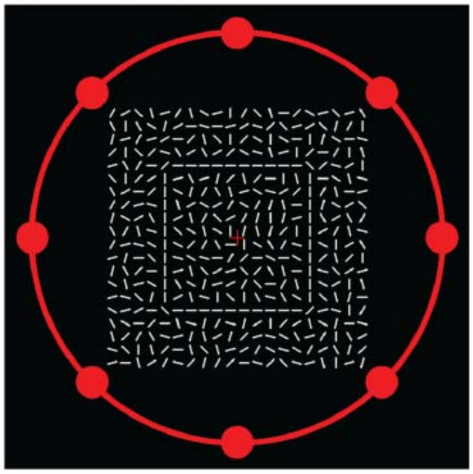
2) Horizontal Rectangle



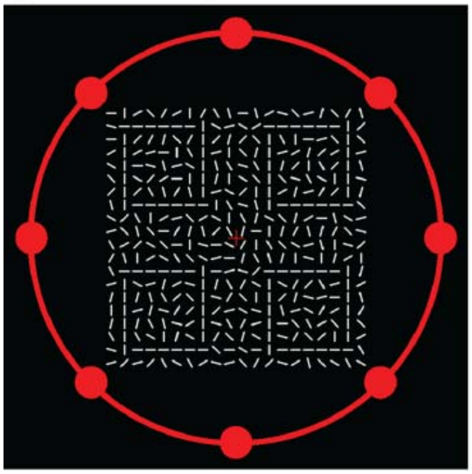
3) X Pattern



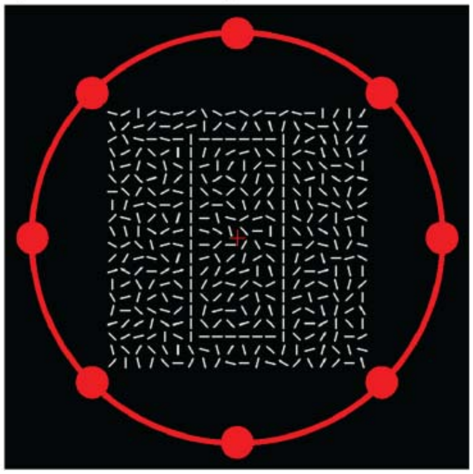
4) One Big Square



5) Four Small Squares



6) Vertical Rectangle



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