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Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness

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ABSTRACT

A primary goal in cognitive neuroscience is to identify neural correlates of conscious perception (NCC). By contrasting conditions in which subjects are aware versus unaware of identical visual stimuli, a number of candidate NCCs have emerged; among them are induced gamma band activity in the EEG and the P3 event-related potential. In most previous studies, however, the critical stimuli were always directly relevant to the subjects' task, such that aware versus unaware contrasts may well have included differences in post-perceptual processing in addition to differences in conscious perception per se. Here, in a series of EEG experiments, visual awareness and task relevance were manipulated independently. Induced gamma activity and the P3 were absent for task-irrelevant stimuli regardless of whether subjects were aware of such stimuli. For task-relevant stimuli, gamma and the P3 were robust and dissociable, indicating that each reflects distinct post-perceptual processes necessary for carrying-out the task but not for consciously perceiving the stimuli. Overall, this pattern of results challenges a number of previous proposals linking gamma band activity and the P3 to conscious perception.

Introduction

A central goal in the scientific study of consciousness is to identify neurophysiological processes that are both necessary and sufficient for a specific conscious percept (Crick and Koch, 2003; Koch, 2004). The contrastive method, a straightforward approach in which brain activity is compared for seen versus unseen visual stimuli, has proven fruitful (for reviews see Dehaene and Changeux, 2011; Railo et al., 2011). In electroencephalographic (EEG) experiments, a number of candidate neural correlates of consciousness (NCC) have emerged, including pre-stimulus alpha phase (8–12 Hz), the P1 event-related potential (ERP) component, the visual awareness negativity (VAN), induced gamma band activity (>30 Hz), and the late positive P3 (also known as P300) component (Batterink et al., 2012; Fisch et al., 2009; Koivisto and Revonsuo, 2010; Mathewson et al., 2009; Pins and ffytche, 2003; Schurger et al., 2006; Sergent et al., 2005). Two of the most intensely investigated of these proposed NCCs, gamma activity and the P3, have been interpreted as neural evidence for Baars' (1989) global workspace theory of consciousness (Baars, 2002; Dehaene and Changeux, 2011; Fisch et al., 2009; Gaillard et al., 2009). The global neuronal workspace theory posits that the transition from non-conscious to conscious processing is marked by the "ignition" of wide-spread cortical networks, including fronto-parietal regions, which enable brain-wide "broadcasting" of conscious content for flexible utilization by other systems, such as language, memory, executive control, and voluntary action (Dehaene and Changeux, 2011; Dehaene and Naccache, 2001; Dehaene et al., 1998).

Recently, however, the contrastive method has faced a major challenge (Aru et al., 2012b). Aru and colleagues argued that when comparing brain activity between aware and unaware conditions, other processes are likely to vary in addition to those associated with the conscious percept itself. Depending on how visual awareness is manipulated and assessed, neural prerequisites that are necessary but not sufficient for conscious perception and neural consequences that are sufficient but not necessary may be confused with the NCC-proper (Aru et al., 2012b). For example, differences in attention, expectation, and/or subtle properties of the physical stimulus can lead to differences in preconscious processing between aware and unaware conditions. Similarly, after a conscious percept has been established, stimuli can be recognized, held in working memory, and accessed for perceptual report while in unaware conditions these subsequent processes are typically absent. We refer to this latter category of processes as "post-perceptual" because they depend on but are not necessary for the formation of the conscious visual percept. Importantly, even when response requirements are equated across aware and unaware conditions (e.g., subjects make forced-choice discriminations on every trial) post-perceptual processing is likely to differ. On aware trials, the time between perception and response includes the access and maintenance

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of perceptual information in addition to decision-making and motor preparation and execution. On unaware trials there is no perceptual information to be accessed or maintained and thus the neural markers of these post-perceptual processes are missing, leaving only those related to deciding, preparing, and executing a "not seen" response. Thus, previous studies that have compared brain activity on aware versus unaware trials may have misinterpreted neural markers of post-perceptual processes as indices of conscious perception per se (Aru et al., 2012b).

To investigate whether two candidate NCCs, induced gamma band activity and the P3 component, reflect perceptual awareness or post-perceptual processing, we carried out a series of experiments in which visual awareness and task relevance were independently manipulated. In each case, we recorded the scalp EEG and analyzed ERPs in the time domain and spectral gamma band amplitude in the time–frequency domain. In experiment 1, an inattentional blindness paradigm was employed to measure neural responses to simple geometric shapes that were task-irrelevant and not perceived, task-irrelevant but clearly perceived, or task-relevant and clearly perceived (Pitts et al., 2012). We hypothesized that if gamma and the P3 are indeed NCCs, they should vary according to perceptual awareness regardless of task relevance. Alternatively, if gamma and P3 reflect post-perceptual processes, they should be modulated by task relevance and should be dissociable from awareness.

Two additional experiments were conducted to verify and extend the results from experiment 1. To create a situation conducive to inattentional blindness, experiment 1 utilized temporally-overlapping, spatially-separated distracter stimuli. Thus the results may have reflected differences in spatial or object-based attention rather than differences in post-perceptual processing. In experiment 2, the stimuli and tasks were adjusted to control for differences in spatial attention between the task-relevant and irrelevant conditions and to ensure that the critical stimuli (shapes) were temporally isolated in the task-irrelevant condition. Finally, because experiments 1 and 2 explored task-relevancy as a binary variable, it was only possible to assess the presence versus absence of gamma and P3. In experiment 3, the degree of task-relevance was manipulated (across five levels) by varying perceptual similarity to the target. Taken together, this series of experiments was aimed at determining whether gamma band activity and/or the P3 reflect processes necessary and sufficient for conscious perception or instead post-perceptual processes that depend on but are not necessary for visual awareness per se.

Materials & methods — experiment 1

Participants

Thirty-eight healthy adults participated in experiment 1. This experiment utilized the same raw data as our previous study (Pitts et al., 2012), in which only the time domain ERPs were reported. All participants were recruited as volunteers and gave informed consent prior to the beginning of the experiment. Data from six participants were later excluded due to excessive EEG artifact. The final group consisted of thirty-two participants (mean age 21 years old; 19 females). The experimental procedures were approved by the University of California San Diego institutional review board in compliance with the Declaration of Helsinki.

Stimuli & procedure

Detailed methods for experiment 1 have been published in Pitts et al. (2012). Briefly, stimuli consisted of a 20 × 20 grid of small white line segments (visual angle = 6.2° × 6.2°). The grid was surrounded by a red ring (9.8°) of eight evenly-spaced disks (each 1.0°). The orientations of the line segments alternated between a random configuration during the inter-stimulus interval (duration = 600–800 ms) and one of three possible stimulus configurations (duration = 300 ms): a square pattern (3.5°), a diamond pattern (3.2°), or another random configuration. Stimuli were presented in random order with the following probabilities: square patterns (40%), diamond patterns (10%), and random configurations (50%). The red ring of disks alternated between a standard position and one of two rotated positions (15° clockwise or counterclockwise) simultaneous with the changes in line segment orientation. Example stimuli are shown in Fig. 1 and an example block of trials can be viewed as an online video at http://youtu.be/8-9NAFUn_CI.

The experiment was divided into three phases. For all phases, the stimuli were physically identical. Each phase consisted of ten 1 min runs, 60 stimuli per run, totaling 600 stimuli per phase (240 of which were square patterns). Observers took self-paced breaks after each run, with a mandatory extended break after every 5 runs. Prior to phase 1, subjects completed 5 practice runs attending to the ring of disks in which no shape patterns were presented.

During phase 1, subjects were instructed to attend to the ring of disks in order to detect occasional dim target disks that appeared randomly at one of the eight disk positions on 10% of trials. This dim-disk distracter task was designed to elicit inattentional blindness to the shape patterns in roughly half of the subjects. Immediately following phase 1, subjects were given an awareness questionnaire to ascertain whether they had noticed any of the shape patterns. The questionnaire included a combination of open-ended questions and recognition-based confidence ratings. The complete questionnaire is available in Pitts et al. (2012). In addition to assessing awareness, this intervening questionnaire served as a cue for subjects who were inattentionally blind in phase 1 to notice the shape patterns in phase 2.

After completing the questionnaire, subjects were instructed to continue performing the dim-disk distracter task during phase 2. Importantly, the shape stimuli remained task-irrelevant in phase 2 so that changes in awareness from phase 1 to phase 2 could be isolated from changes in task-related, post-perceptual processing. Following phase

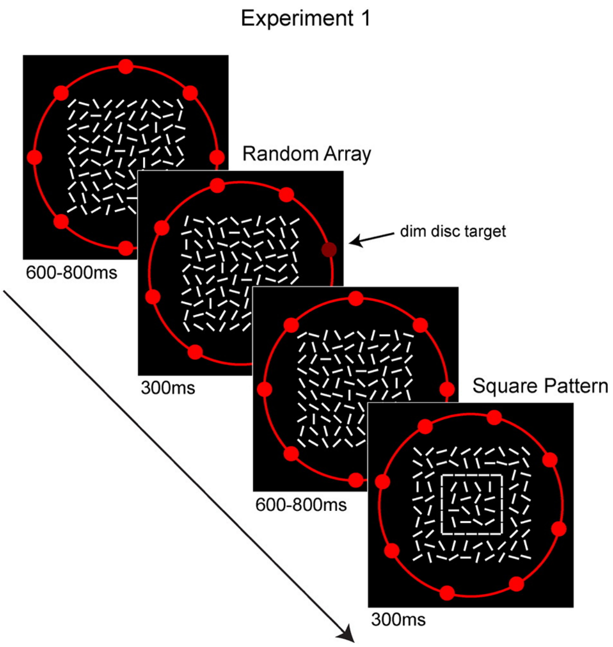

Fig. 1. Example stimulus sequence from experiment 1. Stimuli were identical across the three phases of the experiment. In phases 1 and 2 subjects attended to the outer red ring of disks to detect occasional dim disk targets. Half of the subjects in phase 1 did not notice (i.e., were inattentionally blind to) the shape patterns formed by the line segments. In phase 3 subjects attended to the line segments to detect occasional diamond shaped targets (not shown). ERPs and spectral analyses were time-locked to changes in line orientations. Note that actual stimuli consisted of 20 × 20 grids of lines and are displayed here as 10 × 10 grids for demonstration purposes. A video example can be viewed online: http://youtu.be/8-9NAFUn_CI.

2, the same awareness questionnaire was given again. Finally, in phase 3 subjects were instructed to ignore the ring of disks and attend to the line segment array in order to detect the diamond patterns that appeared on 10% of the trials. Thus, the shape patterns became task-relevant only in the third phase of the experiment. In all phases, the square patterns and random arrays were non-targets so that the ERPs of interest remained uncontaminated by motor preparation and response execution potentials.

EEG/ERP methods

In Pitts et al. (2012) we focused on the two earliest ERP differences between square pattern and random array stimuli (components labeled Nd1, Nd2). Here, we analyzed the same data to investigate the P3 and induced gamma band activity. Brain electrical activity was recorded non-invasively 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) 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 (electrooculogram) recordings. A right mastoid electrode served as the reference for all scalp channels and the vertical EOG. Left and right horizontal EOG channels were recorded as a bipolar pair.

Raw EEG data were analyzed separately in the time domain (ERPs) and the time–frequency domain. In both cases, EEG signals were time-locked to the line segment orientation changes and 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 12.7% of trials per individual were rejected due to these artifacts (mean number of trials after artifact rejection: 171 for square stimuli, 222 for random stimuli). Trials in which a manual response was made to the non-target squares or random arrays within a −500 ms to +1000 ms time window relative to stimulus onset were excluded. Prior to ERP analysis, data were re-referenced to the average of the left and right mastoid channels, segmented into −100 to 600 ms epochs, baseline corrected from −100 to 0 ms, low-pass filtered at 30 Hz, and averaged across trials. The time window and electrode locations for analysis of the P3 effect (square pattern–random array) were chosen based on the peak amplitudes and scalp distributions in the grand-averaged P3 waveforms across all conditions, using previous studies as a guide (Polich, 2007, 2012). In-house software (ERPSS) was used for all ERP analyses.

For time–frequency analysis, data were re-referenced to the average of all channels, segmented into −1000 to +1000 ms epochs, low-pass filtered at 150 Hz, and analyzed on a single-trial basis via complex Morlet wavelets prior to averaging. For each subject, condition, electrode, trial, and time point (every 2 ms) spectral amplitude was estimated via 8 cycle wavelets at 28 different frequencies increasing logarithmically from 19 Hz to 85 Hz (at 35 Hz, time–frequency resolution = 72 ms × 8.75 Hz). Single trial spectral amplitudes were then averaged across trials, segmented into −400 to +600 ms epochs, and mean baseline amplitude (−350 to −50 ms) was subtracted from each individual time point for each frequency separately. Data preprocessing was carried out using a combination of EEGLAB (Delorme and Makeig, 2004) and ERPLAB (Lopez-Calderon and Luck, 2014) toolboxes. Wavelet analyses and subsequent data processing were conducted using custom scripts in Matlab (R2009b, MathWorks), following the methods of Lakatos et al. (2004) and Torrence and Compo (1998). The time window, frequency window, and electrode locations for analysis of gamma amplitude were chosen based on the peak amplitudes and scalp distributions in the grand-averaged spectra across all conditions, again using previous measurements of induced gamma in M/EEG experiments as a guide (Melloni et al., 2007; Vidal et al., 2006; Wyart and Tallon-Baudry, 2008).

Results & discussion — experiment 1

Behavioral results

Based on the awareness questionnaire data obtained after phase 1, sixteen out of the thirty-two subjects were deemed inattentionally blind to the square patterns (Pitts et al., 2012). The questionnaires given after phase 2 indicated that all subjects were aware of the square patterns during this phase. All subsequent behavioral and electrophysiological analyses treated these two groups of subjects separately (hereafter, the "inattentionally blind" and the "noticer" subject groups). Detailed questionnaire results are available in Pitts et al. (2012).

Critical for the current analysis, behavioral performance on the dim-disk distracter task was not adversely affected by subjects noticing the task-irrelevant square patterns. ANOVA for reaction times (RT) and d-prime (d') with the within subjects factor phase (1, 2) and the between subjects factor group (inattentionally blind, noticers) showed no significant main effects or interactions other than a main effect of phase on reaction times, $F(1, 30) = 4.65$, $p = .039$. This RT effect, however, was in the opposite direction than one would expect if noticing an additional stimulus interfered with performance on the primary task [mean RT (sem): phase 1 = 614 ms (9 ms); phase 2 = 601 ms (11 ms)]. This lack of performance decrement suggests that while awareness of the squares differed between inattentionally blind subjects and noticers in phase 1 and within the inattentionally blind group between phases 1 and 2, post-perceptual processing related to the distracter task remained unchanged.

Performance on the diamond detection task in phase 3 was better than the dim-disk distracter task in phases 1 and 2 in terms of d' but not RT. ANOVA including all three phases showed no main effects or interactions for RTs, a main effect of phase on d', $F(2, 60) = 9.38$, $p = .001$ (Greenhouse–Geisser corrected), and no interactions between group and phase for d'. Mean d' (sem): phase 1 = 2.98 (0.15); phase 2 = 3.11 (0.16); phase 3 = 3.63 (0.09).

EEG/ERP results

The contrasts of interest for both the P3 and gamma were between square pattern and random array stimuli (stimulus factor) across the three phases of the experiment (phase factor) and between the inattentionally blind and noticer subjects (group factor). Initial omnibus repeated measures ANOVAs were conducted for the P3 and gamma separately to confirm the expected stimulus × phase interaction and to test for a potential stimulus × phase × group interaction. Follow-up one-way repeated measures ANOVAs with the factor stimulus were then conducted for each group and each phase separately.

Mean P3 amplitudes from 350 to 550 ms post-stimulus were assessed at 9 central-parietal electrode sites (C1, CZ, C2, CP1, CPZ, CP2,

Table 1
Experiment 1: P3 results.

	Amplitudes			F (1, 15)	p
	Square pattern	Random array	Difference		
Phase 1					
IB group	0.94 (0.34)	0.90 (0.34)	0.04	0.04	0.85
Noticer group	0.02 (0.36)	0.09 (0.28)	−0.07	0.09	0.76
Phase 2					
IB group	0.69 (0.39)	0.46 (0.31)	0.23	0.69	0.42
Noticer group	0.26 (0.21)	−0.08 (0.36)	0.34	1.77	0.20
Phase 3					
IB group	4.29 (0.58)	1.23 (0.46)	3.06	39.54	0.00002*
Noticer group	4.52 (0.63)	0.42 (0.37)	4.10	58.78	0.000001*

Amplitudes (sem) are mean voltages (μV) from 350 to 550 ms across 9 central-parietal electrodes.
"IB" = group of subjects inattentionally blind in phase 1.
* Indicates significance for an alpha of $p < .05$.

P1, PZ, P2). The initial omnibus ANOVA with the factors stimulus, phase, electrode, and group revealed a significant stimulus × phase interaction, F(2, 60) = 58.47, $p < .000001$ (Greenhouse–Geisser corrected), while the three-way interaction between stimulus × phase × group was not significant. Follow-up ANOVAs confirmed that the stimulus × phase interaction was due to significant P3s only in the third phase of the experiment. No significant differences between P3 amplitudes for square and random stimuli were evident during phase 1 or 2 for either group of subjects. In phase 3, both the inattentionally blind and noticer subjects showed robust P3 effects, F(1, 15) = 39.54, p = .00002; F(1, 15) = 58.78, p = .000001, respectively. Mean P3 amplitudes averaged across the 9 central-parietal channels, along with statistical results from the one-way ANOVAs are provided in Table 1. Grand averaged ERPs and difference topographies for the inattentionally blind group of subjects are plotted in Fig. 2. The same data for the noticer subjects is provided in Supplementary Fig. S1.

Mean gamma band amplitude was measured from 360 to 440 ms and from 30 to 40 Hz in left and right hemisphere clusters of occipital–parietal electrodes (PO7, PO3, P7, P5, O1, and PO8, PO4, P8, P6, O2), based on the time–frequency distribution and scalp distribution of the grand average across all conditions. Similar to the P3 results, an initial omnibus ANOVA with the factors stimulus, phase, hemisphere, electrode, and group resulted in a significant stimulus × phase interaction, F(2, 60) = 18.08, p = .00005 (Greenhouse–Geisser corrected), while the three-way interaction between stimulus × phase × group was not significant. Although there were no 2 or 3-way interactions with the factor hemisphere, there was a significant 4-way interaction between hemisphere × stimulus × phase × group, F(2, 60) = 3.72, p = .03 (G–G corrected). This interaction was explained by the inattentionally blind subjects having increased gamma activity over the left hemisphere compared to the noticer subjects for the square stimulus in phase 3.

Follow-up ANOVAs confirmed that the interaction of greatest interest (stimulus × phase) was due to a significant difference in gamma amplitude between the square and random stimulus in phase 3 for both inattentionally blind and noticer subjects, F(1, 15) = 10.99, p = .005; F(1, 15) = 9.23, p = .008, respectively, while no significant differences in gamma activity were evident during phase 1 or 2 for either group of subjects. To confirm these results, we also tested mean gamma amplitude against zero for each stimulus and each phase separately (all subjects combined). The only condition showing gamma amplitude significantly different from zero was the square stimulus in phase 3; i.e., when it was task-relevant [t(31) = 4.17, p = .0002]. Table 2 provides mean gamma amplitudes averaged across the 10 occipital–parietal electrodes, along with statistical results from the one-way ANOVAs. Fig. 2 shows the grand averaged spectral amplitude over time as well as difference topographies for the inattentionally blind group of subjects. Supplementary Fig. S1 provides the same (and

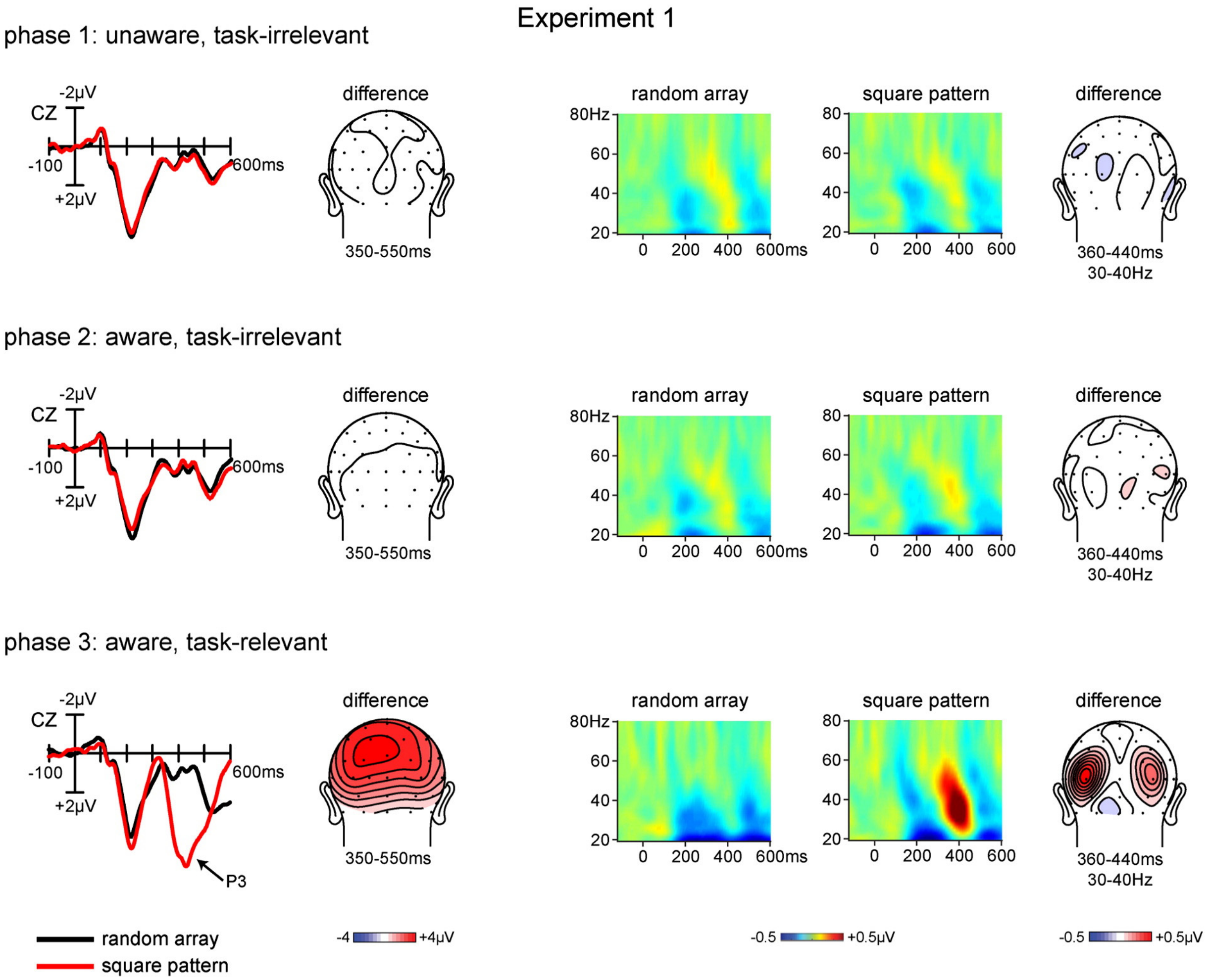

Fig. 2. (Left) Grand averaged ERPs at a representative electrode site (CZ) and difference wave scalp topographies (square minus random; posterior view of scalp) during each phase of the experiment. (Right) Grand averaged time–frequency plot of spectral amplitude at electrode PO7 along with difference topographies for the same three phases of the experiment. Note that only data from the group of subjects (N = 16) who were inattentionally blind to the square patterns during phase 1 of the experiment are shown here. Similar data for the group of subjects (N = 16) who spontaneously noticed the square patterns in phase 1 are provided in Supplemental Fig. S1.

Table 2
Experiment 1: Gamma results.

	Amplitudes			F (1, 15)	p
	Square pattern	Random array	Difference		
Phase 1					
IB group	0.009 (0.019)	0.028 (0.019)	−0.019	1.13	0.30
Noticer group	−0.002 (0.022)	0.003 (0.019)	−0.005	0.05	0.83
Phase 2					
IB group	0.043 (0.026)	0.020 (0.020)	0.023	0.92	0.35
Noticer group	0.012 (0.027)	0.029 (0.013)	−0.017	0.63	0.44
Phase 3					
IB group	0.243 (0.080)	−0.047 (0.014)	0.290	10.99	0.005*
Noticer group	0.197 (0.071)	0.003 (0.018)	0.194	9.23	0.008*

Mean spectral amplitudes (μV) and (sem) from 360 to 440 ms, 30–40 Hz for 10 occipito-parietal electrodes.
"IB" = group of subjects inattentionally blind in phase 1.
* Indicates significance for an alpha of p < .05.

virtually identical) data for the noticer group of subjects, and Supplementary Fig. S2 shows the gamma response amplitudes for a larger set of individual scalp sites.

While the gamma response observed in phase 3 (from 360 to 440 ms, 30–40 Hz) likely reflects induced activity, the analysis outlined above measures total amplitude which may include both induced (non-phase-locked) and evoked (phase-locked) activity. To determine whether the gamma activity in phase 3 was induced, we analyzed phase-locking values (PLVs) in the same time–frequency windows and electrodes used to measure the amplitude effects. To calculate PLV, the same complex wavelet decompositions used for amplitude analyses were normalized on every trial and then averaged across trials. The resulting PLVs are thus amplitude-independent and measure spectral phase consistency across trials on a scale from zero to one (Lakatos et al., 2005; Mishra et al., 2012). Supplemental Fig. S3 shows PLVs for both stimuli in phase 3 at individual electrode sites.

ANOVA for phase-locking values with the factors stimulus, phase, hemisphere, electrode, and group showed a main effect of stimulus, F(1,30) = 16.08, p = .0003 (G–G corrected), and a main effect of phase, F(2,60) = 13.50, p = .00003 (G–G corrected), while the interaction between stimulus × phase was not significant. These main effects were explained by small but consistent increases in PLV for square versus random stimuli, and for phase 3 versus phases 1 & 2 [mean PLV (sem): phase 1 square = 0.13 (0.009); phase 1 random = 0.11 (0.008); phase 2 square = 0.12 (0.009); phase 2 random = 0.12 (0.008); phase 3 square = 0.15 (0.010); phase 3 random = 0.13 (0.010)]. In all phases of the experiment, two clear peaks in PLV were evident at 120 ms and 420 ms corresponding to phase-locked activity evoked at 120 ms post-stimulus-onset and 120 ms post-stimulus-offset, respectively (Fig. S3). The scalp distribution of these peaks in PLV (central occipital) was very different from the distribution of the amplitude effects described above (bilateral occipital–parietal), and the frequency at which PLV reached a maximum was 30 Hz (compared to 35 Hz for the amplitude effects). These differences in timing, frequency, and scalp topography between gamma amplitudes (Fig. S2) and PLV (Fig. S3), along with the different pattern of results across conditions (i.e. no interaction between stimulus × phase for PLV) indicate that the gamma activity elicited by the task-relevant squares was induced rather than phase-locked.

Discussion

If induced gamma band activity and the P3 component were neural correlates of conscious perception, one would expect them to be absent in phase 1 for the inattentional blind group of subjects and present in phase 2 for this same group of subjects once they became aware of the shape stimuli. Gamma activity and P3 should also have been present in both phases 1 and 2 for the subjects who spontaneously noticed the square patterns. The current data, however, provide no evidence for either gamma activity or the P3 component in perceptually aware but task-irrelevant conditions. Instead, gamma and the P3 were evident only in phase 3 when the stimuli became relevant to the task. This suggests that gamma and the P3 do not index perceptual awareness, but instead reflect post-perceptual processes that rely on this perceptual information to fulfill immediate task demands.

Because these findings run counter to the majority of previous studies on visual awareness (see General discussion below), it is important to consider the possibility that our specific implementation of the inattention paradigm may have included a confounding factor that affected the aware versus unaware comparison. For example, in phase 2, even though all subjects reported noticing the square patterns frequently, their spatial attention was focused on the surrounding red ring of disks in order to complete the distracter task. Also, the distracter ring was always simultaneously present with the square patterns and thus may have been treated by the visual system as a separate object competing for limited attentional resources. Either of these factors may have contributed to the absence or active suppression of gamma and/or the P3 during the task-irrelevant conditions.

In order to provide ample opportunity for elicitation of gamma and the P3 by consciously-perceived but task-irrelevant stimuli, we designed a follow-up experiment that controlled for spatial attention and competition between objects. The surrounding red ring of disks was removed, shape patterns were presented without competition, and a new task was implemented in order to make the shape patterns task-irrelevant. During separate blocks of trials, subjects performed one of two tasks (order counterbalanced across subjects), in which either the shape patterns were relevant or arrays containing color patches were relevant. In both conditions, subjects were aware of the shape stimuli. Importantly, the shape patterns were presented in a randomized sequence with the color-patch arrays, and all stimuli were presented in overlapping spatial positions. Gamma responses and P3s elicited by the shape patterns were then measured and compared according to task relevance.

Materials & methods — experiment 2

Participants

Twenty-eight healthy adults participated in experiment 2. All were recruited as volunteers and gave informed consent prior to the beginning of the experiment. Data from six participants were later excluded due to excessive EEG artifact and data from two participants were excluded due to inattentional blindness (see Stimuli & procedure section). The final group consisted of twenty participants (mean age 21.15 years old; 16 females). The experimental procedures were approved by the University of California San Diego institutional review board in compliance with the Declaration of Helsinki.

Stimuli & procedure

The same 20 × 20 grid of line segments from experiment 1 was used in experiment 2 while the surrounding red ring of disks was removed. Stimulus timing was identical to experiment 1. For this experiment, random arrays were presented on 33.3% of trials, rectangle patterns on 33.3% of trials, and arrays with patches of red colored lines on 33.3% of trials. The rectangle patterns were the same as the square patterns used in experiment 1, except they were elongated by one grid row on either the vertical (3.5° × 2.85°) or horizontal (2.85° × 3.5°) axes. Each type of rectangle was presented equiprobably on 16.67% of trials. The arrays with color contained clusters (patches), each made of four adjacent red lines. The color-patch arrays had either 3 or 4 clusters of red lines, each presented equiprobably on 16.67% of trials. The spatial positioning of the color patches across trials was pseudo-randomized with the following restrictions: all color patches appeared at spatial locations that overlapped with locations of the rectangle edges on shape trials; the 4-patch stimuli contained color patches positioned over the top, bottom, left, and right edges of where the rectangles appeared; the 3-patch stimuli were identical to the 4-patch stimuli except with one cluster randomly removed; color patches were separated from each other by at least one column and one row of white lines. Fig. 3 shows example stimuli, and an online video can be viewed here: http://youtu.be/RpcEWi7iB_4.

At the beginning of the experiment, all subjects were shown examples of both the rectangle and color patch stimuli (to prevent inattentional blindness to the task-irrelevant stimuli) and were trained to perform one of two tasks for the first half of the experiment. For the color task, half of the subjects were instructed to press a response key whenever they saw 3 patches of color and half of the subjects whenever they saw 4 patches of color. For the shape task, half of the subjects responded to vertical rectangles while the other half were assigned horizontal rectangles as targets. After finishing the first half of the experiment, which consisted of 1200 trials (400 random stimuli, 400 color stimuli, 400 shape stimuli) subjects were given a brief questionnaire similar to experiment 1 to ensure that they had perceived the task-irrelevant stimuli. Based on this questionnaire, 2 subjects were deemed inattentionally blind to the rectangles during the color task and were excluded from further analysis. Subjects were then trained to perform the second task (attend-color or attend-shape) and completed a second round of 1200 trials. The stimuli were identical for both tasks and task order was counterbalanced across subjects with ten subjects completing the color then shape task and ten completing the shape then color task.

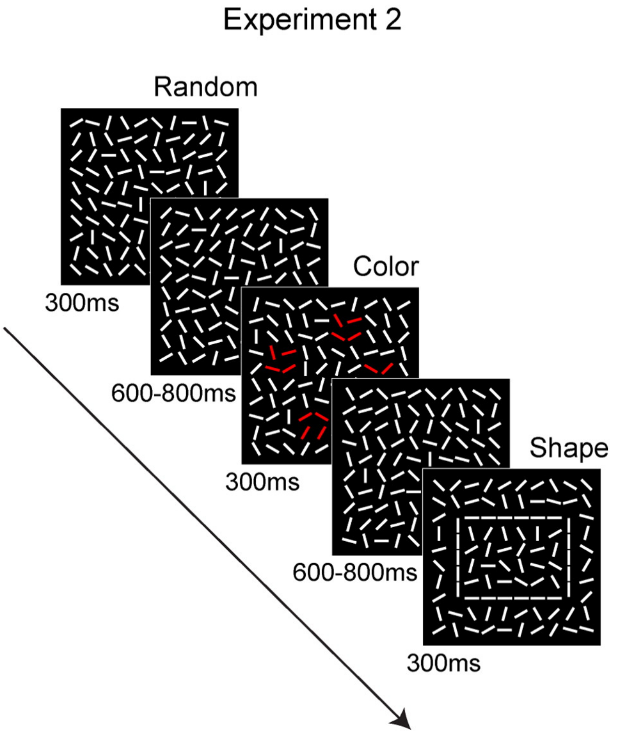

Fig. 3. Example stimulus sequence from experiment 2. Task relevance of the shape and color patch stimuli was manipulated across blocks of trials. Subjects attended to either the color stimuli or the shape stimuli to detect designated targets (3 or 4 patches of color; vertical or horizontal rectangles). As in experiment 1, actual stimuli consisted of 20 × 20 grids of lines and are displayed here as 10 × 10 grids for demonstration purposes. A video example can be viewed online: http://youtu.be/RpcEWi7iB_4.

EEG/ERP methods

EEG recording and data preprocessing for both ERPs and induced gamma band activity were identical to experiment 1. The comparisons of interest for this experiment were between P3s and gamma responses elicited by the non-target rectangles when they were task-relevant (shape task) versus task-irrelevant (color task). On average 18.7% of trials per individual were rejected due to artifacts (mean number of trials after artifact rejection: 253 for rectangle stimuli, 257 for random stimuli). As in experiment 1, the shape-elicited EEG responses (P3 and gamma) were contrasted with responses to the random arrays. Here, the primary EEG analyses included the within subjects factors stimulus (shape, random) and task (shape task, color task), and the between subjects factor task order (shape then color, color then shape). To ensure that detection difficulty for particular shape and color stimuli was equivalent, the behavioral analysis also included the between subjects factors target-shape (vertical, horizontal) and target-color (3-patches, 4-patches).

Results & discussion — experiment 2

Behavioral results

Discrimination accuracy (d') and RTs were assessed via ANOVAs with the within subjects factor task (shape, color) and the between subjects factors target-shape (vertical, horizontal), target-color (3-patches, 4-patches), and task order (shape then color, color then shape). No significant main effects or interactions were found for either measure. Mean d' (sem): vertical rectangles = 4.17 (0.05), horizontal rectangles = 4.35 (0.04), 3-color-patches = 4.24 (0.05), 4-color-patches = 4.26 (0.04). Mean RT: vertical rectangles = 509 ms (28 ms), horizontal rectangles = 487 ms (23 ms), 3-color-patches = 500 ms (26 ms), 4-color-patches = 507 ms (22 ms). These results indicate that the shape and color tasks as well as detection of each type of color/shape target did not differ in difficulty.

EEG results

Mean P3 amplitudes for non-target shape and random array trials were assessed over a 380–580 ms time window [±100 ms around the latency of the peak amplitude (480 ms) of the grand average across all conditions]. P3 was maximal at the same electrode sites as in experiment 1. Fig. 4 shows grand averaged ERPs and difference topographies for the task-relevant and task-irrelevant conditions. ANOVA with the factors stimulus, task, electrode, and task order revealed a significant stimulus × task interaction, $F(1, 18) = 58.78$, $p < .0000001$, while the three-way interaction between stimulus × task × task order was not significant. Follow-up ANOVAs for each task separately revealed that this stimulus × task interaction was due to a significant P3 difference only when the shapes were task-relevant, $F(1, 18) = 74.67$, $p < .0000001$ [mean amplitudes (sem): rectangles = 6.45 μV (0.44 μV); random = 2.04 μV (0.27 μV)]. The P3 was not significantly different between shape and random-array trials when the shapes were task-irrelevant, $F(1, 18) = 0.43$, $p = .51$ [mean amplitudes (sem): rectangles = 1.49 μV (0.21 μV); random = 1.36 μV (0.23 μV)].

Mean gamma amplitude was measured in the same manner as described for experiment 1, except the time window was adjusted slightly (here 340–420 ms, compared to 360–440 ms in experiment 1) to better capture the peak of the gamma response as observed in the grand average across conditions. ANOVA with the factors stimulus, task, hemisphere, electrode, and task order revealed a significant stimulus × task interaction, $F(1, 18) = 5.17$, $p = .035$, while the three-way interaction between stimulus × task × task order was not significant. Follow-up ANOVAs confirmed a significant difference in gamma activity between the rectangle and random stimuli when the rectangles were task-relevant, $F(1, 19) = 8.71$, $p = .008$ [mean amplitudes (sem):

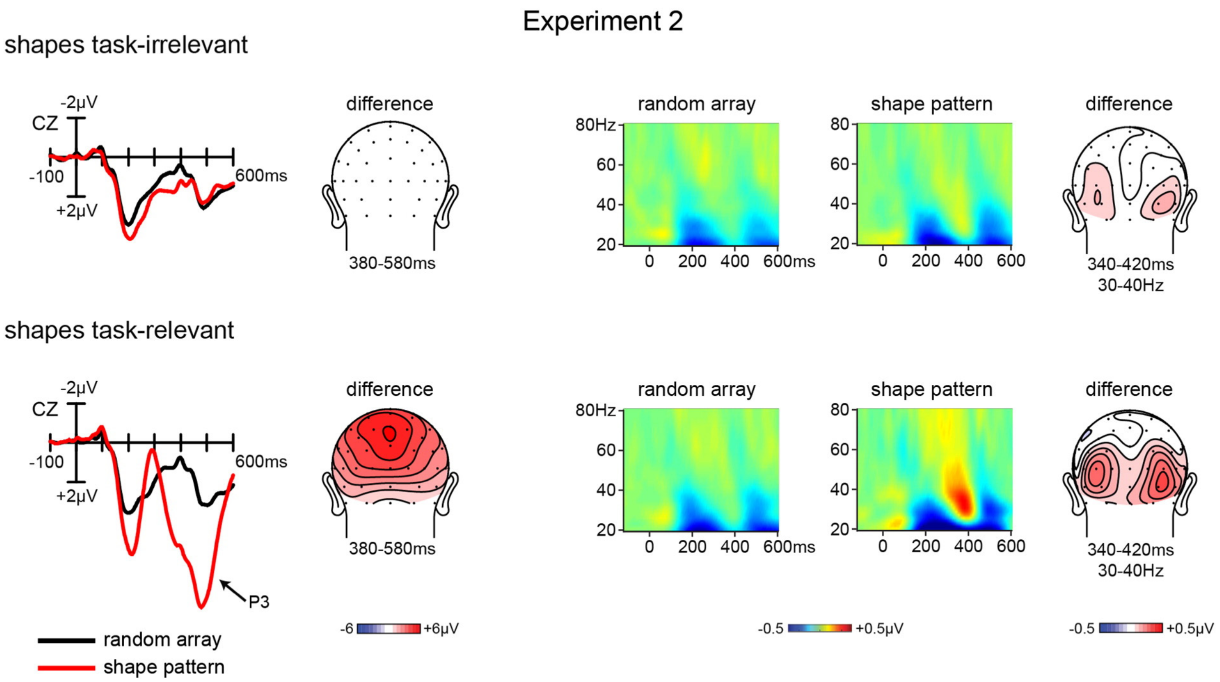

Fig. 4. Grand averaged ERPs and difference topographies (shape minus random) during conditions in which the shapes were irrelevant (top) or relevant (bottom) to the task. Grand averaged spectral amplitude for electrode PO8 along with difference topographies are plotted to the right of the ERP data for each condition. ERPs and gamma band activity elicited by the color stimuli are provided in Supplemental Fig. S4.

rectangles = 0.13 μV (0.05 μV); random = −0.02 μV (0.02 μV)]. The difference in gamma amplitude when the shapes were task-irrelevant was much smaller, but remained statistically significant, F(1, 19) = 8.44, p = .009 [mean amplitudes (sem): rectangles = 0.02 μV (0.03 μV); random = −0.03 μV (0.02 μV)]. However, when each of the four means were tested against zero, only the gamma response to the rectangle stimuli in the task-relevant condition differed significantly from zero, t(19) = 2.47, p = .02. Gamma activity elicited by the rectangles in the task-irrelevant condition, t(19) = 0.99, p = .33, as well as random stimuli in the task-relevant, t(19) = −1.39, p = .18, and irrelevant conditions, t(19) = −1.68, p = .11, did not differ significantly from zero. Fig. 4 shows grand averaged spectral amplitude as well as difference topographies for the task-relevant and irrelevant conditions.

While the main focus here was on the planned comparisons between the shape and random stimuli, we also conducted exploratory analyses on the P3 and gamma elicited by the color-patch stimuli. The overall pattern of results for the color-patch stimuli was the same as for the shape stimuli: both P3 and gamma activity were present when color was task-relevant and absent when color was task-irrelevant. However, the spatio-temporal characteristics of the gamma response to the color-patch stimuli differed from those of the shape stimuli. Namely, gamma elicited by task-relevant color-patch stimuli was earlier (200–280 ms), higher in frequency (60–80 Hz), and focused over more ventral occipito-temporal scalp regions. Supplementary Fig. S4 summarizes these exploratory results.

Discussion

Results from experiment 2 were consistent with those of experiment 1 in that both gamma activity and the P3 were absent following consciously perceived but task-irrelevant stimuli and appeared only when these stimuli became directly relevant to the task. Importantly, this experiment demonstrated that even when spatial attention was allocated to the location of the stimuli, the stimuli appeared in isolation, and subjects were perceptually aware of the stimuli, gamma activity and the P3 were evident only when subjects were required to access this perceptual information in order to complete the task. These results provide additional evidence for a post-perceptual interpretation of these two candidate NCCs.

In both experiments 1 and 2, whenever the P3 was present, gamma responses were also present, and whenever the P3 was absent, gamma activity was also absent. This pattern of results suggests that the P3 and gamma might reflect similar or closely linked post-perceptual processes. In a recent attentional blink experiment, however, Batterink et al. (2012) reported a dissociation between gamma and the P3. To further investigate the relationship between these two EEG components, a final experiment was conducted in which all stimuli were potentially task-relevant while the degree of relevance of different outline shapes was manipulated by varying perceptual similarity to the target shape.

Materials & methods — experiment 3

Participants

Twenty-five healthy adults participated in experiment 3. All were recruited as volunteers and gave informed consent prior to the beginning of the experiment. Data from five participants were later excluded due to excessive EEG artifact. The final group consisted of twenty participants (mean age 21 years old; 15 females). The experimental procedures were approved by the University of California San Diego institutional review board in compliance with the Declaration of Helsinki.

Stimuli & procedure

The stimuli consisted of random arrays (33.3%), arrays containing rectangles (33.3%), and arrays containing ellipses (33.3%). Half of the rectangles were oriented vertically (3.75° × 2.85°) and half horizontally (2.85° × 3.75°) as in experiment 2. Similarly, half of the ellipses were oriented vertically (4.5° × 3.25°) and half horizontally (3.25° × 4.5°). In order to keep the center of each line segment locked in position while creating the four types of shapes solely by changing line orientation, the line segments were positioned pseudo-randomly with extra space between each line (lower line density) compared to experiments 1 and 2. Stimulus timing was identical to experiments 1 and 2. Example stimuli are shown in Fig. 5 and an online video is available here: http://youtu.be/lTZgY42s1YE.

Subjects were familiarized with all four shape stimuli and were then instructed to attend to either the rectangles or the ellipses for the entirety of the experiment. Each subject was assigned the vertical or horizontal version of their attended shape as the target for the first half of the experiment and the other orientation for the second half of the experiment (counterbalanced across subjects). Ten subjects were assigned ellipse targets and the other ten subjects were assigned rectangle targets. A total of 3000 trials was completed by each subject, 1000 random, 1000 rectangles, and 1000 ellipses. Trials were sorted according to target similarity (most to least similar) as follows: target shape, same shape different orientation, different shape same orientation, and different shape different orientation. In other words, for a subject who was assigned the vertical ellipse as the target shape, the horizontal ellipse (same shape diff orient) was considered most similar, the vertical rectangle (diff shape same orient) was of intermediate similarity, and the horizontal rectangle (diff shape diff orient) was least similar. On average 12.19% of trials per individual were rejected due to artifacts (mean number of trials after artifact rejection: 830 for random arrays, 381 for target stimuli, 406 for same shape diff orient, 409 for diff shape same orient, 413 for diff shape diff orient). Based on previous work (Azizian et al., 2006a, 2006b), we expected the P3 to be modulated by target similarity, with the largest amplitudes for the target, followed by shapes most confusable with the target, and the smallest amplitudes for shapes most easily distinguishable from the target. The question of interest was whether gamma band activity would follow a similar pattern of amplitude modulation by target similarity.

Results & discussion — experiment 3

Behavioral results

Discrimination accuracy (d′) and RTs were assessed via ANOVAs with the within subjects factor target-orientation (horizontal, vertical) and the between subjects factor target-shape (ellipse, rectangle). No significant main effects or interactions were evident. Mean d′ and RTs (sem) for vertical ellipse, horizontal ellipse, vertical rectangle, and horizontal rectangle targets were 4.11 (0.09), 4.17 (0.14), 4.19 (0.16), 4.23 (0.12), and 536 ms (10 ms), 534 ms (10 ms), 524 ms (15 ms), 520 ms (15 ms), respectively. These results confirmed that the four target detection tasks were approximately equivalent in difficulty and that our counter-balancing protocol was sufficient.

EEG results

P3 amplitudes were measured over a 390–590 ms interval (based on ± 100 ms around the peak latency of 490 ms across all conditions) at the same electrodes as in experiments 1 and 2, but in this case were assessed via $5 \times 9 \times 2$ ANOVA with the within subjects factors stimulus (random, target shape, same shape diff orient, diff shape same orient, diff shape diff orient) and electrode (9 central-parietal channels), and the between subjects factor target shape (ellipse, rectangle). No main effects or interactions were evident for the between subjects factor, therefore, all subsequent analyses were collapsed across this dimension. A main effect of stimulus was evident, $F(4,72) = 96.60$, $p < .0000001$ (Greenhouse–Geisser corrected), and follow-up paired t-tests confirmed that P3 amplitudes were significantly larger for the target shape versus the same shape different orientation ($t(19) = 10.03$, $p < .0000001$), as well as the same shape different orientation versus different shape same orientation ($t(19) = 4.64$, $p = .0002$). P3 amplitudes for the two different shape stimuli did not differ significantly from each other ($t(19) = 0.05$, $p = .96$), although both differed significantly from the random stimuli ($t(19) = 5.43$, $p = .00003$; $t(19) = 5.92$, $p = .00001$). Mean amplitudes (sem) for each stimulus: random = 2.03 μV (0.26); target = 10.51 μV (0.83); same shape diff orient = 4.49 μV (0.46); diff shape same orient = 3.14 μV (0.35); diff shape diff orient = 3.14 μV (0.34). Fig. 6 shows grand averaged ERPs at a representative electrode site (Pz) for all five stimuli.

Unlike the pattern of results obtained for the P3, gamma activity did not vary in amplitude as a function of target similarity. Gamma amplitudes were measured over the same time windows and electrodes as in experiment 1. ANOVA with the within subjects factors stimulus, hemisphere, and electrode, and a between subjects factor target shape (ellipse, rectangle) revealed a main effect of stimulus, $F(4,72) = 8.48$, $p = .003$ (Greenhouse–Geisser corrected), with no significant interactions. This main effect was explained by the absence of gamma for the random stimulus. Paired t-tests between the stimuli confirmed that gamma amplitude for each shape stimulus differed significantly from the random stimulus [target: $t(19) = 3.40$, $p = .003$; same shape diff orient: $t(19) = 2.96$, $p = .008$; diff shape same orient: $t(19) = 3.85$, $p = .001$; diff shape diff orient: $t(19) = 3.53$, $p = .002$] while gamma amplitude did not differ between any two of the shape stimuli. For consistency with experiments 1 and 2, we also tested mean gamma amplitude against zero for each stimulus separately. While gamma amplitude did not differ from zero for the random stimulus [$t(19) = -0.99$, $p = .33$], the other four stimuli showed significant gamma responses [target: $t(19) = 2.30$, $p = .03$; same shape diff orient: $t(19) = 2.04$, $p = .05$; diff shape same orient: $t(19) = 2.75$, $p = .01$; diff shape diff orient: $t(19) = 2.29$, $p = .03$]. Time–frequency plots for each type of stimulus along with summary bar graphs comparing P3 and gamma amplitudes across the four shape stimuli are shown in Fig. 6.

Discussion

In experiments 1 and 2, gamma and P3 were absent when shape stimuli were task-irrelevant and present when the same stimuli became task-relevant. This suggested that these two EEG components might

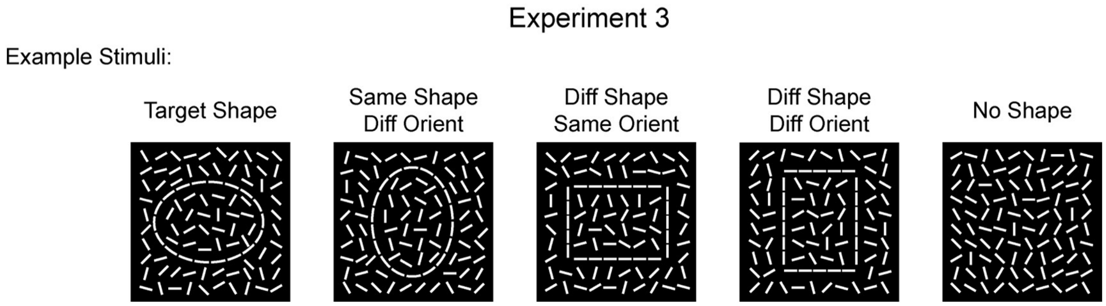

Fig. 5. Example stimuli from experiment 3. The shapes were always task-relevant while the target stimulus was manipulated across blocks of trials. Each of the four shapes served as a target in some conditions and the non-target stimuli were categorized according to target-similarity. Note that the actual stimuli consisted of 20 × 20 grids of line segments and were arranged less densely than shown here. A video example can be viewed online: http://youtu.be/lTZgY42s1YE.

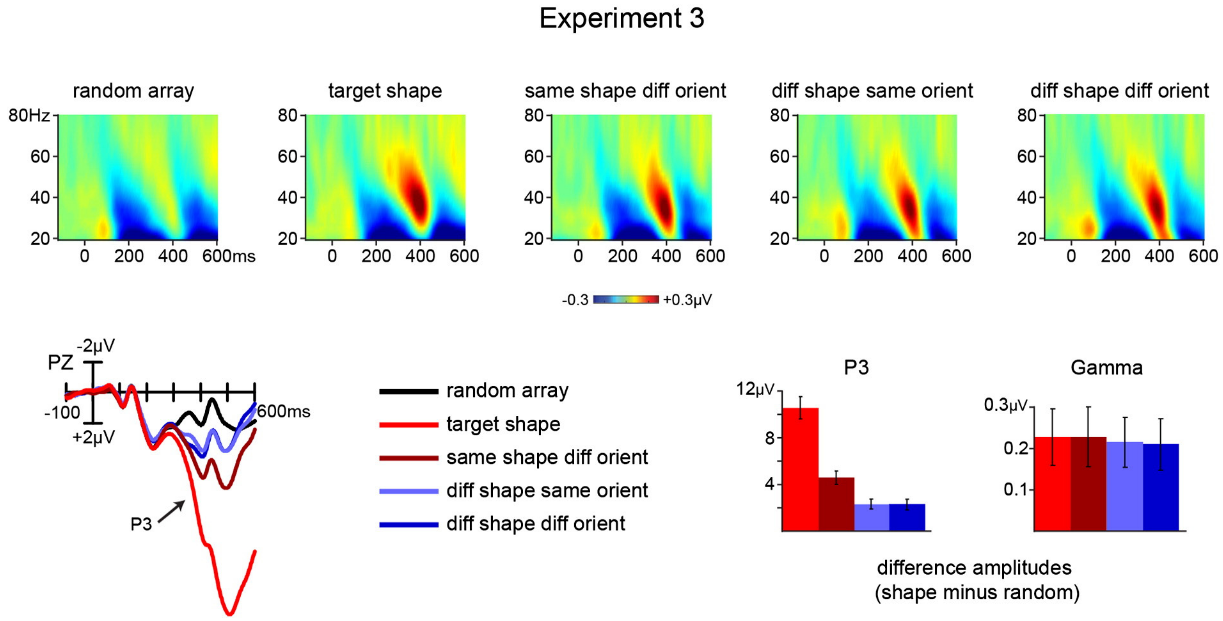

Fig. 6. Grand averaged spectral amplitude for electrode PO8 (top) and grand averaged ERPs for electrode PZ (bottom left) for each stimulus category in experiment 3. P3 (390–590 ms) and gamma (360–440 ms; 30–40 Hz) difference amplitudes (shape minus random) are plotted for the same electrodes (bottom right; colors same as in ERPs).

index similar or closely linked post-perceptual processes. Results from experiment 3, however, argue against this possibility by demonstrating a substantial modulation of P3 amplitude with an accompanying lack of gamma modulation according to target similarity. This dissociation between gamma and P3 is consistent with results from a recent attentional blink study (Batterink et al., 2012). However, Batterink and colleagues argued that gamma and the P3 should each be interpreted as reflecting distinct NCCs. The present results, on the other hand, suggest that neither gamma nor the P3 should be considered as NCCs but rather as indices of distinctive post-perceptual processes.

General discussion

Gamma band activity: preconscious, post-perceptual, or an NCC?

Results from experiment 1 support the view that induced gamma band activity (30–40 Hz) recorded in the scalp EEG should not be considered a neural correlate of conscious perception (NCC); not only was gamma activity equally absent in inattentionally blind subjects who failed to see the stimulus shapes and in subjects who did notice the stimuli, but it was also absent within the inattentionally blind group as they transitioned from unaware to aware conditions. A distinct gamma response having an onset latency of around 350 ms and a frequency range of 30–40 Hz was present only when the stimuli were directly relevant to the task. In a recent study, Aru et al. (2012a) found that induced gamma activity correlated with sensory evidence (gamma power increased for less degraded stimuli) but did not correlate with previous exposure to stimuli. Because both stimulus degradation and previous exposure affected perceptual visibility equally, Aru et al. (2012a) concluded that these gamma responses were not related to visual awareness but instead reflected a preconscious process that is necessary but not sufficient for awareness. Results from the current series of experiments, however, suggest that gamma band activity rather indexes a post-perceptual process that is sufficient but not necessary for visual awareness.

While the current results and those of Aru et al. (2012a) support the conclusion that gamma band activity is not a NCC (see also Schurger et al., 2008), the question still remains as to whether such activity reflects preconscious processes, as Aru et al. (2012a) propose, or post-perceptual processing, as our data suggest. First, it is important to note that Aru et al. (2012a) measured gamma band responses via intracranial EEG (iEEG) and found broadband increases in gamma power (~50–140 Hz) that were sustained over hundreds of milliseconds (~200–500 ms). The scalp recorded gamma activity reported here was narrow-band (maximal at 30–40 Hz) and temporally discrete (maximal at 340–440 ms). The exact relationship between gamma activity recorded intracranially and at the scalp is currently unclear, although it is likely that some of the iEEG signal is resolvable with scalp EEG and MEG (Buzsaki et al., 2012; Dalal et al., 2009; Lachaux et al., 2012). Second, all stimuli in Aru et al.'s (2012a) experiment were task-relevant and thus each elicited a gamma band response, regardless of stimulus degradation. The magnitude of the gamma response varied according to physical stimulus properties. In our experiments we did not vary the physical stimulus but instead manipulated its task-relevance and found that the gamma response could be completely abolished when non-degraded stimuli were rendered task-irrelevant.

The onset latency of a particular gamma response may provide clues regarding its functional significance, with very early responses being more indicative of preconscious activity and very late responses post-perceptual activity. However, the onset of most induced gamma activity (e.g. Aru et al., 2012a; Fisch et al., 2009; Moratti et al., 2014; Vidal et al., 2014) falls within a mid-latency period (~200–400 ms) making it difficult to use timing as a decisive factor in distinguishing between pre- versus post-perceptual processing. It is also likely that post-perceptual processing begins before preconscious processing ends and this temporal overlap can further complicate functional interpretations based on gamma response latencies (Aru et al., 2012b). In addition, it is becoming increasingly clear that gamma band activity is not a unitary phenomenon (Buzsaki and Wang, 2012). For example, Vidal et al. (2006) provide clear evidence for perceptual-grouping related gamma activity at high frequencies (70–120 Hz) and attention-related gamma activity at lower frequencies (44–66 Hz), whereas, Wyart and Tallon-Baudry (2008) distinguish awareness-related and attention-related activity at low versus high gamma bands, respectively. With respect to the current study, it is possible that the gamma activity measured here is indeed post-perceptual, while other types of gamma responses reflect preconscious activity, or even conscious activity. We would emphasize, however, that regardless of the specific type of gamma response (low, mid, or high frequency gamma, measured with iEEG, ECoG, or M/EEG), contrasts between aware and unaware conditions are typically confounded with differences in post-perceptual processing. When the stimuli are task-relevant, aware trials will inevitably contain extra activity related to maintaining information in working memory and accessing this information for discrimination or reporting purposes, while unaware trials lack such activity.

In addition to weighing against a direct role of gamma activity in conscious perception, the current study provides initial clues regarding the type of processing that is indexed by the scalp-EEG gamma responses (30–40 Hz; 340–440 ms) recorded here. In experiments 1 and 2, gamma was absent for clearly perceived but task-irrelevant stimuli, whereas in experiment 3, gamma was present (and equivalent in magnitude) for all stimuli, including the less relevant shapes (i.e. shapes more dissimilar from the target). One interpretation of this pattern of results follows from differences between the experiments in the manipulation of task relevance: In experiment 1, the shapes were task-irrelevant when subjects attended to a *different object* (the peripheral red ring of disks); in experiment 2, the shapes were irrelevant when subjects attended to a *different feature* (color); in experiment 3, however, the less-relevant stimuli were still within the *same object/feature* category as the relevant target stimulus (all were outline shapes). Thus, the presence/absence of this gamma-band response may depend critically on whether or not the eliciting stimulus is of the same object-type as the task-relevant target. Interestingly, the P3 showed a graded response in experiment 3 according to target similarity, whereas gamma did not. A possible explanation for this finding is that the gamma response may be more closely linked to the maintenance of task-relevant visual information in working memory, while the P3 reflects operations performed on that information according to task demands. Such an account is consistent with the current results as well as those of Aru et al. (2012a), Moratti et al. (2014), and Vidal et al. (2014); however, in each of these previous studies the stimuli were always task-relevant making it difficult to distinguish between activity related to conscious perception per se and activity related to carrying out the task. Further studies in which conscious perception is manipulated for task-irrelevant stimuli are required to more thoroughly evaluate this interpretation.

Gamma in scalp EEG versus intracranial EEG

Several recent experiments aimed at testing the relationship between gamma band activity and visual awareness have employed intracranial EEG (iEEG) recordings or electrocorticography (ECoG), in which electrodes are inserted into or placed directly on the surface of the cortex in awake human patients undergoing invasive monitoring to locate epileptic foci (Aru et al., 2012a; Fisch et al., 2009; Gaillard et al., 2009). The major advantages of iEEG compared to scalp EEG are the higher signal-to-noise ratio, especially for high-frequency activity, and the improved spatial resolution, as iEEG electrodes are sensitive to local field potentials generated by directly adjacent cortical tissue (Jerbi et al., 2009b). Of course, the primary disadvantages of iEEG are the invasiveness of the recordings and the limited subject pool. The location of electrodes used in iEEG is also somewhat restricted and depends on where the epileptic monitoring happens to be taking place. Scalp EEG on the other hand records the far field of the same neural electrical activity, which is necessarily weaker and spatially blurred due to signal decay and intervening bone and tissue, but can be measured noninvasively in any healthy adult population.

The recent controversy concerning artifactual eye movement (microsaccade) versus brain generated gamma has raised concerns with the interpretation of scalp EEG gamma and in some cases even with iEEG gamma (Jerbi et al., 2009a; Melloni et al., 2009; Yuval-Greenberg et al., 2008, 2009). The current recordings of gamma activity do not appear to be attributable to ocular artifacts for several reasons. First, the scalp distribution of the gamma band activity was highly focal and strictly posterior, with gamma appearing in a small subset of electrodes bilaterally over the occipital scalp. Second, gamma was absent in the EOG channels during similar time frames and was not widely distributed across anterior EEG channels as is commonly observed for the microsaccade artifact (see Supplemental Fig. S2). Finally, the frequency range and time-course of the gamma observed here (30–40 Hz; ~340–440 ms) differ from the broadband (30–100 Hz) and shorter latency (200–300 ms) gamma indicative of micro-saccades (Yuval-Greenberg and Deouell, 2009; Yuval-Greenberg et al., 2008). These characteristics point towards a neural source as opposed to an eye movement artifact for the gamma responses observed in the current series of experiments.

In both Fisch et al.'s (2009) and Aru et al.'s (2012a) experiments, category specific gamma band responses were measured. For example, in Fisch et al. (2009) some electrodes showed increased gamma for faces compared to man-made objects while other electrodes showed the inverse. The current results are not directly comparable to these findings as we did not manipulate stimulus category and focused only on gamma elicited by simple geometric shapes. Interestingly however, in an exploratory analysis of data from experiment 2, we analyzed gamma elicited by stimuli containing patches of colored lines (Supplementary Fig. S4). We found that task-relevant stimuli containing color patches elicited gamma band activity that differed from the shape-elicited gamma in latency (color: 200–280 ms; shape: 340–420 ms), frequency (color: 60–80 Hz; shape: 30–40 Hz), and scalp distribution (color: ventral occipito-temporal; shape: middle-occipital). These results are consistent with the emerging view that different sub-bands in the gamma range may reflect functionally distinct processes (Vidal et al., 2006; Wyart and Tallon-Baudry, 2008). These preliminary findings also suggest that it may be possible to measure category-specific gamma even at the scalp; however, further research is necessary to fully evaluate this possibility. It would also be worthwhile for future iEEG experiments to include conditions in which subjects are made aware of task-*irrelevant* stimuli to determine whether the gamma responses recorded on the surface of the cortex disappear when subjects are not required to access or maintain perceptual information to meet task demands.

P3: sufficient but not necessary for conscious perception?

In a variety of experiments employing masking, attentional blink, and change detection paradigms, the P3 component (also called "P300" or "P3b") has been found to distinguish aware from unaware trials, and its amplitude correlates tightly with subjects' visibility ratings (Babiloni et al., 2006; Batterink et al., 2012; Del Cul et al., 2007; Fernandez-Duque et al., 2003; Lamy et al., 2009; Sergent et al., 2005). At first glance, it would seem that the consistency of this effect across a wide variety of paradigms strengthens the case for interpreting this component as a NCC. The current results, however, along with a handful of previous studies, argue against this interpretation (Bachmann, 2009; Hillyard et al., 1971; Koivisto et al., 2008; Railo et al., 2011; Squires et al., 1973; Verleger, 2010). The results reported here show that stimuli that are clearly perceived but that do not require post-perceptual processing for decision and response-related purposes *do not* produce a P3 component. These results are consistent with classic signal detection experiments in which the P3 correlated closely with subjects' confidence in having perceived the stimuli during active tasks, but was absent during passive tasks, even when stimuli were well above threshold (Hillyard et al., 1971; Squires et al., 1973). A common objection to these claims is that readily visible (unmasked) stimuli might not be perceived when they are unattended and task-irrelevant (Dehaene and Changeux, 2011), thus the lack of P3 in such conditions might correspond to a lack of awareness instead of a lack of post-perceptual processing (for a related example from the fMRI literature, see Tse et al., 2005). While we agree that one cannot assume awareness of a stimulus solely based on its being unmasked, experiment 2 of the current study was specifically designed to ensure visibility of task-irrelevant stimuli. Here, task-irrelevant shape stimuli were presented for 300 ms, in isolation (without any spatial/temporal competition from other stimuli), and in spatially attended locations, and conscious perception of these stimuli was confirmed via post-test questionnaires. Taken together, the current study along with numerous previous studies demonstrates that the P3 is not *necessary* for conscious perception.

A separate question is whether the P3 is a *sufficient* marker of visual consciousness. In other words, if a clear P3 is observed can one be absolutely certain that the subject was conscious of the stimulus? This latter question has substantial practical relevance even if the P3 is not directly related to conscious perception per se. For example, if the P3 is a sufficient marker of visual awareness, it could be used as positive evidence when assessing consciousness in clinical situations (e.g. coma, vegetative state), in infants, or in nonhuman animals (Bekinschtein et al., 2009; Faugeras et al., 2012; Harrison and Connolly, 2013; Kouider et al., 2013; Paller et al., 1992; Sambeth et al., 2003; Schnakers et al., 2008). The current results are indeed consistent with the notion that P3 is a sufficient index of conscious perception, although our experiments were not designed to explicitly examine sufficiency. To directly assess whether the P3 is a sufficient marker of awareness, one must look for cases in which the P3 might be present during unaware conditions (e.g. Bernat et al., 2001). While this is still an open question, the current consensus is that whenever a P3 is observed (specifically the P3b), the subject must have been conscious of the stimulus (Dehaene and Changeux, 2011; Railo et al., 2011).

If not gamma or P3, which EEG/ERP components do correlate with awareness?

While the present analyses focused on gamma band activity and the P3, we previously reported results from experiment 1 in which an earlier ERP component, a bilateral posterior negativity from ~200–300 ms, was found to correspond closely with visual awareness (Pitts and Martinez, 2014; Pitts et al., 2012). We labeled this negativity the "Nd2" because it was the second negative difference in the ERPs elicited by shapes versus random arrays. An earlier negativity (Nd1) was found even during inattentional blindness and was thus interpreted to reflect preconscious processes such as automatic contour integration. The Nd2 was elicited only in conditions in which subjects were aware of the shapes regardless of whether the shape information needed to be accessed to fulfill immediate task demands. Fig. 7 summarizes these results (for more details, see Pitts et al., 2012).

To further explore the relationship between these ERP components and the current gamma results, we conducted correlational analyses between gamma amplitudes and Nd1, Nd2, and P3 to determine whether subjects that showed increased gamma activity also showed increased ERP amplitudes. None of these correlations (gamma × Nd1; gamma × Nd2; gamma × P3) was significant (see Supplementary Table 1). In addition to the results based on our experimental manipulations, these null correlation results provide further support for our conclusions that the induced gamma activity measured here is post-perceptual (gamma did not correlate with the preconscious Nd1 component), does not reflect awareness (there was no relationship between gamma and Nd2), and is distinct from the P3 (there was no correlation between gamma and P3).

Previous studies have reported ERP negativities with scalp distributions and latencies very similar to the Nd2 when comparing aware versus unaware conditions in backward masking and attentional blink paradigms (Koivisto and Revonsuo, 2003, 2007; Koivisto et al., 2006, 2008, 2009; Sergent et al., 2005). While some have labeled this ERP component the "visual awareness negativity" or "VAN" (for a review see Railo et al., 2011), it may be premature to attribute such a functionally discrete label to this component. It is important to note that in experiment 1 of the current study, in order to manipulate awareness, we manipulated attention by employing an inattentional blindness paradigm. Thus, we cannot be certain that a difference between our aware and unaware conditions reflects differences in attention or differences in awareness, as both varied concurrently. While the relationship between some forms of attention (spatial, exogenous) and awareness have been challenged (Koch and Tsuchiya, 2007; Tsuchiya and Koch, 2009; Wyart and Tallon-Baudry, 2008) recent results support the view that attention is necessary for awareness (Cohen et al., 2011, 2012).

One possible interpretation of the Nd2 (VAN) is that it is a marker of phenomenal conscious content that is accessible (but need not be accessed), while gamma and the P3 reflect processes involved in the conscious access of perceptual information by other systems (Block, 2005, 2007, 2011). It is also possible that the Nd2 reflects conscious access and activity in the global neuronal workspace (Dehaene and Changeux, 2011), because even though subjects in phase 2 were not required to access perceptual representations of the shape stimuli for reporting purposes, they must have maintained this information in memory in order to report their percepts after the phase commenced. The current results suggest that gamma and the P3 should not be considered markers of global neuronal workspace activity, as these signals disappear when the stimuli are rendered task-irrelevant (despite being consciously perceived). It would be interesting to run experiment 1 with fMRI to assess whether the brain regions that generate the Nd2 include fronto-parietal networks assumed to play a critical role in the global neuronal workspace. Finally, it remains possible that the N2d (VAN) reflects a certain type of interaction between attention and visual representations in the ventral stream that in itself constitutes the neural basis of visual awareness (for a similar view see Cohen and Dennett, 2011).

The inattention paradigm versus other paradigms

The primary advantage of the inattention paradigm as implemented here is that awareness and post-perceptual processing can be assessed independently. In phase 1, for inattentionally blind subjects, conscious perception of the shape stimuli was absent, and thus post-perceptual processing was absent as well. In phase 2, conscious perception was present but subjects continued to perform the distracter task and were not required to access information about the shape stimuli until after phase 2 terminated. In phase 3, conscious perception and post-perceptual processing were present because subjects were required to compare the target held in memory (the diamond) to the current non-target stimulus (the square) in order to decide whether to respond. In other words, awareness and task relevance were added in a step-wise fashion across the three phases of the experiment. Results from phase 3 compared to phase 1 are largely consistent with the literature in that gamma activity and the P3 component were present during phase 3 (aware) and absent during phase 1 (unaware). For example in the experiment of Tallon-Baudry (2003), a hidden Dalmatian dog elicited gamma only when subjects consciously perceived it, but the task in the aware condition was to discriminate which direction the dog was facing. Results from phase 2 of our experiment would predict that if Tallon-Baudry's (2003) subjects had clearly perceived the hidden dog but did not have to access this information in order to perform the task, gamma would have been absent. Similarly, backward masking and attentional blink experiments have generally included conditions comparable to phase 1 and phase 3 of the inattention paradigm wherein stimuli were either not perceived, or perceived and immediately accessed and reported (e.g. Del Cul et al., 2007; Sergent et al., 2005)

While the separation of awareness and immediate access is a clear advantage of the inattention paradigm, several weaknesses exist in comparison to other paradigms. One weakness is that trial-by-trial assessment of awareness is not possible in the inattention paradigm because such an assessment would ruin the inattentional blindness effect. Thus, we cannot be sure exactly how many times out of the 240 presentations the subject was aware of the stimulus. To address this concern, we asked subjects to estimate how frequently they perceived the shapes. While we cannot place too much confidence on the accuracy of these estimates, our results showed that Nd2 amplitudes correlated

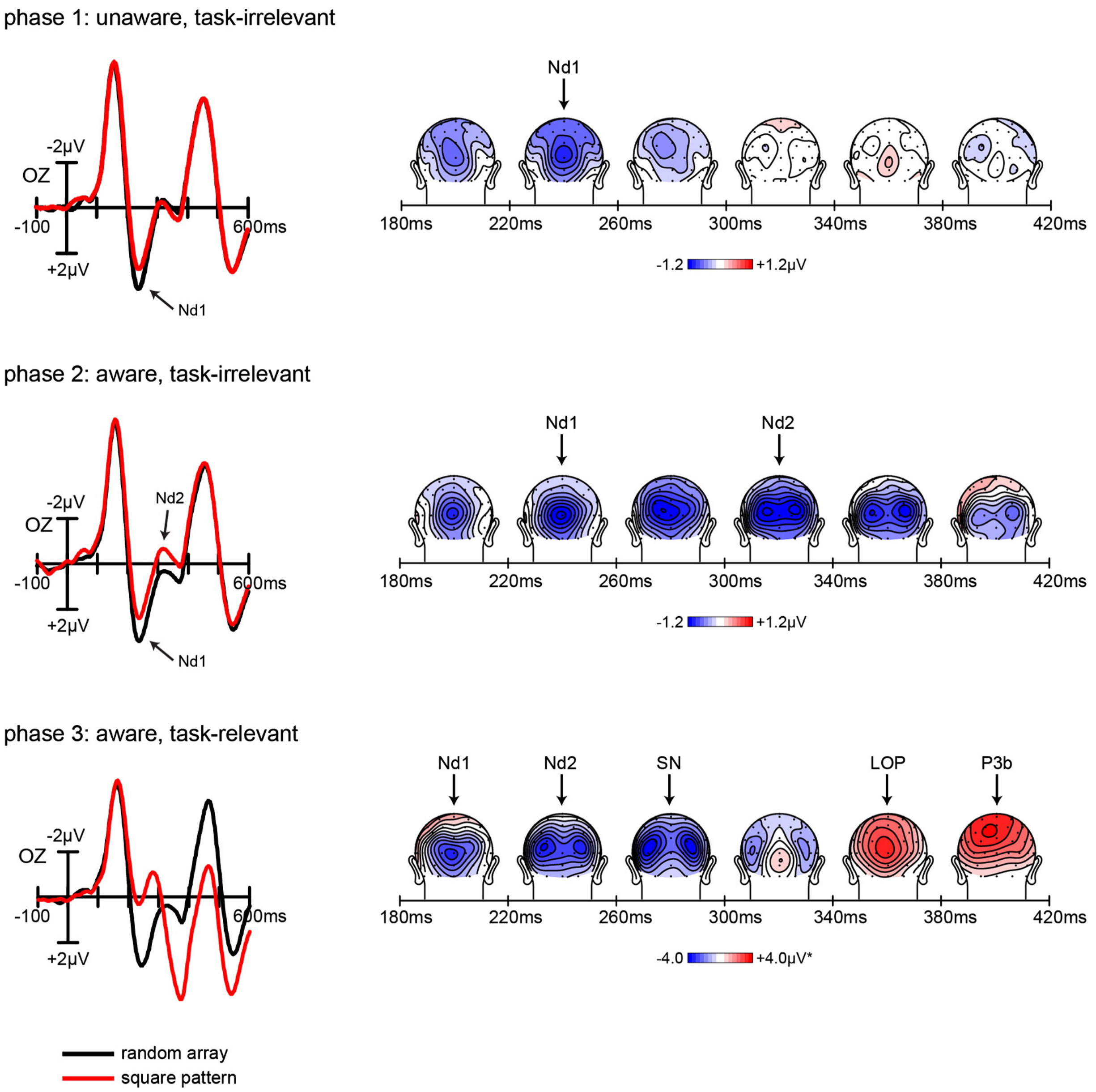

Fig. 7. Grand averaged ERPs (left) and difference wave maps (right) showing the earlier ERP effects (Nd1, Nd2) observed in experiment 1. The ERPs are plotted for a representative electrode (OZ), and the difference maps (square minus random) reflect mean amplitudes across successive time intervals. For more details, see Pitts et al. (2012) and Pitts and Martinez (2014). Nd1 = first negative difference; Nd2 = second negative difference; SN = selection negativity; LOP = late occipital positivity; P3b = centro-parietal positivity. *Note that all maps in phase 3 are scaled from −4 to +4 μV except the first map (Nd1) which is scaled from −1.2 to +1.2 μV.
Reproduced from Pitts and Martinez (2014).

with reported frequency of perceiving the square (Pitts et al., 2012), while P3 and gamma amplitudes did not correlate with this measure.

Another concern is that the inattention paradigm necessitates running each condition in the same order; i.e., counterbalancing is not possible. This concern would indeed be troubling if we had directly compared ERPs elicited by square patterns in phase 2 versus phase 1 because ERP amplitudes may vary over time due to sensory adaptation, habituation, fatigue, etc. However, the inclusion of random array stimuli allowed us to always compare ERPs elicited by shapes and random stimuli within the same phase. Comparisons of this ERP *difference* across phases should not be confounded by adaptation effects. Also, it should be noted that counterbalancing was possible in experiment 2, and similar gamma and P3 results were obtained regardless of condition order.

A further weakness of the inattention paradigm, at least for identification of the NCC-proper, is that attention and awareness may have co-varied. As the name of this paradigm implies, in order to manipulate awareness, one must ensure that some subjects pay absolutely no attention to the stimuli. This means that any differences in brain activity between phases 1 and 2 (or differences between aware and unaware subjects in phase 1) might index attentional processes rather than awareness-related processes. Other paradigms such as masking, attentional-blink, and threshold detection are also subject to this confound, however, since trial-to-trial variations in attention might determine whether or not a stimulus is consciously perceived (Squires et al., 1973). In previous studies employing these other paradigms, a bilateral occipital–parietal negativity from ~200 to 300 ms (Nd2 or "VAN") has been reported for aware versus unaware conditions in addition to gamma band activity and the P3. While the inattention paradigm is limited in the sense of confounding attention and awareness, if results are compared across paradigms, the only consistent marker of awareness appears to be the Nd2, while results from the inattention paradigm allow us to attribute gamma and the P3 to post-perceptual processing.

Neuronal "ignition" underlying conscious perception?

In previous masking and attentional blink experiments visual awareness appeared to be associated with substantial increases in gamma power and P3 amplitudes, thereby prompting the supposition that conscious perception is akin to a neuronal "ignition" of activity in widely-distributed cortical networks (Dehaene and Changeux, 2011; Fisch et al., 2009; Gaillard et al., 2009). This metaphor is meant to describe how a small change in perception (the "spark" of crossing the threshold to awareness) leads to large and longer-lasting changes in brain activity (the "flame" of the NCC). Dehaene and Naccache (2001) and Dehaene et al. (1998) postulated that this wide-spread cortical activity observed in studies contrasting aware versus unaware conditions may reflect the neuronal instantiation of the global workspace theory of consciousness (Baars, 1989, 2002). In the current study, however, the transition from non-conscious processing to conscious perception was found to coincide with a modest change in brain activity (Nd2), while a more robust "ignition" of cortical activity was found to correspond to changes in post-perceptual processing (gamma and P3).

It is likely that the "ignitions" of neural activity observed in the task-relevant conditions of the current study are similar to what previous studies have observed in aware conditions, and in all cases we would argue that these neural activity patterns are indicative of differences in post-perceptual processing such as maintenance in working memory and access for immediate report (see also Aru et al., 2012b; Railo et al., 2011). In contrast to the masking and attentional blink paradigms, in which all stimuli are task-relevant and must be accessed on every trial, the inattention paradigm allows us to compare brain activity under conditions involving identical post-perceptual processing by delaying the assessment of awareness (i.e. after 240 presentations of the stimulus). A critical question for future research will be whether manipulations of task relevance will similarly eliminate gamma and P3 components across various paradigms in which aware versus unaware contrasts are possible (e.g. backward masking, attentional blink). The questions of whether the difference between conscious and non-conscious perception depends on local or wide-spread changes in neural activity and whether these changes reflect phenomenal consciousness, global workspace activity, or interactions between attention and perceptual representations remain open and should continue to be investigated as experimental paradigms continue to be improved and refined.

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