Distinct and independent correlates of attention and awareness in a hemianopic patient

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\textbf{A B S T R A C T}

Attention and awareness are intimately related concepts. Nevertheless, the two phenomena are empirically dissociable: visuo-spatial attention can act in the absence of visual awareness. We used magnetoencephalography (MEG) to record cortical neural activity from hemianopic patient GY while he performed a peripheral orientation-discrimination task in the context of an attention-cueing paradigm. The luminance contrast of target stimuli was set at GY’s threshold for reports of awareness (a feeling “that something happened” in his blind visual field). GY’s accuracy was significantly greater than chance and comparable, with or without awareness. GY was significantly faster to respond correctly on valid-cue versus invalid-cue trials, even in the absence of awareness, confirming the action of visuo-spatial attention in the absence of awareness. Time-frequency analysis of spectral power in the gamma frequency range (30–90 Hz), averaged over left parieto-occipital sensors, revealed effects of cue-validity independent of reported awareness, and effects of awareness independent of cue-validity. GY’s reports of awareness were not, however, independent of his pre-target attentional state (gamma-band response to the central cue), consistent with a one-way, but not a two-way, dissociation between attention and awareness. Our evidence suggests that the observed cue-validity effect is an awareness-independent involuntary re-orienting response, and that the neurodynamics underlying the exogenous capture of attention are similar with or without awareness. The finding of a significant awareness-independent effect in the area of 40 Hz implies that a stimulus-induced modulation of power in the canonical gamma band is not a sufficient condition for sensory awareness.

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What is the relationship between attention and awareness? Traditionally, attention has been thought of as a means by which some of the information actively being processed, or about to be processed, in the (objective) brain is selected for an appearance in the (subjective) mind. Notions of attention conceived from the first-person point of view, such as the “spotlight” metaphor, leave little room for a concrete empirical distinction to be drawn between attention and awareness. In recent years, neuroscience has provided a radically different conception, expressed in terms of objective neural resources rather than subjective cognitive resources. Attention is now widely thought of in terms of a bias in neural information processing (Desimone & Duncan, 1995). Stimuli compete for “representation” by the neuron(s) whose receptive field they inhabit, and attention acts (through enhancement or suppression) to bias that representation toward the attended stimulus.

This model of attention is mostly silent on the subject of awareness, but for the intuition that contents “selected” by attention are more likely to “reach” awareness.

A number of recent studies demonstrate that attention (in the form of enhanced processing) and awareness (in the form of subjective report) can in fact be empirically dissociated, both in the patient studied here (Kentridge, Heywood, & Weiskrantz, 1999, 2004) and in normal subjects (Bahrami, Lavie, & Rees, 2007; Jiang, Costello, Fang, Huang, & He, 2006; Kentridge, Nijboer, & Heywood, 2007; Montaser-Kouhsari & Rajimehr, 2004; Sumner, Tsai, Yu, & Nachev, 2006). Kentridge (Kentridge et al., 2004) used a version of Posner’s classic attention-cueing paradigm (Posner, Snyder, & Davidson, 1980) to test behaviorally for the effects of visuo-spatial attention in the blind hemifield (BF) of hemianopic patient GY. A central arrow (visible to GY) directed his attention to either the upper or lower quadrant of his BF, and then an oriented bar (not consciously seen by GY) appeared in either the cued (80%) or uncued (20%) quadrant. GY was significantly faster to correctly guess the orientation (vertical versus horizontal) of the target bar when it
appeared in the cued location compared to when it appeared in the uncued location. This effect of cue validity on reaction time was cited as evidence of visuo-spatial attention without awareness (of the attended target).

Although GY is functionally blind in his right hemifield, visual stimuli with certain properties (esp. high luminance contrast, rapid onset/cutoff, flicker, quick movement) sometimes provoke a report from GY of a sensation “that something happened” (Schurger, Cowey, & Tallon-Baudry, 2006; Weiskrantz, Barbur, & Sahraie, 1995; Zeki & Ffytche, 1998) in his blind hemifield. However, GY’s accuracy on at least two different tasks (direction of motion and orientation discrimination) is independent of this form of awareness (Schurger et al., 2006a; Weiskrantz et al., 1995). Using stationary stimuli with moderate luminance contrast and/or gradual onset/cutoff, GY continues to exhibit greater-than-chance accuracy without acknowledged awareness (true “blindsight”).

GY therefore exhibits (a) comparable accuracy with or without awareness and (b) visuo-spatial attention with or without awareness. These two phenomena together in the same patient provide a unique opportunity to study the relationship between attention and awareness. To this end, we recorded brain activity from patient GY performing an attentional cueing task almost identical to that of Kentridge (Kentridge et al., 2004) (see Fig. 1), using magnetoencephalography (MEG), in order to identify macroscopic electrophysiological features of cortical neural activity that correlate separately with awareness and attention-without-awareness.

Although the task (orientation discrimination) and method of cueing (central arrow consciously visible to GY) were the same as those used by Kentridge, our paradigm (Schurger, Cowey, & Tallon-Baudry, 2006b) was different in one important respect: prior to running the cueing experiment, we used a psychophysical staircase procedure (similar to that of Taylor and Creelman, 1967, but developed independently) to estimate the contrast threshold at which GY reported a “feeling that something happened” in response to the target approximately 50% of the time. We used this contrast for the remainder of the experiment, resulting in “aware” responses on ~53% of trials (714/1351, total before rejection of trials with MEG signal artifacts; see Table 1). Only trials on which GY responded correctly (CORRECT, ~56% of trials) were included in MEG and reaction-time (RT) analyses. This provided us with a two-by-two experimental design matrix, with factors AWARENESS (AWARE/UNAWARE) and CUE-VAILDIY (VALID/INVALID). Enhanced processing (e.g. faster correct responses) of targets presented in the cued versus the uncued location would indicate the action of visuo-spatial attention within GY’s blind hemifield, allowing for the effects of cue-validity to be interpreted in terms of attention. If GY’s reports of awareness vary independently of cue-validity, then we can attempt to identify neural dynamics associated with both awareness and attention independent of awareness. A modulation of spectral power in the gamma band has previously been linked separately to both attention (Fries, Reynolds, Rorie, & Desimone, 2001; Gruber, Muller, Keil, & Elbert, 1999; Muller, Gruber, & Elbert, 2000; Muller, Gruber, & Keil, 2000) and awareness (Meador, Ray, Echauz, Loring, & Vachtsevanos, 2002; Schurger et al., 2006a; Summerfield, Jack, & Burgess, 2002). We therefore focused our analyses on the gamma band.

1. Methods

1.1. Subject

GY (male, born 1956, age 49 at the time of the experiment) was an automobile accident at the age of 8 during which he suffered trauma to his left occipital cortex, restricted almost entirely to V1 (with slight damage also to dorsal areas V2 and V3). He also has significant visual field defects (Weiskrantz et al., 1991; Zeki & Ffytche, 1998). Details concerning the extent of GY’s lesion (Barbur, Watson, Frackowiak, & Zeki, 1993; Baseler, Morland, & Wandell, 1999) are available (Barbur, Ruddock, & Waterfield, 1980; residual visual sensitivity (Barbur et al., 1980, 1993; Weiskrantz, Harlow, & Barbur, 1991), and his ability to guess without awareness (Weiskrantz et al., 1995; Zeki & Ffytche, 1998) may be found elsewhere. For a general review of blindsight, see (Stoerig & Cowey, 1997) and (Cowey, 2004). GY gave informed consent to participate in the study.

1.2. Testing environment and MEG recording

The experiment was conducted at the Centre MEG of the Hôpital de la Salpêtrière, Paris, France in July of 2005. MEG recording was carried out using a whole-head MEG system, manufactured by CTF Systems, Canada, with 151 radial gradiometers over the head and 29 reference gradiometers and magnetometers.

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**Table 1**

<table>
<thead>
<tr>
<th>Condition</th>
<th>COR</th>
<th>ERR</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Valid-cue (total)</td>
<td>313</td>
<td>217</td>
<td>530</td>
</tr>
<tr>
<td>UN</td>
<td>263</td>
<td>224</td>
<td>487</td>
</tr>
<tr>
<td>Total</td>
<td>576</td>
<td>441</td>
<td>1017</td>
</tr>
<tr>
<td>B. Invalid-cue (total)</td>
<td>102</td>
<td>82</td>
<td>184</td>
</tr>
<tr>
<td>UN</td>
<td>83</td>
<td>67</td>
<td>150</td>
</tr>
<tr>
<td>Total</td>
<td>185</td>
<td>149</td>
<td>334</td>
</tr>
<tr>
<td>C. Valid-cue (after MEG artifact rejection)</td>
<td>252</td>
<td>183</td>
<td>435</td>
</tr>
<tr>
<td>UN</td>
<td>218</td>
<td>185</td>
<td>403</td>
</tr>
<tr>
<td>Total</td>
<td>470</td>
<td>368</td>
<td>838</td>
</tr>
<tr>
<td>D. Invalid-cue (after MEG artifact rejection)</td>
<td>81</td>
<td>69</td>
<td>150</td>
</tr>
<tr>
<td>UN</td>
<td>65</td>
<td>48</td>
<td>113</td>
</tr>
<tr>
<td>Total</td>
<td>146</td>
<td>117</td>
<td>263</td>
</tr>
</tbody>
</table>

There were a total of 1440 trials (18 blocks of 40 trials), but 89 trials were rejected due to inappropriate behavioral responses (response too early or too late, or missing response), leaving a total of 1351 “good” trials. Behavioral statistics are reported for all “good” trials (1351), before MEG artifact rejection, since none were rejected due to eye-movement artifacts—only eye-blink, muscle, and other signal artifacts. The pattern of behavioral results was similar before and after MEG artifact rejection.

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Fig. 1. Task and reaction times. (A) A schematic of the trial sequence (illustrating an invalid-cue trial); not drawn to scale (the central cue fit entirely within a region of spared sight around the macula, and was clearly visible to GY). (B) GY’s average reaction times for CORRECT trials, showing main effect of cue validity (invalid > valid) and main effect of awareness (aware < unaware). Mean reaction times (from left to right) are 1028, 508, 800, and 770 ms. Numbers at the base of each bar are number of trials averaged. GY was significantly faster to respond correctly on validly cued trials, even without awareness (p < 0.015, one-tailed t-test), thus replicating the result of Kentridge et al. (2004). Results of two-way ANOVA with factors cue-validity and awareness: significant main effect of cue validity (F = 4.27, p < 0.04); significant main effect of awareness (F = 25.63, p < 0.000001); no significant interaction (F = 1.56, p > 0.22).
ANOVA on the average energy within PT2 revealed a significant main effect of CUE-VALIDITY (could appear in either the cued (region of macular sparing, and so was consciously visible to GY. The arrow remained 75\% of trials) or uncued quadrant, and remained on the screen for 500 ms. After the target had disappeared, GY was prompted (with the word “Orient?”) to guess the orientation of the bar – either “top-leaning-left” (upper) or “top-leaning-right” (lower). The nearest edge of any stimulus to the fixation cross was never closer than 6.2°, well outside of GY’s region of macular sparing (2.5–3.0°). Screen dimensions were 47 cm × 34.5 cm at a resolution of 1024 × 768 pixels. Stimulus contrast was 0.88 (Michelson) with mean luminance of ~21 cd/m² (approximately isoluminant with the gray background of ~20 cd/m²). Stimuli were back-projected onto a translucent screen via a computer data projector. Each trial began with the appearance of a fixation cross in the middle of the screen, which remained throughout the entire trial. After a brief interval (randomly 500–700 ms), a small central arrow appeared extending outward from the fixation cross, directing GY’s (covert) attention to either the upper (50% of trials) or lower quadrant of his blind (right) visual hemifield.1 The arrow fit entirely within GY’s region of macular sparing, and so was consciously visible to GY. The arrow remained on for 500 ms, and its disappearance signaled the onset of the target. The target bar could appear in either the cued (75% of trials) or uncued quadrant, and remained on the screen for 500 ms. After the target had disappeared, GY was prompted (with the word “Orient?”) to guess the orientation of the bar – either “top-leaning-left” (135°) or “top-leaning-right” (45°). GY was given 1750 ms to respond (by button press) before a second prompt appeared (the word “Aware?”) at which point GY was to indicate (again by button press) whether or not he had experienced a feeling “that something happened” in his blind hemifield in response to the target bar. In between trials the fixation cross disappeared (gray background only) for a random interval of 1000–2000 ms.

1 GY’s eye movements were monitored via electrooculogram (four ocular electrodes), which was calibrated prior to the experiment using a simple saccade task. EOG traces were visually inspected off-line and trials that showed any signs of eye movements were excluded from the analysis.

Fig. 2. Distinct and independent correlates of cue-validity and awareness. (A) Time-frequency plot of grand average over all CORRECT trials, at sensor LP31 (shown in D). Two distinct responses were evident based on visual inspection, and windows around these were labeled PT1 (280–410 ms, 44–76 Hz), and PT2 (430–580 ms, 38–58 Hz). PT refers to “post-target” time period. Topography (similar for both PT1 and PT2) was focused within a left occipito-parietal region, similar to our previous study with this patient (Schurger et al., 2006a). All subsequent analyses were carried out on the average across this topographical ROI (eight sensors, shown in D). B and C show the averaged responses across trials for each condition (CORRECT trials only) within PT2 and PT1, respectively. A two-way ANOVA (cue-validity × awareness) on the average energy within PT1 revealed a significant main effect of AWARENESS (F = 8.07, p < 0.005), no main effect of cue (F = 0, p = 0.96), and no interaction (F = 0.09, p = 0.77). The same two-way ANOVA on the average energy within PT2 revealed a significant main effect of CUE-VALIDITY (F = 7.72, p = 0.006), no significant effect of awareness (F = 1.15, p = 0.29), and no interaction (F = 0.27, p < 0.61). Levene’s test for homogeneity of variance: p > 0.8 for PT1 and PT2. The N in (B) and (C) differ from those in Fig. 1 by the number of trials excluded from MEG analysis due to signal artifacts. (D) shows the mean of the topographies of PT1 and PT2 (which were highly similar).

for ambient field correction. Signals were digitized at a sampling rate of 1250 Hz (0–200 Hz bandwidth) during epochs lasting 5 s, beginning 1 s prior to stimulus onset. Eye movements were monitored via electrooculogram (four ocular electrodes), which was calibrated on a simple saccade task. Ambient lighting was mesopic.

1.3. Stimuli and task

Target stimuli were oriented rectangular bars made up of a random elongated checkerboard pattern (see Fig. 1). Stimulus size was 6° × 15° at a viewing distance of 85 cm. Stimulus placement (r, δ in polar coordinates, from fixation to center of bar) was either 9.2°, 45° (upper) or 9.2°, −30° (lower). The nearest edge of any stimulus to the fixation cross was never closer than 6.2°, well outside of GY’s region of macular sparing (2.5–3.0°). Screen dimensions were 47 cm × 34.5 cm at a resolution of 1024 × 768 pixels. Stimulus contrast was 0.88 (Michelson) with mean luminance of ~21 cd/m² (approximately isoluminant with the gray background of ~20 cd/m²). Stimuli were back-projected onto a translucent screen via a computer data projector.

Each trial began with the appearance of a fixation cross in the middle of the screen, which remained throughout the entire trial. After a brief interval (randomly 500–700 ms), a small central arrow appeared extending outward from the fixation cross, directing GY’s (covert) attention to either the upper (50% of trials) or lower quadrant of his blind (right) visual hemifield.1 The arrow fit entirely within GY’s region of macular sparing, and so was consciously visible to GY. The arrow remained on for 500 ms, and its disappearance signaled the onset of the target. The target bar could appear in either the cued (75% of trials) or uncued quadrant, and remained on the screen for 500 ms. After the target had disappeared, GY was prompted (with the word “Orient?”) to guess the orientation of the bar – either “top-leaning-left” (135°) or “top-leaning-right” (45°). GY was given 1750 ms to respond (by button press) before a second prompt appeared (the word “ Aware?”) at which point GY was to indicate (again by button press) whether or not he had experienced a feeling “that something happened” in his blind hemifield in response to the target bar. In between trials the fixation cross disappeared (gray background only) for a random interval of 1000–2000 ms.

1.4. Analysis of MEG data

Time-varying MEG data were divided into epochs spanning the time period from 500 ms before the onset of the cue through 1000 ms after the onset of the target. MEG and EOG traces were visually inspected off-line and any trials with signal artifacts (eye movement, eye blink, muscle) were excluded from the analysis. Estimates of spectral power for frequencies in the range 30–90 Hz (in steps of 2 Hz) at each time point were computed by convolution with complex morlet wavelets (Tallon-Baudry, 1997). The resulting spectral power estimates (in matrices of time × freq, one per trial) were log transformed to approximate a normal distribution and then sorted by experimental condition (VALID/INVALID, AWARE/UNAWARE). Only data from trials on which GY correctly guessed the orientation of the bar (CORRECT) were included in the analysis. Levene’s test for homogeneity of variance was negative (p = 0.8 for PT1 and PT2), indicating similar variance among the four cells. MEG data processing and analysis was carried out using in-house software. Statistical analysis and data visualization were performed using MatLab (MathWorks, Inc.) with the help of the Statistics Toolbox.

1.4.1. Selection of topographical region of interest (ROI)

Visual inspection of the wavelet-transformed MEG data was carried out on the grand average over all CORRECT trials, so as to avoid “cherry picking” effects of interest. Visual inspection was focused on the left occipito-parietal region, where attention-related modulation of gamma-band responses has previously been observed in normal subjects (Gruber et al., 1999; Muller, Gruber, & Elbert, 2000; Muller, Gruber, & Krol, 2000; Vidal, Chaumont, O’Regan, & Tallon-Baudry, 2006), and where awareness-related modulation has previously been observed in this same patient with similar stimuli and task (Schurger et al., 2006a). A significant increase in gamma power was identified at approximately 300–500 ms post-target, 38–70 Hz, in the area around sensor LP31 (left occipito-parietal). The topography of the average spectral power over the window 300–500 ms, 38–70 Hz was used...
to delimit a roughly circular ROI, centered on sensor LP31 (Fig. 2). Eight sensors were included: LT16, LP32, LP22, LO12, LP31, LO11, ZP02. Unless otherwise indicated, all subsequent analyses were performed on the average over these eight sensors.

1.4.2. Point-wise statistical analyses of time-frequency space

Point-wise statistical analyses in TF space were performed over the post-cue and post-target intervals in order to identify possible effects that were not apparent in the grand average. A two-way ANOVA with factors AWARENESS (AW/UN) and CUE-VALIDITY (VAL/INV) was performed on the average [log(f difference in spectral power for that effect (INV − VAL and AW − UN, respectively). Only clusters that survived a multiple comparisons test at p < 0.05 are shown (see Methods). Besides the clusters shown, no other cluster survived the multiple comparisons correction at a threshold lower than p < 0.15. (B and D) Spectra of the difference in power (averaged over the corresponding highlighted time windows in A and C) corresponding to the main effect of cue-validity (INV − VAL, red), main effect of awareness (AW − UN, green), and interaction ([VAL/UN + INV/AW] − [VAL/AW + INV/UN], blue). C (inset) shows mean spectral power (log − log(BL)) in the window 38–90 Hz, 170–210 ms post-cue, for each condition, illustrating the interaction. All vertical error bars are SEM, and horizontal error bars in B show standard error of the peak frequency in the difference spectra, estimated using a bootstrap procedure (see Section 1).

1.4.3. Correction for multiple comparisons in statistical maps

TF data were first down-sampled (using MatLab's resample function) by a factor of 16 along the time axis in order to render the test computationally tractable on our computer. Due to the temporal "smearing" inherent in the wavelet transform, this level of down-sampling does not alter the overall layout of features in TF space—i.e. distinct features in TF space at full temporal resolution also appear distinct at 1/16 of full temporal resolution, given that 16 samples at 1250 Hz is approximately 12 ms. After down-sampling, the trials were randomly shuffled between the four conditions (VALID/AWARE, VALID/UNAWARE, INVALID/AWARE, INVALID/UNAWARE). The number of trials within each condition was kept the same for all shufflings. Then the point-wise multiple-ANOVA procedure described above was applied to the shuffled data. Recall that this procedure results in three separate statistical maps: one for the main effect of cue-validity, one for the main effect of awareness, and one for the interaction. A point-wise threshold was applied to each map (p < 0.05 for the post-target interval, and p < 0.10 for the post-cue interval). Then, separately for each map, all contiguous clusters were identified and the size of each cluster recorded. This process was repeated 1000 times. The resulting cluster-size data were used to construct a null distribution of cluster sizes for each of the three probability maps (two main effects, one interaction). The corrected p-value for a given observed cluster of size S was taken to be the number of clusters in the null distribution with size greater than or equal to S divided by the total number of clusters in the null distribution. There were no marginally significant clusters in either the post-cue or post-target epochs: apart from the clusters shown in Fig. 3, A and C, no other cluster survived the multiple-comparisons correction at a threshold lower than p < 0.15.

1.4.4. Bootstrap procedure for testing differences in peak-power frequency

Data were first sorted by experimental condition into four groups (again, only CORRECT trials were included): VALID/AWARE, VALID/UNAWARE, INVALID/AWARE, INVALID/UNAWARE. Bootstrap (Efron & Tibshirani, 1998) re-samplings were drawn, with replacement, from each of these groups (each re-sampling had the same number of samples as the group from which it was drawn). For each trial's data, average spectra were taken over the time interval 300–400 ms post-target, for the awareness effect, and 425–525 ms, for the cue-validity effect (Fig. 3A, shaded regions). The spectrum of the AWARENESS effect was computed as the mean spectrum over VALID/AWARE trials minus the mean spectrum over UNAWARE trials. The spectrum of the CUE-VALIDITY effect was computed as the mean spectrum over INVALID-CUE trials minus the mean spectrum over VALID-CUE trials (see Fig. 4). The frequency of the peak in each of these difference spectra was recorded. This procedure was repeated 1000 times. The variance of the peak difference frequency for each effect across bootstrap re-samplings is an unbiased estimator of the actual variance. These two variance estimates were used to compute a z-score with the observed peak-difference frequency as the mean for each sample: (m1 − m2)/sqrt(v1 + v2), where m and v are the mean and variance estimates, respectively.

2 Because the cue-validity effect had a bi-modal spectrum, for this effect only we took the peak within the range 30–60 Hz, rather than over the entire range of frequencies (whether or not we restricted the range made little difference in the resulting estimate of variance).
without awareness was not significant (binomial). The difference in accuracy between responses with and time-frequency (TF) analysis (see Section 1). Our analyses were reports of awareness were related to the appearance of a stimulus.

2. Results

2.1. Behavioral

GY was significantly faster to correctly guess the orientation of the bar on valid-cue versus invalid-cue trials, even on trials in which he indicated that he was unaware of the target (Fig. 1B), thus confirming the action of visuo-spatial attention in the absence of awareness, and replicating the result of Kentridge (Kentridge et al., 2004). GY guessed the orientation of the bar significantly better than expected by chance whether he reported awareness (58%, 415/714, p < 0.00001 binomial) or not (54%, 346/637, p < 0.02 binomial). The difference in accuracy between responses with and without awareness was not significant (χ² = 1.98, p < 0.16) as in previous studies (Schurger et al., 2006a; Weiskrantz et al., 1995). Cue-validity did not have any measurable effect on either GY’s reports of awareness (χ² = 0.156, p < 0.70) or his accuracy (χ² = 0.16, p < 0.69). GY was substantially and significantly faster to respond on trials in which he reported awareness (Fig. 1), consistent with results from a previous experiment of ours with GY (Schurger et al., 2006a).

Because we were primarily interested in awareness in response to a stimulus (not of purely endogenous origin) we performed an analysis aimed at determining whether or not GY’s reports of awareness were indeed tied to the appearance of a stimulus: Due to known inhomogeneities in GY’s blind field (Kentridge, Heywood, & Weiskrantz, 1997) we reasoned that the probability of GY reporting awareness might vary slightly depending upon the precise location and/or orientation of the target bar. A three-way log-linear analysis was applied to the number of observations in each combination of (a) vertical position (upper or lower quadrant), (b) orientation (top-leaning-left or top-leaning-right), and (c) awareness (yes or no). This analysis revealed a significant three-way interaction (G² = 13.16; d.f. = 4; p < 0.0015), confirming that GY’s reports of awareness were related to the appearance of a stimulus.

2.2. Magnetoencephalography

Time-varying MEG signals were subject to a wavelet-based time-frequency (TF) analysis (see Section 1). Our analyses were focused on a roughly circular topographical region of interest (ROI) over left occipito-parietal cortex (Fig. 2D), chosen from an analysis of the grand average over all CORRECT trials (i.e. the ROI was selected before the data were sorted by condition, in order not to bias our choice). Within this topographical ROI, we identified two ROIs in TF space during the post-target time interval (“PT”, 100–600 ms after target onset) that showed increases in power (Fig. 2A), and labeled these PT1 (280–410 ms, 44–76 Hz) and PT2 (430–590 ms, 38–58 Hz). Separate two-way ANOVA’s were performed on the average TF energy within each of these windows (only CORRECT trials were included). PT1 showed a significant main effect of AWARENESS (AWARE > UNAWARE, p < 0.005), but no effect of cue-validity, and PT2 showed a significant main effect of CUE-VALIDITY (INVALID > VALID, p < 0.006), but no effect of awareness. There was no significant interaction at either ROI (p > 0.6). The difference in spectral power INVALID – VALID at PT2 is therefore an effect of attention that is independent of awareness.

In order to reveal effects not apparent in the grand average, we performed a statistical analysis of the entire region of TF space from 250 to 600 ms post-target, and 30–90 Hz (in steps of 2 Hz). At each point in TF space we performed a two-way ANOVA across all CORRECT trials with factors AWARENESS and CUE-VALIDITY (Fig. 3A; see Section 1 for details). This analysis revealed the same two regions, PT1 (main effect of awareness) and PT2 (main effect of cue-validity), identified previously, plus a third region also with a main effect of cue-validity, temporally coincident with PT2 (~450–550 ms), but in a higher frequency range (~60–90 Hz). All three clusters survived a randomization test for multiple comparisons (see Section 1 for details) at p < 0.02, p < 0.02, and p < 0.002, respectively. No other cluster survived a threshold lower than p < 0.15.

The finding of an attention-related response that is independent of awareness suggests that attention might act in a similar way, with or without awareness. However, the preceding TF analyses were restricted to a single topographical ROI (Fig. 2D). Differences in the action of attention with and without awareness might be revealed by differences in topography. Therefore we compared the average topographies of the low-gamma cue-validity effect (PT1, INVALID – VALID) for AWARE versus UNAWARE trials (Fig. 5A and B). Taking into account differences in latency, the spatial correlation between the AWARE and UNAWARE topographies was significant (r = 0.1826, p < 0.026). However, the amount of variance accounted for was relatively small (3.3%), so we performed an additional analysis aimed at detecting differences between the AWARE and UNAWARE topographies: For each of the 150 MEG sensors, we performed a two-way ANOVA with factors cue-validity (VALID, INVALID) and awareness (AWARE, UNAWARE). A differential effect of cue-validity depending upon level of awareness should result in a significant interaction. No cluster in the (topographical) interaction map was significant at a threshold of p < 0.10, after correcting for multiple comparisons (false discovery rate with independence assumption, FDRi), and only one sensor (RC21) was significant (p < 0.01) without correction. Hence, a relatively conservative test (spatial correlation) provides evidence of similarity, and a relatively sensitive test (multiple sensor-wise ANOVA’s) with a liberal threshold fails to reveal any difference between the low-gamma effect of spatial attention with and without awareness.

The high-gamma (56–76 Hz) cue-validity effect was not as focused in time-frequency space as its low-gamma counterpart (Fig. 5A and B), making it problematic to test for a difference in average latency between AWARE and UNAWARE trials (no significant difference was found, although there was an apparent lag of about 20 ms for UNAWARE versus AWARE). However, the topographies of the high-gamma effect, averaged over the time interval 425–525 ms, with and without awareness were significantly correlated (r = 0.21, p < 0.02). The same correlation at a later time interval
Fig. 5. Comparison of cue-validity responses with and without awareness. The cue-validity response in the low gamma range peaked approximately 50 ms later on UNAWARE trials ($p < 0.03$, bootstrap estimate of std err; compare A and B) and results of a comparison of the topographies are consistent with this difference in timing: (C) shows the average topography of the cue-validity effect (INVALID − VALID) in the low gamma range (38–48 Hz) for AWARE and UNAWARE trials, during two different time windows (“early” = 450–550 ms, “late” = 500–600 ms). The early-AWARE topography is significantly correlated with the late-UNAWARE topography, but not with the early-UNAWARE. The average time-course of the high-gamma response (56–76 Hz) for UNAWARE trials was bimodal, making it problematic to test for differences in peak latency. Both the rise time and return-to-baseline of the entire high-gamma response lagged behind by approximately 20 ms for UNAWARE versus AWARE trials, but the difference was not significant ($p < 0.15$, bootstrap estimate of std err).

(490–590 ms) was not significant ($r = 0.10$, $p < 0.25$). We also performed the same sensor-wise ANOVA as above, looking for signs of an interaction between cue-validity and awareness at any sensor. Again, after correcting for multiple comparisons (FDRi) no sensor heralded a significant interaction at a liberal threshold ($p < 0.1$). By contrast, two sensors (RP34 and ZF01) showed a significant main effect of awareness ($p < 0.05$ corrected), and one (LP32, at the center of our topographical ROI, as expected) showed a significant main effect of cue-validity ($p < 0.01$ corrected).

Previous work has highlighted the role of gamma oscillations in perceptual integration (Engel & Singer, 2001) and sensory awareness (Meador et al., 2002; Schurger et al., 2006a; Summerfield et al., 2002). Our data revealed a correlate of awareness (at PT1), independent of cue-validity, and a correlate of attention (at PT2), independent of awareness, in what appeared to be the very same frequency range. In order to more carefully examine the frequency relationship between these two responses, we used a bootstrap procedure (see Section 1) to statistically compare the peak-power frequency (PPF) for the awareness effect at the time of PT1 and the cue-validity effect at the time of PT2 (Figs. 3B and 4). The average PPF was 42 Hz for the cue-validity effect and 46 Hz for the awareness effect, and the difference between the two frequencies was not significant. Therefore a significant stimulus-induced response in the canonical gamma band (~40 Hz) seems not to be, in this patient, a sufficient condition for sensory awareness, because an effect of cue-validity, entirely independent of awareness, also manifests in this same frequency range.

3 We use the term “peak-power frequency” for simplicity. To be more precise, the variable of interest is the frequency of the peak difference between two spectra (which is a difference in spectral power). For the main effect of awareness, the difference is AWARE − UNAWARE, and for the main effect of cue-validity, the difference is INVALID − VALID (see Fig. 3).
It is usually held that attention should increase gamma oscillations (Fries et al., 2001; Fries, Schroder, Roelfsema, Singer, & Engel, 2002; Gruber et al., 1999; Muller, Gruber, & Elbert, 2000; Muller, Gruber, & Keil, 2000), so it is perhaps counter-intuitive that the effect of cue validity should manifest as INVALID > VALID, rather than the other way around (see Fig. 4). This observation, along with the relatively late timing of the effect, is consistent with it being an attention “re-orienting” response. Visual signals prime the oculomotor system in hemianopic humans (Rafal, Smith, Krantz, Cohen, & Brennan, 1990), and evidence suggests that covert orienting (and presumably re-orienting) of attention is carried out by the same neural system that drives saccades (Moore, Armstrong, & Fallah, 2003). In order to test this hypothesis we examined a time interval during which we knew GY was making a voluntary shift of attention in response to a stimulus that appeared in his intact visual field: the interval immediately following the onset of the cue. We used the same statistical analysis as for the post-target interval (described under Fig. 3 and Section 1). This analysis revealed a significant cue-validity/awareness interaction across a broad range of frequencies at approximately 180 ms post-cue (p < 0.05, corrected; Fig. 3C), that we labeled PC1 (PC = “post-cue”). The average spectrum of this interaction effect (Fig. 3D) is qualitatively similar to that of the cue-validity effect in the post-target interval (Fig. 3B): both are bimodal with a sharp peak in the low gamma range (∼42 Hz), and a second broad peak in the high gamma range (∼60–90 Hz).

In order to quantitatively compare these spectra, we performed a statistical test on the trial-by-trial difference in energy between the low (38–58 Hz) versus high (60–90 Hz) gamma range, comparing the interaction effect at PC1 (∼330 to ∼290 ms), the awareness effect at PT1 (300–400 ms), and the cue-validity effect at PT2 (425–525 ms) (Fig. 6). On the basis of this metric, PC1 and PT2 were indistinguishable from each other and from zero (p > 0.35), while PT1 was significantly different from both PC1 (p < 0.04) and PT2 (p < 0.02).

Finally, a third test was performed similar to the one we used to test for topographical differences between the effect of attention with and without awareness during the post-target interval. Time-frequency data were averaged over the range 38–90 Hz, during two different time windows, ∼300 to ∼290 ms (post-cue interaction effect) and 425–525 ms (post-target cue-validity effect). These data (two measurements for each trial) were combined and grouped using two dummy variables. One coded for “time” (post-cue or post-target) and the other coded for whether this datum belonged on the left- or right-hand side of the relevant subtraction corresponding to the effect that was observed at that time: Data belonging to the post-target cue-validity response were coded with a 1 if from an INVALID-CUE trial, and 0 if from a VALID-CUE trial (since the relevant subtraction was INVALID – VALID). Data belonging to the post-cue interaction effect were coded with a 1 if from a VALID/UNAWARE or INVALID/AWARE trial, and a 0 otherwise (the relevant subtraction for an interaction effect is between the two diagonals of the design matrix, which in this case is [VALID/UNAWARE + INVALID/AWARE] – [VALID/AWARE + INVALID/UNAWARE]). If the effect (coded by the second dummy variable) is different depending upon the time (post-cue or post-target, coded by the first dummy variable), then this should appear as an interaction effect in an analysis of variance. A separate ANOVA was performed on this data for each of the 150 MEG sensors, and the resulting interaction map was inspected. No significant interaction effect was found at any central, posterior, or temporal sensor at a sensor-wise threshold of p < 0.05 (uncorrected). Two right-frontal regions showed signs of an interaction effect: one centered at sensor RFS1 (p < 0.0001, uncorrected), and a nearby region over right fronto-temporal cortex, centered at sensor RT11 (p < 0.05 uncorrected) (see Fig. 7).

Taken together, these analyses reveal a similar response pattern in the post-cue endogenous orienting response and post-target cue-validity response, consistent with the latter reflecting a true (but perhaps involuntary) re-orienting of attention. This is particularly relevant to theories that argue for different mechanisms for voluntary and involuntary shifts of attention (Prinzmetal, McCool, & Park, 2005). Given that the cue (central arrow positioned in GY’s region of macular sparing) was consciously seen by GY, it is interesting that the spectral properties of its effect were similar to those of the post-target cue-validity effect in response to stimuli not consciously seen by GY (the targets appearing in his blind hemifield).

3. Discussion

Although significantly better than chance, GY’s accuracy was not as high as has been the case in previous reports (Kenrtridge et al., 2004; Weiskrantz et al., 1995; Zeki & Ffytche, 1998). It was, however, consistent with results of a previous experiment of ours using the same stimuli and task (Schurger et al., 2006a). GY’s guessing accuracy on any blind-field task is a function of stimulus and task parameters. A solid bar, differing in overall luminance from the background, and oriented either horizontally or vertically can yield an accuracy of ∼80% correct (Kentridge et al., 2004). The stimuli in our experiment, on the other hand, were, on average, isoluminant with the background. The random checkerboard pattern made the orientation information less salient (it could not be inferred locally, as in the case of a solid bar). Also, the orientations we used were

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4 The use of the term “orienting” here should not be taken to imply a “top-down” or voluntary process, as is often the case. If the appearance of a stimulus in an unexpected location causes the biasing effect of attention to shift to this new location, then we can say that attention has been “re-oriented,” regardless of whether the shift was driven by “bottom-up” or “top-down” forces.

5 “Awareness” here refers to GY’s report of a “feeling that something happened” in his blind hemifield in response to the subsequent target stimulus. The central cue was always visible to GY, as it was positioned within his region of macular sparing.
oblique, which are less discriminable than horizontal versus vertical. One or a combination of these three factors likely explains the difficulty of the task.

The fact that GY’s accuracy was less than 60% correct and no different on valid- than on invalid-cue trials might raise concern, however, since a significant proportion of his correct trials may have been correct by chance – just lucky guesses, not due to stimulus information – and only very few trials would have contributed to his above-chance accuracy. The fact that we find significant effects in both the reaction-time and MEG data, is perhaps an adequate answer, but not the only answer: It is perfectly reasonable for attention to vary with the cue, even in the absence of any effect on accuracy (and we provide evidence that it does). Attention may act to enhance a selected sensory signal, even if that enhancement is insufficient to improve accuracy—and it is the enhancement itself that is at issue. Therefore, even if GY was utterly at chance, we might still have seen measurable effects of attention. In fact, the relative difficulty of the task might have made the neural effects of attention even more pronounced.

One could argue that a significant modulation in gamma-band activity independent of awareness in GY (i.e. the cue-validity response at PT2) may not generalize to the uninjured brain. Perhaps the observed cue-validity effect in the gamma frequency range is “cut off” from awareness in this patient owing to his V1 lesion. But then it becomes difficult to explain why there is a significant effect of awareness in the very same frequency range, in response to the same stimuli, just 100 ms prior. Also, it seems unlikely that damage to V1 would fundamentally change the mechanism by which perceptual contents “reach” awareness, regardless of what those contents may be (e.g. “a rectangular checkerboard” or “a feeling that something happened”). Nevertheless, further studies involving normal subjects will have to be carried out in order to determine whether or not this particular result generalizes to the healthy population. As mentioned previously, the behavioral effect being investigated in the present study has been demonstrated in normal subjects (Kentridge et al., 2007; Sumner et al., 2006).

Although it may seem so, our study does not address the possibility of awareness without attention. This is difficult to do when awareness is indexed by subjective report, because the act of reporting may necessarily draw attention to the information being reported on. But then how are we to explain the main effect of awareness at PT1? Bear in mind that awareness independent of cue-validity is not identical to awareness independent of attentional state. The interaction effect in response to the cue (Fig. 3C) suggests that awareness was not independent of pre-target attentional state. Also, GY’s awareness was of an event (“something happened”) not of an object or a location. Awareness without attention in this case would imply a sensation “that something happened” without a bias in information processing toward the neural activity underlying that sensation. Our design does not address this possibility. Our data reveal evidence that the immediate neurodynamic effects of attention (capture, shift, and bias) can occur, without awareness of the visual stimulus driving those effects, or of the effects themselves. Our data are not consistent with awareness operating independent of attentional state.

It is commonly held that the “bias in neural information processing” associated with attention has two possible proximal causes in the brain—“top-down” and “bottom-up”. Our results reveal an intriguing similarity in neural dynamics between the unconscious exogenous re-orienting (or “capture”) of attention and the conscious endogenous orienting of attention, suggesting that the two may share a common mechanism (Fig. 3B and D, and associated analyses). Future studies should examine whether or not the same neurodynamic effects (i.e. the biasing mechanism) might be similarly engaged in either case.

In summary, our paradigm involved the voluntary orienting of attention in response to a consciously seen endogenous cue (central arrow). We examined the effects of attention (operationally defined in terms of cue-validity) within the blind hemifield of a hemianopic patient, in response to targets that were not consciously seen, but which sometimes provoked a sensation “that something happened”. We identified distinct and independent neural responses (to unseen targets) in the gamma frequency range associated with awareness and attention-without-awareness. Our results suggest that the exogenous capture/reorienting of attention manifests in a similar fashion with and without awareness, and that processes independent of sensory awareness can produce significant modulations in the gamma frequency range. We also reveal an apparent spectral and topographic similarity between exogenous and endogenous covert orienting processes that merits further study.

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6 With 0° and 90° orientations the distance between the leftmost corner of the stimulus and the vertical mid-line is confounded with orientation, so we chose to use oblique orientations.
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