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ABSTRACT

Whether visual spatial attention can modulate feedforward input to human primary visual cortex (V1) is debated. A prominent and long-standing hypothesis is that visual spatial attention can influence processing in V1, but only at delayed latencies suggesting a feedback-mediated mechanism and a lack of modulation during the initial afferent volley. The most promising challenge to this hypothesis comes from an event-related potential (ERP) study that showed an amplitude enhancement of the earliest visual ERP component, called the 'C1', in response to spatially attended relative to spatially unattended stimuli. In the Kelly et al. study, several important experimental design modifications were introduced, including tailoring the stimulus locations and recording electrodes to each individual subject. In the current study, we employed the same methodological procedures and tested for attentional enhancements of the C1 component in each quadrant of the visual field. Using the same analysis strategies as Kelly et al., we found no evidence for an attention-based modulation of the C1 (measured from 50–80 ms). Attention-based amplitude enhancements were clear and robust for the subsequent P1 component (90–140 ms). Thus, despite using methods specifically designed to reveal C1 attention effects, the current study provided no confirmatory evidence for such effects.

Introduction

Attending to a particular location in the visual field is known to improve detection, discrimination, and even alter the appearance of stimuli at that location (e.g., Carrasco, Ling, & Read, 2004; Hawkins et al., 1990; Hillyard, Vogel, & Luck, 1998; Luck et al., 1994; Posner, 1980). Where in the visual pathway spatial attention first modulates afferent information, however, remains controversial. While single-unit recordings in nonhuman primates have suggested spatial attention modulations of afferent input to V1 (Briggs, Mangun, & Usrey, 2013; McAdams & Reid, 2005; Motter, 1993; Sharma, Sugihara, Katz, Tenenbaum, & Sur, 2014), or even prior to V1 in the lateral geniculate nucleus (LGN) of the thalamus (McAlonan, Cavanaugh, & Wurtz, 2008), similar results in humans have remained elusive. Human studies employing fMRI have observed modulations of neural activity in V1 during spatial attention (e.g., Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Martinez et al., 1999), but these anatomically early effects may

be temporally delayed, with attention first modulating activity in extra-striate areas prior to feedback to V1 (Di Russo, Martinez, & Hillyard, 2003; Lamme & Roelfsema, 2000; Martinez et al., 1999, 2001; Noesselt et al., 2002). The temporally sluggish nature of fMRI is unsuitable for assessing the precise time course of attention effects on stimulus processing.

The majority of evidence from studies that employed event-related potentials (ERPs) has suggested a lack of attentional modulation of feedforward input to V1 (e.g., Mangun, Hillyard, & Luck, 1993; Clark & Hillyard, 1996; Di Russo et al., 2003; reviewed in Ding, Martinez, Qu, & Hillyard, 2014). In these and similar studies, amplitudes of the earliest visual-evoked potential, the 'C1' component (~50–80 ms poststimulus), elicited by physically identical stimuli at a particular location, were compared when subjects focused attention on that location versus on a different location. The most consistent finding has been a lack of C1 amplitude modulation in the ERPs to attended versus unattended stimuli, followed by robust modulations of subsequent components, the

P1 (~90–140 ms) and the N1 (~150–180 ms). Source localization analyses, as well as the polarity inversion observed for stimuli presented in the upper versus lower visual fields, suggest that the C1 component is primarily generated in V1, while the P1 and N1 components are generated in extra-striate cortical regions (e.g., Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Di Russo et al., 2012; Martinez et al., 2001). While it is likely that neural generators in visual areas V2 and V3 also contribute to the scalp-recorded C1 component (Ales, Yates, & Norcia, 2010, 2013), an analysis of the C1's voltage topography by Kelly, Vanegas, Schroeder, and Lalor (2013) reinforced the hypothesis that area V1 is the dominant generator of the C1. Slotnick (2013) has designated the aforementioned pattern of results – a lack of attentional modulation of the C1 together with clear attention effects on the P1/N1, and fMRI-measured attention effects in V1 – as representing the current 'majority view' with respect to the spatiotemporal locus of visual spatial attention modulations.

Despite the wealth of evidence supporting the majority view (Aine, Supek, & George, 1995; Clark & Hillyard, 1996; Ding et al., 2014; Di Russo et al., 2003, 2012; Fu, Caggiano, Greenwood, & Parasuraman, 2005; Fu et al., 2008; Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Gratton, 1997; Heinze & Mangun, 1995; Hopfinger & West, 2006; Johannes, Munte, Heinze, & Mangun, 1995; Mangun et al., 1993, 2001; Martinez et al., 1999, 2001; Noesselt et al., 2002; Proverbio, Del Zotto, & Zani, 2010; Wijers, Lange, Mulder, & Mulder, 1997; Woldorff et al., 1997, 2002; Yoshor, Ghose, Bosking, Sun, & Maunsell, 2007), one study in particular has provided solid counterevidence. Kelly, Gomez-Ramirez, and Foxe (2008) identified a potential weakness in all previous studies that had reported an absence of C1 attention effects. Due to well-known variation in V1 cortical anatomy across individuals, the scalp topography of the C1 is highly variable (Clark et al., 1995; Foxe & Simpson, 2002; Jeffreys & Axford, 1972; Proverbio, Del Zotto, & Zani, 2007). Therefore, when studies employ uniform measurements of C1 across individuals (i.e., the stimulus position and electrode locations are held constant, which is common practice in ERP experiments), these measures may be underpowered, and small amplitude modulations may be missed. To circumvent this problem, Kelly et al. (2008) implemented a procedure in which stimulus locations and recording electrodes optimally placed for measuring the C1 were identified for each subject in an initial 'probe' experiment, and these individually tailored parameters were then used in a subsequent spatial attention experiment. Kelly et al. (2008) added several other features to their design, including a demanding task that promoted attention to low-level visual features (detecting targets defined by low-contrast luminance decrements), adaptive titration of task difficulty to encourage sustained effort on the task, stimuli that are known to elicit robust V1 activity (high-contrast-oriented patterns of high-spatial frequency), and trial-by-trial cueing of endogenous spatial attention. With these methodological improvements, Kelly et al. (2008) found significant attention-based modulations of C1 amplitude (50–80 ms), thus challenging the majority view in the field.

Surprisingly, almost 10 years later, there exist no published replications or even close extensions of the Kelly et al. (2008) experiment. To address this gap, the present study aimed to further investigate whether the C1 can be modulated by attention by utilizing the innovative experimental procedures of Kelly et al. (2008). In this study, we replicated the major aspects of the Kelly et al. (2008) experiment with one small modification. In the Kelly et al. (2008) experiment, two stimulus locations were selected for each subject and these locations were always diagonally opposed, thus crossing both the vertical and horizontal meridians of the visual field (e.g., upper left versus lower right). In the current study, we selected four stimulus locations, one in each quadrant of the visual field, and during separate blocks of trials presented stimuli either in the upper or lower visual fields. Attention was cued on each trial to either the left or right location, as in Kelly et al. (2008), but in this case, the attended and unattended stimulus locations were only horizontally opposed instead of diagonally opposed. If visual spatial attention indeed modulates C1 amplitude, we reasoned that it should do so for attend-left versus attend-right conditions regardless of whether the attended and unattended locations cross the horizontal meridian.

Methods

Subjects

Twenty-one healthy paid volunteers between the ages of 18 and 24 participated in the experiment (7 male, 14 female) and 17 individuals were included in the final analysis (7 male, 10 female). All individuals had normal or corrected-to-normal visual acuity and no history of neurological disorders. All procedures were approved by the Reed College Institutional Review Board and closely followed the methods of Kelly et al. (2008). Each subject participated in three EEG recording sessions on three separate days: one probe session to determine the optimal stimuli locations and electrodes for recording the C1 and two identical sessions for the main spatial attention task. Participants were paid $10 for completing each session ($30 total). Data from one subject were excluded from analysis due to excessive EEG artifacts and from three subjects due to absence of a measurable C1 (defined by a visible negative-going peak for upper field stimuli and a positive-going peak for lower field stimuli between 50–80 ms poststimulus) at any of the eight locations in the probe experiment.

Apparatus

Scalp EEG was recorded using a custom 96-channel electrode cap (EASYCAP, Herrsching, Germany) with Ag/AgCl electrodes arranged with equidistant spacing. Signals were digitized at 500 Hz and amplified using three 32-channel amplifiers (Brain Amp Standard, Brain Products) with a recording bandpass of 0.05–100 Hz. Eye movements and blinks were monitored using left and right horizontal electrooculogram (HEOG) channels and a vertical EOG channel under the left eye. During recording, an electrode at CPz was used as the reference. Subjects sat 57 cm from the computer monitor and responded with computer mouse clicks. All of the raw EEG data collected in this experiment have been uploaded for sharing via the open science framework: https://osf.io/taakn/.

We did not perform simultaneous eye-tracking as in Kelly et al. (2008) but relied on the averaged HEOG to verify that fixation was maintained during the cue-target interval. The maximum deviation of the HEOG in the cue-target interval (400–700 ms post cue onset) averaged 1.53 uV (SD = 1.31) following cues directing attention to the left and −1.96 uV (SD = 1.60) following cues directing attention to the right. These averaged HEOG deviations correspond to average eye fixation deviations of approximately 0.15° to the left and 0.20° to the right, respectively, following the calculations of Mangun and Hillyard (1991). These minimal deviations from fixation are unlikely to have an appreciable effect on the ERPs, and if they did the effect would actually be to increase the amplitudes of ERPs to attended stimuli.

Stimuli

As described by Kelly et al. (2008), nontarget stimuli used in all sessions were Gabor patches that appeared for a duration of 100 ms with a spatial frequency of 6 cycles/degree and a diameter of 1.0° at half-contrast. Each stimulus had an equal probability of being oriented at 45° or 135°; these orientations were irrelevant to the assigned task. Target stimuli during the probe session consisted of a black ring superimposed on the Gabor patch. During the spatial attention task, the luminance of the dark ring in the target stimuli was dynamically adjusted to maintain a constant level of task difficulty using an interleaved staircase procedure. All stimuli were presented on a gray (RGB: 187,187,187) background on a 1920 × 1200 pixel LCD screen, Planar SA2311w23 (refresh rate = 60 Hz), with a custom psychtoolbox Matlab code shared by Simon Kelly to correct for the gamma function of the stimulation monitor. Timing of stimulus onset relative to the event codes was measured via a photodiode attached to the screen and connected to StimTracker (Cedrus). A consistent delay of 38 ms was detected (typical for modern LCD monitors) during pilot testing and was corrected by delaying the output of all trigger codes to match the true time zero measured by the photodiode. Stimuli were created and controlled by a custom script written in psychtoolbox for Matlab (Mathworks), also generously shared by Simon Kelly. The final Matlab scripts used in the probe and attention experiments are available via the open science framework: https://osf.io/taakn/.

Probe session

The probe session was used to determine the best stimulus locations for eliciting the C1 component in each individual subject, independent from attentional effects. Subjects were instructed to maintain fixation on a small white dot (0.12°) in the center of

the screen while Gabor patches appeared in a random sequence at one of eight equidistant locations surrounding the fixation point, at an eccentricity of 4°. These locations were identical to those used in Kelly et al. (2008), but in the current study four of these locations were selected per subject for use in the main attention experiment. On 11% of trials, a target stimulus was presented, which was the same as the target from the easiest level of difficulty in the experimental task. Subjects were instructed to respond with a mouse click whenever they detected a target stimulus, and to do nothing in response to nontarget stimuli. This task encouraged subjects to distribute their attention evenly across all stimulus locations. Only ERPs elicited by nontarget stimuli were considered in the analyses. A total of ~200 nontarget stimuli were presented at each of the eight locations during the probe session.

Experimental sessions

Following the probe session, on two separate days, subjects completed two identical sessions of the visual spatial attention task (Figure 1). This attention task closely followed the task employed by Kelly et al. (2008), except that in the current experiment each block of trials contained stimuli that appeared at mirror image right and left locations only in the upper *or* lower visual field. In the work by Kelly et al. (2008), the attended versus unattended locations were always diagonally opposed, such that upper *and* lower visual field locations were stimulated in each block of trials. Due to this change, we added the second experimental session in order to collect data from the same number of trials per stimulus location as by Kelly et al. (2008).

During each block of the attention experiment, two of the stimulus locations chosen for that subject (a left–right pair in either the upper or lower visual field) were marked by virtual squares (2.75° x 2.75°) made of 4 white dots at the corners (each a single pixel in size, or .027°). Separate left–right pairs of stimulus locations were chosen for the upper and lower fields based on which locations produced the largest C1 amplitudes during the probe session. While subjects fixated on the central dot, a cue appeared to the left or right of this fixation point for 100 ms directing them to covertly attend to that
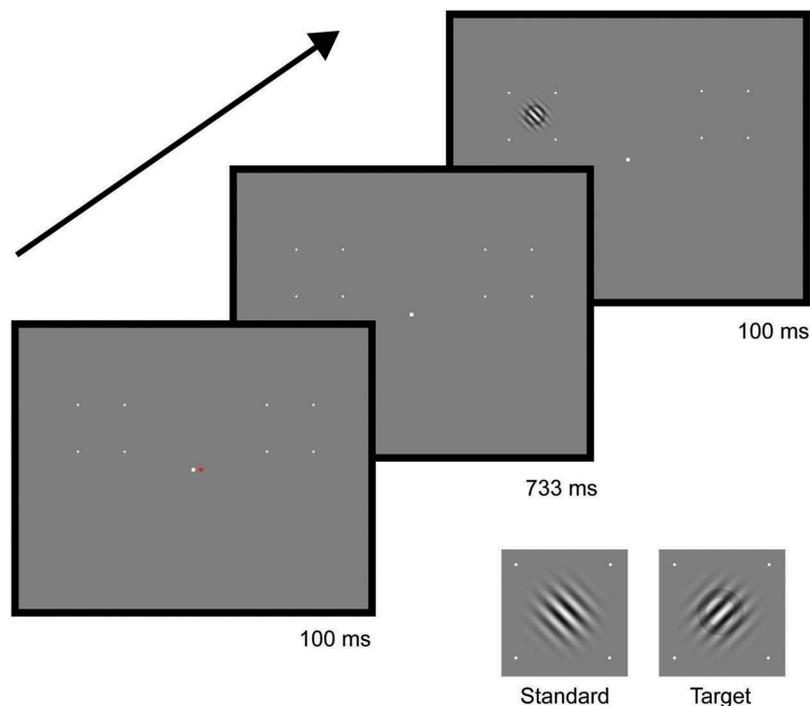

Figure 1. Sample trial of the spatial attention task.
Attention was cued on a trial-by-trial basis to either the left or right location. If a target appeared at the attended location, subjects responded with a button press. All stimuli presented at the unattended location were task-irrelevant. ERPs elicited by nontarget stimuli at a given location were used to compare mean amplitudes of the C1 when that location was attended versus unattended. Upper field and lower field locations were tested during separate blocks, and attention was a cued to either the left or right. Stimuli in this figure were adapted for ease of viewing and are not identical to those actually used.

side while keeping their gaze fixed in the center. Different from the 'L'-shaped white cue used by Kelly et al. (2008), the cue was a small red dot (4 x 4 pixels; RGB: 255, 0, 0) that appeared immediately adjacent to the fixation dot. After a delay of 733 ms, a Gabor patch stimulus was presented for a duration of 100 ms in either the attended or unattended location with an equal probability of occurring on either side. In synchrony with the Gabor patch stimulus, the white marker dots that surrounded it slightly increased in size to 2 x 2 pixels (.054°). If the stimulus that appeared at the attended location was a target stimulus (which occurred randomly on 30% of trials), the subject responded with a mouse click. If the attended stimulus was a nontarget or if a stimulus appeared in the unattended location, no response was required. Thus, the unattended location was always irrelevant and could be ignored.

The cue-to-stimulus interval was 833 ms, and each trial was separated by an inter-trial interval of 1533 ms. In order to encourage sustained effort on the task, the difficulty of target detection was adapted according to the performance of the subjects by adjusting the luminance of the dark ring in target stimuli. That is, following two sequential correct responses, the ring would become lighter and thus more difficult to detect, while following one miss or two sequential false alarms (for either valid or invalid trials), the ring would become darker and thus easier to detect. This differs slightly from the Kelly et al. (2008) procedure, which only took into account validly cued trials. Since the number of false alarm responses to invalidly cued stimuli here was very small (0.3% of trials), the procedures used in the two studies were essentially the same. To achieve the adjustment of task difficulty in the present study, gray scale brightness values of the dark ring were multiplied by 0.76–0.98 to create a total of 12 possible levels of luminance which was applied after the saturation of Gabor stimuli, and each block began at level 7. This adjustment was slightly different from the luminance adaption applied by Kelly et al. (2008), which used 11 levels of luminance (with multiplication factors of 0.4–0.9). During the breaks between blocks of trials, high performance on the task was encouraged by providing on-screen feedback of hit rates over the preceding block and reminding participants to put as much effort as possible into detecting the targets. Each block consisted of 100 stimulus

presentations and blocks alternated between upper and lower visual fields. During each experimental session, a total of 24 blocks were administered, 12 with upper field stimuli and 12 with lower field stimuli, the order of which was counterbalanced across subjects.

Data analysis

Individual electrodes that showed extended periods of noise were interpolated from nearby channels, but no interpolated channels were used for individual C1 analysis. After interpolating noisy channels, trials containing blinks, eye movements, or muscle artifacts were detected and rejected semi-automatically on a trial-by-trial basis for each subject. This procedure was recommended by Luck (2014) and involves setting automatic artifact-detection thresholds, visually inspecting the flagged and unflagged trials to verify the decision to accept or reject those trials, adjusting the detection threshold if necessary, and rechecking the data until a balance is achieved between detecting as many genuine artifacts as possible and avoiding discarding too many artifact-free trials. On average, 12.8% of trials were discarded due to artifacts in the probe session, and 11.6% in the experimental sessions. The mean number of trials retained after artifact rejection for the main attention experiment was 184 per stimulus location (min: 121; max: 227). ERPs were then re-referenced to the average of all 94 scalp channels, low-pass filtered at 45 Hz (half amplitude cutoff; 12dB/oct roll-off), epoched from −80 ms before to 200 ms after stimulus onset, and baseline-corrected from −80 to 0 ms.

ERPs elicited by nontarget stimuli in the probe task were analyzed to determine the best stimulus locations for eliciting the C1 component and the optimal electrode for measuring C1 amplitude at that location. These stimulus locations and corresponding electrode locations were selected by examining topographical maps and ERP traces during the C1 time window. Following Kelly et al. (2008), the C1 was defined by having an onset of 50 ms or earlier, rising above baseline amplitudes before 80 ms, and demonstrating a positive polarity for stimuli that appeared in the lower visual field and a negative polarity for stimuli that appeared in the upper visual field. The C1 was evaluated for stimuli at each of the eight probe locations independently for time of

onset, amplitude at 80 ms relative to baseline, clarity of the C1 waveform (as distinguished from EEG noise modulations), and topographical distribution. A single ideal electrode per stimulus location was determined by choosing the electrode at the center of the topographical map of the C1 during the 50–80 ms time window.

A total of four stimulus locations were chosen for each individual subject – two locations in the upper hemifield and two in the lower hemifield were studied on separate blocks in each session (Figure 2). Selected right and left locations in each hemifield (upper or lower) were always symmetrical about the vertical meridian, though the location of pairs could differ between upper and lower fields. This means that out of the possible pairs in the probe session, a given subject could be assigned locations 1 and 8, or 2 and 7, for the upper field, though never 1 and 7 or 1 and 2 (see Figure 2 for the eight possible locations). However, subjects could be assigned 1 and 8 for the upper field and 5 and 6 for the lower field, as these locations were tested on separate blocks of trials. If multiple pairs of locations per

hemifield showed a clear C1, amplitudes were compared to determine the best pair for the upper and for the lower hemifield.

In the attention task, ERPs elicited by nontarget stimuli that appeared in the same physical location were compared between conditions in which the subject was attending to that location versus conditions in which the subject was not attending to that location, with false alarm trials excluded from analysis. For the main analysis, in order to keep comparisons as similar as possible to Kelly et al. (2008), only data from the best upper field location and the best lower field location (for each individual subject) were included in the analysis. For the statistical analysis of C1, ERPs elicited by upper-field stimuli were polarity inverted (to make the C1 measure uniformly positive), and mean amplitudes from 50–80 ms at the designated optimal electrodes were compared using a 2 x 2 (attended/unattended, upper/lower field) repeated-measures analysis of variance (ANOVA). Follow-up analyses were conducted on all the ERP data from the four visual quadrants in a 2 x 4 ANOVA
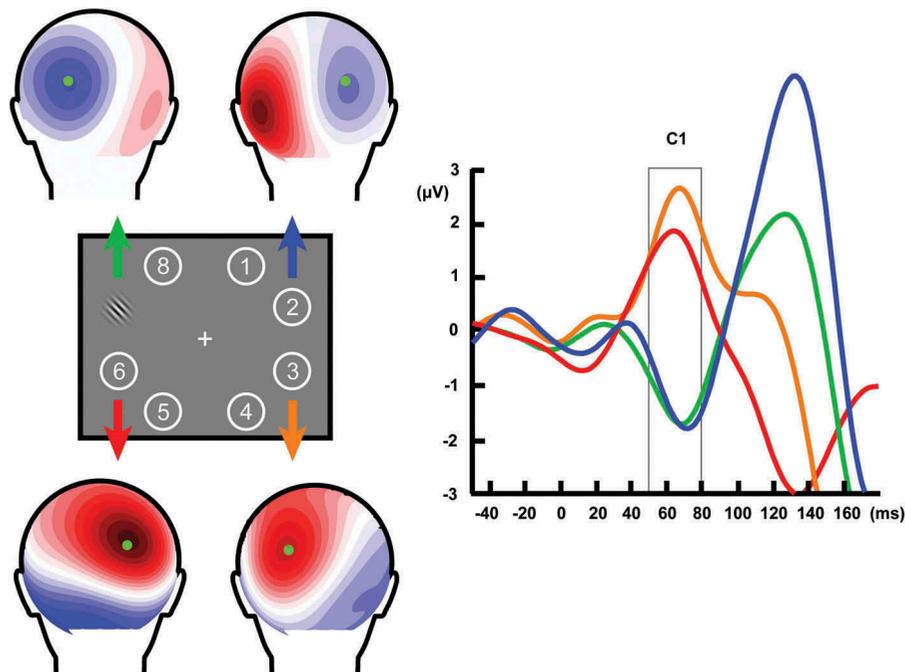

Figure 2. Example probe data for a single subject.
All 8 locations were randomly probed during the initial probe experiment. A pair of locations in the upper field and a pair of locations in the lower field that elicited the largest amplitudes in the C1 time window (50–80 ms) were selected for the main attention experiment, and ERPs were analyzed at the ideal electrode locations (indicated here by green dots on the posterior-view scalp maps). Selected location pairs were always symmetrical (7/2 or 8/1, and 6/3 or 5/4). For this subject, locations 7 and 2 were selected for the upper field, and 6 and 3 for the lower field. ERPs from the probe session at each of these 4 locations, for each of the four optimal electrode positions are plotted on the right. Stimulus in figure is adapted for ease of viewing and not identical to those actually used.

as well as post-hoc *t*-tests for each quadrant separately.

Attentional effects on the early (90–110 ms) and late (110–140 ms) phases of the P1 component were also evaluated. Electrode sites for measuring the P1 were chosen on the basis of grand-averaged probe data for each of the eight locations, with an optimal contralateral electrode used for the early P1 and an ipsilateral electrode for the late P1 (see Kelly et al., 2008). Mean amplitudes for the early and late P1 were compared between attended and unattended conditions. Here, separate 2 x 4 (attended/unattended x upper-left/upper-right/lower-left/lower-right) repeated-measures ANOVAs were employed to examine attention effects during the early and late P1 time windows.

Results

Behavioral and probe session results

In the probe task, subjects detected targets with 98.3% (SD = 2.3) accuracy. In the main attentional task, mean hit rate was 74.7% (SD = 6.6), comparable to the behavioral results from Kelly et al. (2008) of 80.7% (SD = 3.3). The mean false alarm rate was 1.3% (SD = 1.2) for validly cued stimuli and 0.3% (SD = 0.2) for invalidly cued stimuli. As performance typically stabilized toward the end of each block in this adaptive difficulty design, subjects averaged a difficulty level (see Methods section) of 7.7 (SD = 0.99) in the latter third of each

block. Two pairs of ideal stimulus locations (in the upper and lower visual fields) were clearly evident for 17 out of 21 probed subjects (with one subject excluded for excessive EEG artifacts). Three subjects were excluded from the attention sessions due to a lack of a measurable C1 at the locations used in the current study. As reported by Kelly et al. (2008), stimulus locations for the majority of subjects were chosen based on the presence of the C1. When subjects did have multiple pairs of viable C1 locations, amplitude was used to select the better pair. Figure 2 presents example data from a single subject's probe session.

Attention session ERP results

Grand-averaged ERPs for the optimal stimulus and electrode locations are presented in Figure 3, alongside a reprint of Kelly et al.'s (2008) main ERP data. The present study found no evidence for attention-based modulations of C1 amplitude. A 2 x 2 (attention x visual field) repeated-measures ANOVA found no main effect of attention in the present study, $F(1,16) = 2.24$, $p = 0.15$, $\eta_p^2 = 0.15$. Additionally, there was no main effect of visual field, $F(1,16) = 0.07$, $p = 0.79$, $\eta_p^2 = 0.078$, and no significant interaction, $F(1,32) = 0.16$, $p = 0.69$, $\eta_p^2 = 0.010$.

While the foregoing main analysis of attention effects on C1 amplitudes used only the best stimulus location in the upper field and best location in the lower field (to allow for more direct comparisons
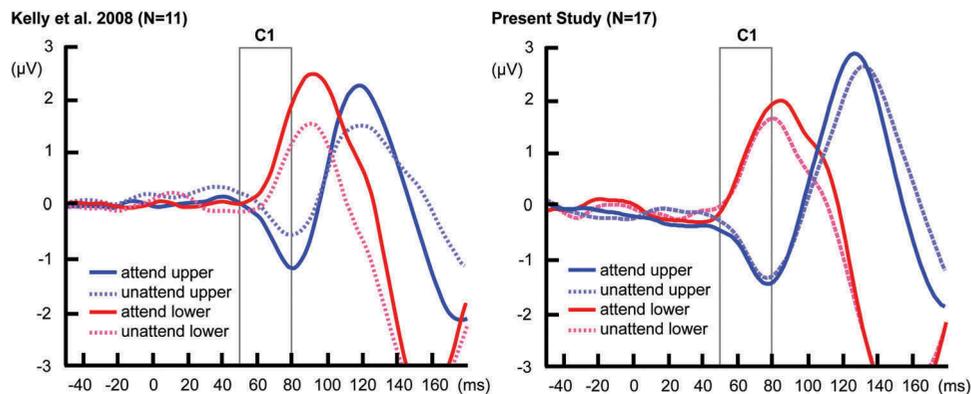

Figure 3. Grand-averaged ERPs from Kelly et al. (2008), left, and from the current study, right.
Mean C1 amplitudes (50–80 ms) were compared between attended and unattended trials. As Kelly et al. (2008) compared only one stimulus location per subject per visual field, our main analysis included only the best stimulus locations per visual field for each subject. While attention-based modulations of the C1 were found in Kelly et al. (2008) study, the current study failed to replicate this effect. The small amplitude difference for lower field stimuli from ~80–120 ms is an attention-based modulation of the early phase of the P1 (see Figure 5).
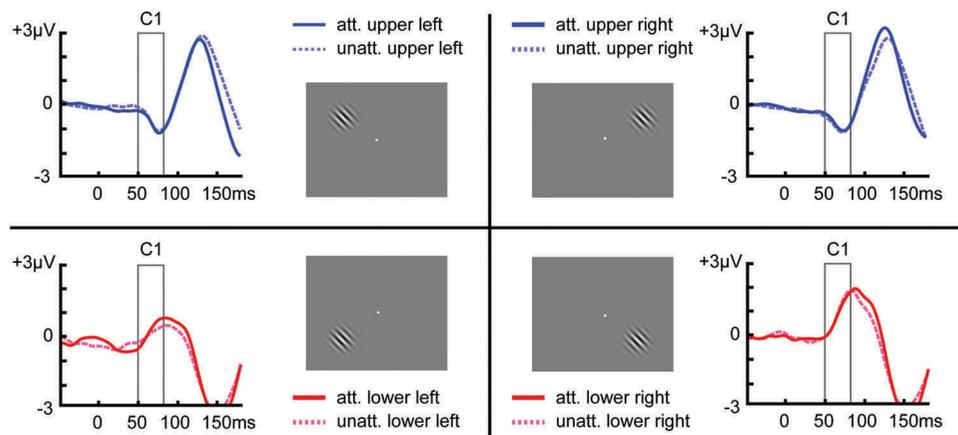
Figure 4. Grand-averaged ERPs in the attention experiment, shown separately for each visual quadrant. These grand-averages combine individual subjects' ERPs elicited by stimuli in the ideal location in each quadrant together with ERPs from the corresponding contralateral location, all measured at optimal electrode sites. Thus, these waveforms include all stimuli presented in the attention experiment. The time-window of the C1 used in the statistical analyses (50–80 ms) is indicated by the outline rectangles. No significant amplitude modulations for attended (att.) versus unattended (unatt.) stimuli were found (see main text for statistical results). Stimuli in figure were adapted for ease of viewing and are not identical to those actually used.

with Kelly et al.'s results), we also conducted subsequent analyses using all of our data – that is, ERPs from all four locations tested (Figure 4). A 2 x 4 ANOVA with the factors attention (toward/away) and visual field quadrant (upper-left/upper-right/lower-left/lower-right) revealed no main effects of attention, $F(1,16) = 0.01$, $p = 0.94$, $\eta_p^2 = 0.00014$, a marginally significant main effect of quadrant, $F(3,48) = 2.55$, $p = 0.07$, $\eta_p^2 = 0.46$, and no significant interaction, $F(3,48) = 0.62$, $p = 0.61$ $\eta_p^2 = 0.037$. Post-hoc *t*-tests confirmed the lack of significant attention effects in all quadrants during the C1 time-window: upper-left, $t(16) = 0.57$, $p = 0.58$, $d = 0.096$; upper-right, $t(16) = −0.70$, $p = 0.49$, $d = 0.14$; lower-left, $t(16) = 0.92$, $p = 0.37$, $d = 0.27$; lower-right, $t(16) = −0.38$, $p = 0.70$, $d = 0.67$.

Attention was found to modulate both the early and late phases of the P1 (Figure 5). A 2 x 4 repeated measures ANOVA with the factors attention and visual quadrant compared mean amplitudes during the early P1 (90–110 ms) and late P1 (110–140 ms) time-windows. For the early P1, ANOVA revealed a significant main effect of attention, $F(1,16) = 12.57$, $p = 0.0027$, $\eta_p^2 = 0.58$, no significant main effect of quadrant, $F(3,48) = 1.09$, $p = 0.36$, $\eta_p^2 = 0.55$, and no significant interaction, $F(3,48) = 0.82$, $p = 0.49$, $\eta_p^2 = 0.049$. Analysis of the late P1 also revealed a significant main effect of attention, $F(1,16) = 11.15$, $p = 0.0042$, $\eta_p^2 = 0.44$, no

significant main effect of quadrant, $F(3,48) = 0.55$, $p = 0.65$, $\eta_p^2 = 0.18$, and no significant interaction, $F(3,48) = 1.82$, $p = 0.16$, $\eta_p^2 = 0.10$.

Because the C1 and P1 were temporally adjacent, we compared scalp topographies of the C1, early-P1, and late-P1 for each visual quadrant. Figure 6 shows scalp maps for the evoked potentials (all stimuli in a given quadrant averaged together) as well as differential amplitudes between attended versus unattended trials. For upper field stimuli, the evoked C1 topography was clearly distinct from the evoked P1 topography, while the difference maps showed modulations only during the P1 time windows. For the lower field stimuli, the evoked C1 and early-P1 topographies were similar, particularly for the lower left field. The only hint of a C1 attention modulation came from the lower left quadrant (see also Figure 4), but this was also the same quadrant where the C1 and early-P1 showed the most spatio-temporal overlap. Overall, attentional modulations were only evident during the P1 time windows (90–140 ms), with no significant modulations during the C1 time window (50–80 ms).

Figure 7 shows ERP waveforms in the attention task from all 17 individual subjects at the optimal stimulus locations and recording electrodes. The individual subjects' waveforms shown here were averaged to form the grand average waveforms presented in
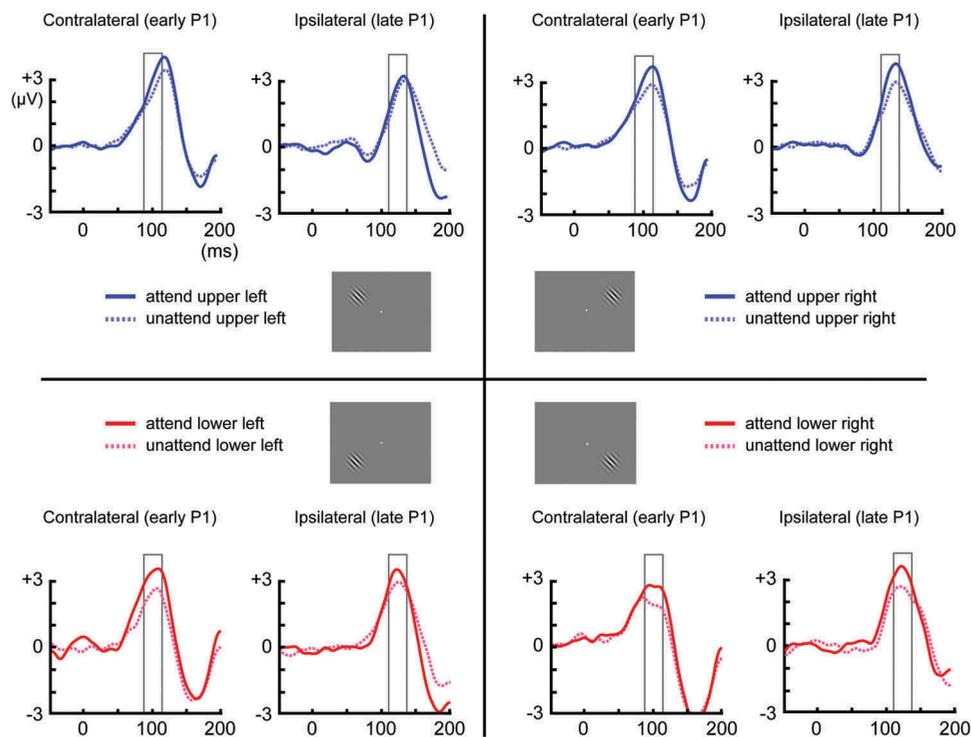
Figure 5. Grand-averaged ERPs in the attention experiment for each of the four visual quadrants recorded from lateral occipital electrodes determined on the basis of the probe data.

Mean amplitudes of early P1 (90–110 ms) and late P1 (110–140 ms) components were compared for attended and unattended trials. A contralateral electrode was used for the early P1 and an ipsilateral electrode was used for the late P1 (see Kelly et al., 2008). Attention-based modulations of P1 amplitudes were evident for both the early and late P1 time windows. Stimuli in figure were adapted for ease of viewing and are not identical to those actually used.

Figure 3. The scalp topography maps shown in Figure 7 were derived from the probe session and indicate the electrode locations that were selected for analysis in the attention experiment.

Discussion

Using experimental procedures pioneered by Kelly et al. (2008) to optimize the detection of possible attentional modulations of afferent V1 activity, the present study failed to find confirmatory evidence of such attentional effects. The earliest visual ERP component, C1 (50–80 ms), did not differ in amplitude when subjects focused attention toward versus away from the location of the stimulus. This lack of attentional modulation of the C1 was found for stimuli at visual field locations that produced the largest C1 amplitudes as well as for averages over all stimulus locations. Attentional effects at slightly later time windows were clearly evident, during both the early (90–110 ms) and late (110–140 ms) phases of the P1 component.

Why did the current study fail to find attention effects on the C1 component while the previous study of Kelly et al. (2008) demonstrated robust attentional modulations of C1 amplitudes? First, it is possible that the one major change we made to the experimental design was pivotal. In Kelly et al.'s (2008) experiment, attended versus unattended locations were always diagonally opposed (crossing both horizontal and vertical meridians of the visual field). In the current study, attended versus unattended locations varied only in the horizontal dimension (left versus right), with stimuli appearing in either the upper or lower visual fields during separate blocks of trials. Given the experimental design of the present study (adopted from Kelly et al.), however, it seems unlikely that this difference in stimulus configuration would account for the difference in C1 modulation between the studies. In particular, since only the cued location was relevant in both studies, there would be no need to suppress information at the uncued (unattended) location. So it should not matter whether the unattended, irrelevant location is situated horizontally or diagonally with
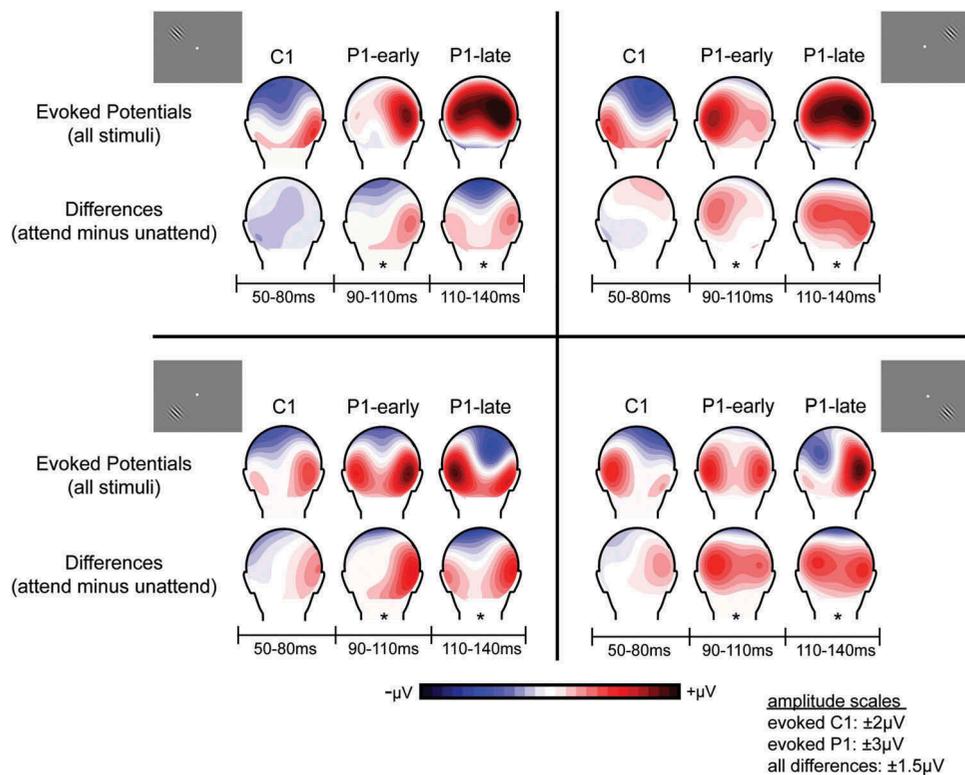
Figure 6. Topographic maps (posterior-view) of ERP components and differences between attended and unattended stimuli for C1 (50–80 ms), early-P1 (90–110 ms), and late-P1 (110–140 ms) shown separately for each visual field quadrant. Asterisks under the difference maps indicate significant differences ($p < .01$). Stimuli in figure were adapted for ease of viewing and are not identical to those actually used.

respect to the attended location. The distance of the attended location from the central fixation point was the same in both cases. It is also important to note that the task performance level achieved here by adaptive luminance adjustment was comparable to (but slightly lower than) the level of the Kelly et al. study, indicating that our lack of C1 modulation could not be attributed to a lesser task difficulty. It should further be noted that a robust enhancement of the P1 component to attended-location stimuli was observed in the present study (like that observed by Kelly et al.), indicating that spatial attention was strongly engaged. If the diagonal positioning of attended and unattended locations is critical for producing a modulation of the C1, this would suggest that such modulation is not a general mechanism of spatial attention but is only engaged in a narrow range of circumstances. Determining the key properties of the circumstances under which a C1 attention modulation may occur will be an important issue for future research.

A second possibility is that C1 attention effects do exist more generally, but the present study failed to detect these effects (i.e., a type 2 error). While possible, such an interpretation is unlikely for several reasons. The current study included data from 17 subjects (compared to 11 subjects in Kelly et al. (2008) experiment) and twice as much data by separating blocks into upper and lower field stimuli, thus testing four locations as compared to the two locations tested by Kelly et al. (2008). Even when ERPs from all locations were entered into the analysis, C1 modulations were still absent, despite the resulting higher signal-to-noise ratios that were obtained. There were some small procedural differences between the present study and that of Kelly et al., including the type of cue and the adaptive luminance procedure, but if C1 is generally modulated by attention, these minor differences should not have precluded such an effect from emerging in the present study. Finally, this interpretation would imply that a large corpus of experiments reported in the literature (reviewed later) may have also resulted in type 2 errors, or used inadequate methods, leading to repeated failures of detecting genuine attention effects on C1 amplitudes.

A third possibility is that attentional modulations of the C1 do not in fact occur, and the results of Kelly et al. (2008) were due to a type 1 or some other form
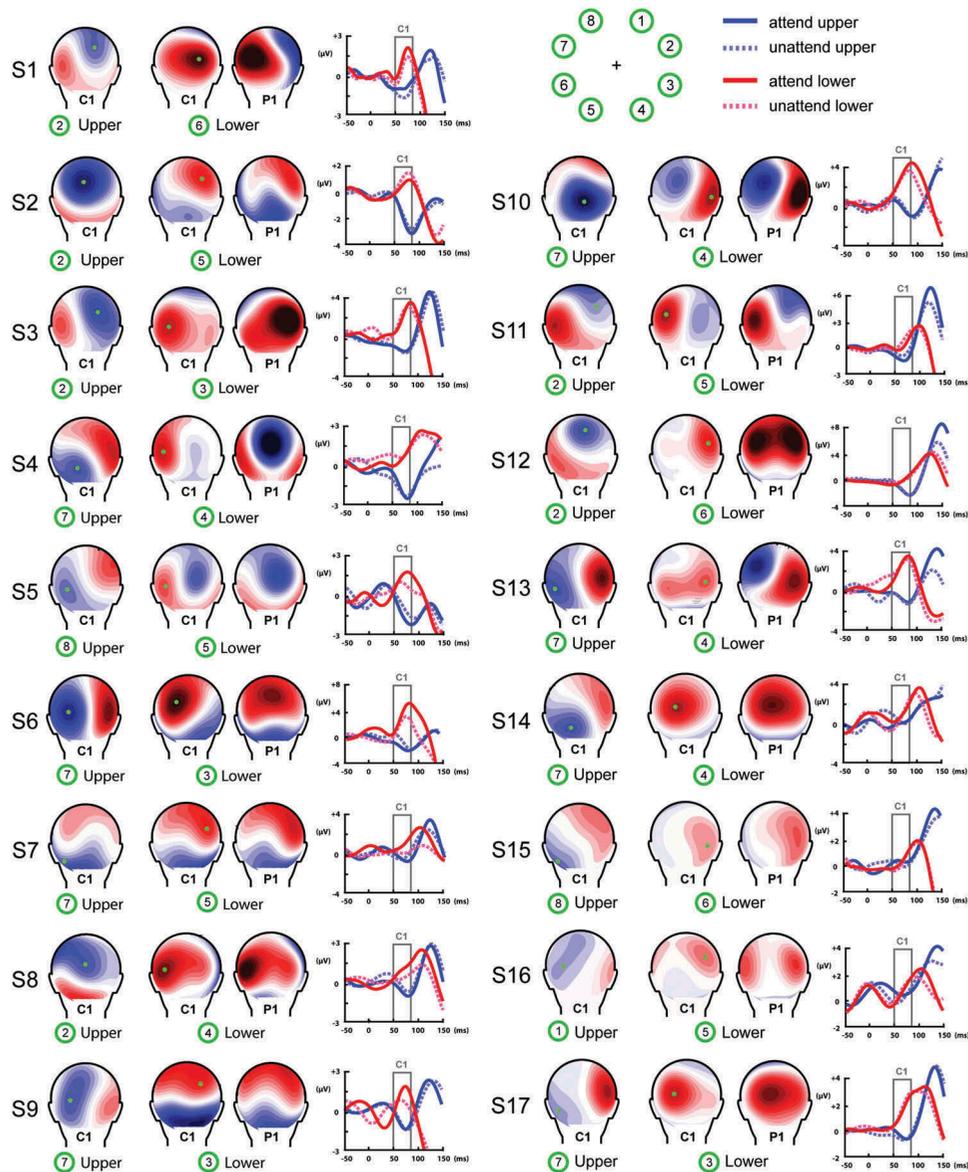
Figure 7. Individual subject scalp topographies from the probe experiment and ERPs from the attention experiment. Topographical maps at 80 ms are shown to demonstrate the location of optimal electrodes for recording the C1 in the best stimulus positions. Topographic maps for the lower field locations are also shown at 100 ms for the P1 component. The time-window for C1 analyses (50-80 ms) is indicated by the light gray boxes in the ERP figures. The grand-averages of these ERPs are shown in Figure 3.

of error. However, this seems unlikely as the data reported by Kelly et al. (2008) appear to have adequate signal-to-noise ratios, the statistical analyses were sound, and appropriate procedures were employed for protecting against confounding factors such as small eye movements toward the attended location. Also, attentional modulations of the C1 were found for both upper and lower visual field locations (in which the polarity of C1 and its modulations inverted), thus potentially ruling out spatio-temporal overlap between the C1 and P1 components. As reviewed later, the results of Kelly et al. (2008) stand out as the

most reliable demonstration to date of C1 modulations by spatial attention, and our failure to replicate such modulations is most puzzling.

Previous studies of C1 modulations by spatial attention

A good deal of evidence has accumulated over the past 24 years in support of the 'majority view' that visual-spatial attention does not modulate the earliest evoked activity in the primary visual cortex reflected in the C1 component (Aine et al., 1995;

Clark & Hillyard, 1996; Ding et al., 2014; Di Russo et al., 2003, 2012; Fu et al., 2005, 2008; Gomez Gonzalez et al., 1994; Gratton, 1997; Heinze & Mangun, 1995; Hopfinger & West, 2006; Johannes et al., 1995; Mangun et al., 1993, 2001; Martinez et al., 1999, 2001; Noesselt et al., 2002; Proverbio et al., 2010; Wijers et al., 1997; Woldorff et al., 1997, 2002; Yoshor et al., 2007). These studies have included a variety of spatial attention manipulations and recording techniques. The general finding was that the earliest modulation of visual processing by spatial attention takes place in extra-striate visual cortex starting at around 80 ms as reflected in the P1 component. In this majority view, the enhanced neural activity in area V1 revealed in fMRI studies can be accounted for by delayed feedback to area V1 following attentional selection that takes place at higher extra-striate levels (Di Russo et al., 2003; Martinez et al., 1999, 2001; Noesselt et al., 2002).

In his recent review, Slotnick (2013) cites three studies in humans that 'provide compelling evidence in favor of the minority view' … 'that attention can rapidly modulate activity in V1' (p. 65), namely Rauss, Pourtois, Vuilleumier, and Schwartz (2009), Slotnick, Hopfinger, Klein, and Sutter (2002), and Kelly et al. (2008). We agree with Slotnick's (2013) warning that 'the majority view can stifle scientific progress if concrete evidence is ignored', thus it's worth examining each of these studies in turn. Rauss et al. (2009) manipulated the attentional load of a visual discrimination task in central vision while recording ERPs to irrelevant peripheral stimuli in the upper and lower visual fields. They found that increasing the central attentional load resulted in a diminished C1 component to the peripheral upper-field stimulus, which was attributed to a concurrent withdrawal of attention from the periphery. The topography of the load-induced modulations of the C1 was not shown, however, and the statistical and source analyses found that the early load effect in the C1 interval (60–100 ms) was only significant at prefrontal regions rather than occipital regions. This suggests that the effect of attentional load may not represent a modulation of the occipitally generated C1 itself, but rather a summation or interaction with other ERP components elicited in this task. To further investigate the effect of attentional load on early visual-evoked activity, Ding et al. (2014) carried out a study that closely paralleled that of Rauss et al. (2009), with

central task stimuli presented in random order while irrelevant peripheral stimuli were presented in the upper and lower visual fields. Like Rauss et al., Ding et al. found that the peripheral stimuli elicited large C1 components that inverted in polarity for upper versus lower field stimuli and were source-localized to the primary visual cortex. Unlike Rauss et al., however, the load manipulation (a simple versus a complex color discrimination) did not affect C1 amplitude in Ding et al.'s study, which used a somewhat different schedule of stimulus randomization than did Rauss et al. The C1 elicited by the central relevant stimuli was similarly unaffected by attention. To ensure a high signal/noise ratio, Ding et al. presented at least 250 stimuli per subject per condition, and their load manipulation was highly effective (mean RT of 440 ms in low-load and 624 ms in high-load) and comparable to the load effect observed by Rauss et al. (mean RT of 478 ms in low-load and 623 ms in high load). The findings of Ding et al. (2014) thus provide evidence in favor of the majority view that the initial cortical processing of both relevant and irrelevant stimuli in area V1 is not substantially modulated by attention.

Slotnick et al. (2002) studied the effects of attention on early visual ERPs in an elegant design where reversing checkerboard stimuli were flickered in rapid and independent order at 60 locations in a circular dart-board-style array. In separate conditions, subjects attended to a small color-changing dot at fixation or in the left or right hemifield. Dipole modeling was conducted on the ERPs elicited in the intervals 50–80 ms and 80–110 ms after stimulus reversal, and difference-of-magnitude values were calculated between dipoles for stimuli at selected locations comparing attended versus unattended conditions. The results showed a small but significant cortical facilitation at the attended locations (mean difference-of-magnitude = 0.04) and a broader region of inhibition surrounding this region of facilitation. These findings are tantalizing, but several features of the experiment suggest caution in interpreting them. First, specific comparisons found that the facilitatory modulation in the critical 50–80 ms interval (that would include C1) was not statistically significant in itself ($p = .22$), while the modulation in the 80–110 ms interval did reach significance ($p < .05$). Second, eye movements were only monitored in one of the three subjects.

With high contrast stimuli fairly close to fixation (attended stimuli had an eccentricity of 2.6 degrees), even small shifts of ocular fixation might modify the visual-evoked potential. Third, information about dipole localization in relation to cortical anatomy was not provided, making it difficult to distinguish cortical generators in striate versus extra-striate visual areas. In sum, the study of Slotnick et al. (2002) provides a strong foundation for more extensive follow-up experiments but hardly provides compelling evidence for attentional modulation of the initial-evoked response (C1 component) in striate cortex.

Of the three human studies cited by Slotnick as supporting the minority view, the results of Kelly et al. (2008) appear to provide the strongest evidence. Yet the present failure to replicate the C1 modulations with attention observed by Kelly et al. under highly similar conditions should give pause to the controversy until the reasons for this discrepancy can be ironed out. Another study favoring the minority view should also be mentioned. In an magnetoencephalography (MEG) study, Poghosyan and Ioannides (2008) reported that spatial attention enhanced an early visual-evoked response with a latency of 55–90 ms that was localized to area V1. The waveforms that demonstrated this effect, however, were averaged over only 18 presentations of each visual stimulus type in each visual field per subject and therefore must have had very low signal/noise ratios. This is another study that calls for replication in an expanded design before accepting its conclusions.

Experiments in nonhuman primates have revealed significant (but often small) attention-related modulations of early stimulus-evoked neural activity in area V1 (Briggs et al., 2013; Chen et al., 2008; Li, Piech, & Gilbert, 2004; McAdams & Reid, 2005; Motter, 1993; Sharma et al., 2014; Wang, Chen, Yan, Zhaoping, & Li, 2015) and even in the lateral geniculate (McAlonan et al., 2008). These findings suggest that comparable effects might be observable in human ERP or MEG recordings if tested under the right conditions and with enough statistical power to reveal small modulations. It is also important to point out that the C1 component is reportedly affected by a number of top-down factors other than visuo-spatial attention. These factors include: attention to spatial frequency (Proverbio et al., 2010), cross-modal attention (Karns & Knight, 2009), perceptual learning (Bao, Yang, Rios, He, & Engel, 2010; Pourtois, Rauss, Vuilleumier, & Schwartz, 2008), and emotional significance (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Stolarova, Keil, & Moratti, 2006). To account for the influence of these diverse factors, Rauss, Schwartz, and Pourtois (2011) have proposed that low-level visual cortex operates as a 'predictive coding' mechanism, whereby incoming sensory information is matched against top-down expectations. If this proposal is on the right track, further studies are needed to elaborate how the interaction between top-down predictions and bottom-up afferent input results in improved perception of attended stimuli.

Conclusion

Determining whether or not afferent activity in human primary visual cortex can be modulated by attention is important because it informs our understanding of how much information is automatically registered and encoded in the visual system. Knowing when attention can first modulate visual processing has implications for the 'cognitive penetrability' debate (Firestone & Scholl, 2016; Siegel, 2012) as well as the debate over the 'richness/sparseness' of visual awareness (Block, 2011; Cohen, Dennett, & Kanwisher, 2016). As reviewed earlier, there is substantial evidence in both humans and nonhuman primates that V1 is not simply an inflexible module that performs an initial feature extraction but rather enacts processing operations that are subject to top-down influences. With respect to the main cognitive function explored in the present study, however, there is little support for the 'minority view' that visual-spatial attention modulates the initial neural response in area V1 as manifested in the C1 component. The studies demonstrating such effects are either very preliminary in nature or have not been confirmed in serious attempts at replication. Until the specific conditions that enable such modulation of C1 can be identified and replicated, the 'majority view', which posits that the initial afferent processing stages in V1 are impenetrable by visual-spatial attention, seems to be the safer bet.

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