Neural Bases of the Interactions between Spatial Attention and Conscious Perception

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Recent behavioral observations suggest that some forms of attentional orienting have the ability to modulate access to perceptual consciousness. However, the neural structures subserving such processes remain uncertain. We used functional magnetic resonance imaging during a visual discrimination task with near-threshold targets preceded by peripheral cues to identify the neural bases of the interactions between spatial attention and conscious visual perception. During the cue–target period critical for spatial orienting, regions within a frontoparietal network, including nodes of the dorsal attentional system, were more strongly engaged for consciously perceived targets than for nonperceived targets at attended locations. Moreover, activation increased for “unseen” targets in more ventral frontoparietal regions, known to be part of a system involved in attentional reorienting. Functional connectivity analyses revealed tighter coupling between frontoparietal nodes for valid cues leading to “seen” reports and for invalid cues leading to unseen reports. We conclude that spatial orienting to peripheral stimuli, subserved by frontoparietal attentional networks, plays a major role in determining the content of our conscious experience.

Keywords: conscious perception, dorsal and ventral attentional networks, fMRI, functional connectivity, spatial attention

Introduction

We can only report a small fraction of all the information reaching our senses. Spatial attention and its underlying neural circuitry have been proposed as the selection mechanism that filters the access of visual information to consciousness (Posner 1994; Dehaene and Naccache 2001; Dehaene et al. 2006; Bartolomeo 2008). However, recent evidence has challenged this hypothesis, by showing that under some situations endogenous or top-down spatial attention may not be crucial for conscious perception (Kentridge et al. 1999, 2004, 2008; Koch and Tsuchiya 2007; Wyart and Tallon-Baudry 2008). In contrast, exogenously triggered spatial attention does seem to be one of the crucial antecedents of our conscious experience (Chica et al. 2010, forthcoming; Chica, Lasaponara, et al. 2011; Chica and Bartolomeo 2012). Peripheral cues are effective in increasing subjective reports of near-threshold targets at the attended location, both when cues are spatially predictive of target appearance and when they are not. However, only spatially predictive peripheral cues (thus provided of an exogenous and an endogenous component) seem to efficiently modulate perceptual sensitivity (d’) as compared with purely endogenous or exogenous spatial signals (Chica, Lasaponara, et al. 2011). This result indicates that once attention has been exogenously triggered by a salient peripheral cue, endogenous maintenance of attention at the cued location increases perceptual sensitivity to consciously perceive near-threshold stimulation. Therefore, the sequence of exogenous attentional capture and endogenous maintenance of attention at the same location sets up the best conditions for modulating conscious perception.

The brain networks related to attentional orienting have been thoroughly explored by means of neuroimaging tools in the last decade (Mesulam 1999; Nobre 2004; Reynolds and Chelazzi 2004; Natale et al. 2009). Based on such evidence, current neurocognitive models (Cortebetta and Shulman 2002; Corbetta et al. 2008) depict a bilateral dorsal frontoparietal network, including the intraparietal sulcus (IPS) and the frontal eye fields (FEFs). This network is proposed to be involved in the orienting of spatial attention. It enables the selection of sensory stimuli based on internal goals or expectations (goal-driven attention) and links them to appropriate motor responses. The dorsal network is preactivated by the expectation of seeing an object at a particular location or with certain features, by the preparation of a specific response, or by the short-term memory of a visual scene. A more ventral frontoparietal network, lateralized to the right hemisphere, and including the middle and inferior frontal gyri (MFG and IFG) and the temporoparietal junction (TPJ), would be responsible for reorienting attention to task-relevant events occurring at unexpected locations. This network is activated when relevant targets (or distractors sharing a task-relevant feature with the target; Serences and Yantis 2007) are presented at unattended or invalid locations. More recently, the right TPJ has also been causally implicated in the orienting of exogenous, but not endogenous, spatial attention (Chica, Bartolomeo, et al. 2011a). Transcranial magnetic stimulation (TMS) was used to causally interfere with right TPJ activity during the orienting of exogenous or endogenous attention, before the target was presented. TMS over this region of the ventral attentional network interfered with late components of exogenous orienting such as inhibition of return, but it had no effect on endogenous orienting processes, indicating that right TPJ is not only important for reorienting attention to task-relevant targets (as proposed by Corbetta and colleagues), but it also plays a causal role in the exogenous orienting of spatial attention.

In contrast, the neural structures implicated in the access to conscious perception remain more elusive and still under debate.
(Tong 2003). Neither activity in primary visual cortices (Rees et al. 2002) nor the recruitment of ventral areas of the lateral temporal cortex seems sufficient to elicit a conscious state by themselves (Rees et al. 2000; Goebel et al. 2001; Vuilleumier et al. 2001). On the other hand, recent studies have stressed that the simultaneous engagement of parietal and prefrontal regions seems to be necessary to achieve consciousness (Beck et al. 2001; Thiebaut de Schotten et al. 2005; for a review, see Dehaene and Changeux 2011). This evidence suggests that attentional networks might indeed provide a neural substrate for the emergence of perceptual consciousness (Chica, Bartolomeo, et al. 2011; Chica, Lasaponara, et al. 2011; Chica et al. forthcoming), but this hypothesis awaits confirmation. Furthermore, it remains unclear if the engagement of frontoparietal networks in conscious reports observed in previous studies is a key feature of conscious processing, or if it is rather related to further attentional demands generated by consciously processed versus nonconsciously processed stimuli.

To determine the neural bases of the interactions between spatial attention and conscious perception, we orthogonally manipulated these variables while using event-related functional magnetic resonance imaging (fMRI). Our behavioral task (see Chica et al. 2010; Chica, Lasaponara, et al. 2011) allowed us to establish how different attentional orienting states may affect the conscious detection rates of subsequent targets. Contrary to numerous previous studies that compared brain activations for consciously "seen" versus "unseen" targets, we focused our analyses on the attentional orienting period and determined whether different attentional orienting states (occurring before target presentation) correlated or not with the subsequent conscious perception of near-threshold targets. Based on previous event-related potentials (ERP) results (Chica et al. 2010), we predicted that during the orienting of spatial attention, the activation of regions within the dorsal frontoparietal network would correlate with increased probability of conscious reports at the attended location. We also expected that conscious reports at attended locations would be associated with increased coupling between frontoparietal regions as assessed by functional connectivity analysis.

Materials and Methods

Participants

Eighteen right-handed voluntaries from Paris, France, took part in the experiment (15 females, mean age 25 years, standard deviation [SD] = 4). They had no neurological or psychiatric conditions and followed all the safety requirements to undergo MRI scanning sessions. All of them were naive to the purpose of the experiment, reported to have normal vision, and were not told the exact amount of trials in which the cue predicted the target's location. They were encouraged to take this information into account in order to respond more accurately. There was a single interstimulus interval (ISI between the onset of the cue and that of the target) of 1200 ms. The target was presented for 32 ms at either the left or the right marker but never at the central location. Participants were asked to provide 2 responses to each target consecutively, by making key presses on a keyboard, for the behavioral experiment and a 2 horizontally aligned button fiber optic box for the fMRI experiment. First, they were required to discriminate the orientation of the gratings (objective task) by pressing, with their right hand, a left situated key if the target was oriented to the left and a right situated key if the target was oriented to the right. Participants were encouraged to respond to every trial as fast and as accurately as possible within 2000 ms after target onset. Even if they did not see the stimulus, they were encouraged to try to guess their response. Second, they saw the question: "Did you see the stimulus?" (subjective task) and the French words for "yes" and "no" situated below the question. Participants were encouraged to take their time to respond correctly by using the same response keys and to report having seen the stimulus only when they felt completely confident about it. The response to the subjective task had to be given within 2000 ms. No target was presented on 14% of the trials. Also for these target-absent trials, participants were required to give the objective response within 2000 ms and to report that no target was seen in the subjective response.

Stimuli

E-prime software was used to control the presentation of stimuli, timing operations, and data collection (Schneider et al. 2002). During the behavioral experiment, stimuli were presented in an eye tracker screen (Tobii Technology AB, Danderyd, Sweden, 17" wide, 1024 × 768, 16 ms refresh rate; temporal and spatial resolution of 50 Hz and 0.25°, respectively) against a gray background. During scanning, images were projected to the head of the bore of the scanner via a display projector (Epson EMP-8300, 1024 × 768, 60 Hz) and viewed with a mirror attached to the head coil. Three black boxes (6° height × 5.5° width) were displayed, one in the center of the display, and the other 2 centered 8.5° to the left and right. The fixation point consisted of a black plus sign (0.5° × 0.5°) presented on the central box. The cue was a square surrounding either the left or the right box (6.7° height × 6.1° width). The target was a grating with a spatial frequency of 3 cycles per degree of visual angle and a diameter of 5.5°. It was tilted by 5° to either the left or the right. There were 25 target stimuli, in which target contrast varied linearly between values of 0.02 and 0.09 Michelson contrast. Target contrast was manipulated before the experimental trials in order to adjust the percentage of consciously perceived targets to ~50%. This titration was done while participants practiced the main task (see Procedure) and was performed independently for valid and invalid trials. All participants started with a high contrast stimulus (Michelson contrast = 0.05), which was well above the threshold of conscious perception. Every 8 trials, target contrast was automatically adjusted using a "one-up-one-down" procedure, until participants perceived ~50% of targets for each condition (valid and invalid trials). That is, if the percentage of correct detection rates was above 55% of the trials, gratings at the immediately following lower contrast level were used for the next block. Inversely, if the percentage of correct detection rates was below 45% of the trials, gratings at the immediately following higher contrast level were used for the next block. The experimental trials started when participants felt comfortable with the task, and performance converged at a target contrast yielding ~50% seen targets for valid and for invalid trials. This titration procedure continued during the whole experiment (this time adjusting target contrast every 14 trials) to prevent factors such as practice or fatigue from influencing conscious perception.

Procedure

All participants performed first the behavioral task outside the scanner. Figure 1 displays the sequence and timing of a trial. Every trial started with an initial fixation period (jitter fixation), with a varied duration corresponding to the MR frames (i.e., ~2-10 s), jittered in increments of 2 s. This fixation period was further extended for 500 ms. The cue was then presented for 300 ms and consisted of a square surrounding one of the peripheral markers, which was predictive about the spatial location of the target on 60% of the target-present trials. Participants were informed about the predictive value of the cue, although they were not told the exact amount of trials in which the cue predicted the target’s location. They were encouraged to take this information into account in order to respond more accurately. There was a single interstimulus interval (ISI between the onset of the cue and that of the target) of 1200 ms. The target was presented for 32 ms at either the left or the right marker but never at the central location. Participants were asked to provide 2 responses to each target consecutively, by making key presses on a keyboard, for the behavioral experiment and a 2 horizontally aligned button fiber optic box for the fMRI experiment. First, they were required to discriminate the orientation of the gratings (objective task) by pressing, with their right hand, a left situated key if the target was oriented to the left and a right situated key if the target was oriented to the right. Participants were encouraged to respond to every trial as fast and as accurately as possible within 2000 ms after target onset. Even if they did not see the stimulus, they were encouraged to try to guess their response. Second, they saw the question: "Did you see the stimulus?" (subjective task) and the French words for "yes" and "no" situated below the question. Participants were encouraged to take their time to respond correctly by using the same response keys and to report having seen the stimulus only when they felt completely confident about it. The response to the subjective task had to be given within 2000 ms. No target was presented on 14% of the trials. Also for these target-absent trials, participants were required to give the objective response within 2000 ms and to report that no target was seen in the subjective response.
The experiment consisted of a total of 280 trials presented in 5 functional scans, 40 of which were target-absent trials. Each of these 5 functional scans lasted 7 min. Valid trials were twice more likely than invalid trials. Valid, invalid, and target-absent trials were presented in a pseudorandomized order during scanning. The jitter fixation and the order of trial types within each scan were determined with an optimal sequencing program designed to maximize the efficiency of recovery of the blood oxygen level-dependent (BOLD) response (Optseq II; Dale 1999). The jitter fixation periods were interleaved with the experimental trials as determined by the optimization program.

**fMRI Data Acquisition**

Whole-brain fMRI was conducted on a 3-T Siemens TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) at the CENIR MRI center (Salpêtrière Hospital in Paris) using a standard whole-head coil. Functional images were acquired using a gradient-echo echo-planar pulse sequence (repetition time = 2000 ms, echo time = 25 ms, 34 axial 2.5 x 2.5 x 3-mm slices, no interslice gap, flip angle = 75°, field of view = 220 mm, 220 volumes acquired per run). Prior to each functional scan, 4 volumes were discarded to allow for $T_1$-equilibration effects. High-resolution $T_1$-weighted anatomical images were also collected. To limit head movement, the area between participants’ heads and the head coil was padded with foam, and participants were asked to remain as still as possible. Snugly fitting headphones dampened background scanner noise and enabled communication with experimenters while in the scanner.

**Behavioral Data Analysis**

Response times (RTs) faster than 150 ms or slower than 1500 ms were eliminated from the RT analyses (0.20% of the trials in the behavioral experiment and 0.12% in the fMRI experiment). Anticipatory responses (0.46% of the trials in the behavioral experiment and 0.09% in the fMRI experiment) were also excluded. For the behavioral experiment, trials with eye movements larger than 2° away from fixation were excluded from further analyses (mean = 3.21%, SD = 2.89). The low rate of eye movements in our participants, together with the fact that those participants with a high eye movement rate were excluded from the study (see Participants) ensured that uncontrolled eye movements did not contaminate our fMRI data.

We analyzed the RT of the objective task and target contrast values for valid and invalid trials by performing 2 repeated-measures analysis of variance (ANOVA) with the factors of Session (behavioral and fMRI), Awareness (seen and unseen trials), and Validity (valid and invalid trials). Accuracy on the objective task was also analyzed with an ANOVA with identical variables. Only significant interactions including Validity are reported in the Results.

**fMRI Data Analysis**

Standard preprocessing routines and analyses were conducted in Statistical Parametric Mapping 5 (SPM5) (Welcome Department of Cognitive Neurology, London). Images were corrected for slice timing acquisition and were realigned and unwarped to correct for movement artifacts. High-resolution anatomical $T_1$ images were co-registered with the realigned functional images to enable anatomical localization of the activations. Functional images were spatially smoothed using 4 mm$^3$ Gaussian kernel. We then used the motion adjustment and artifact repair tools of ArtRepair Software (Stanford Psychiatry Neuroimaging Laboratory) to further correct for motion artifacts. Structural and functional images were spatially normalized into a standardized...
anatomical framework using the default echo-planar imaging template provided by SPM. During normalization, the volumes were sampled to 3-mm$^3$ voxels. Then, functional volumes were spatially smoothed with a 7 mm$^3$ full-width at half-maximum isotropic Gaussian kernel. Finally, time series were temporally filtered to eliminate contamination from slow drift of signals (high-pass filter: 128 s). Statistical analyses were performed on individual participants’ data using the general linear model (GLM). fMRI time series data were modeled by a series of events convolved with a canonical hemodynamic response function (HRF). The 3 phases of each fMRI trial (i.e., Cue, Target, and Subjective Task) were modeled separately. Valid and invalid fMRI trials were sorted as seen or unseen (i.e., Awareness) according to participants’ responses on the subjective task. These events were convolved with an HRF function in SPM 5. Target-absent trials were modeled separately and were excluded from the analyses. The resulting functions were used as covariates in a GLM, along with a basic set of cosine functions that high-pass filtered the data and a covariate for session effects. The least-squares parameter estimates of the height of the best-fitting canonical HRF for each condition were used in pairwise contrasts. Contrast images, computed on a participant-by-participant basis, were submitted to group analyses. At the group level, whole-brain contrasts between conditions were computed by performing one-tailed $t$-tests on these images, treating participants as a random effect.

Whole-brain maps involving all participants were thresholded at $P < 0.001$ corrected (false discovery rate [FDR] correction) for activation contrasts with jitter fixation epochs. Activations were considered significant if they contained at least 5 contiguous voxels. Brain coordinates are reported in Montreal Neurological Institute (MNI) atlas space (Cocosco et al. 1997). Region-of-interest (ROI) analyses were performed with the MARSBAR toolbox for use with SPM 5 (Brett et al. 2002). ROIs consisted of significantly active voxels for contrasts identified from Cue > Jitter Fixation whole-brain comparisons across all participants within specific MARSBAR anatomical ROIs. The center of mass of each ROI is reported in figures. For each region, we performed a repeated-measures ANOVA on the parameter estimates value, with the factors of Validity (valid vs. invalid trials) and Awareness (seen vs. unseen reports). $t$-tests were used to compare parameter estimate of each validity condition for seen or unseen targets. Only regions showing significant modulations of attention in conscious perception ($P < 0.05$) are shown in Figure 3.

We also performed a time course analysis of 2 ROIs (right IFG and supramarginal gyrus, SMG; see Results), which in previous studies have consistently been found to be more activated when suprathreshold targets are presented at invalid versus valid locations (for a review, see Corbetta et al. 2008). MNI coordinates for both brain regions were selected on the basis of local maxima from a previous study (Shulman et al. 2009), which explored stimulus-driven reorienting and expectation in ventral and dorsal frontotemporal networks (right IFG: $x = 48, y = 14, z = 12$ and right SMG: $x = 52, y = -48, z = 32$). BOLD activity time series, averaged across all voxels in a ROI, were extracted for each functional run. Mean time courses for each condition were then constructed by averaging together appropriate trial time courses, which were defined as 12 s windows of activity after each trial onset. These condition-averaged time courses were then averaged across functional sessions and across participants. These time course values were submitted to a repeated-measures ANOVA with the factors of Region (right IFG and right SMG), Validity, Awareness, and Time (with 6 time points every 2 s after cue onset). In order to explore whether the observed effects could be explained by differences in RTs between valid and invalid conditions or by RT differences between seen and unseen responses, we also calculated an index of validity (RT on valid minus RT on invalid trials) and an index of RTs to the subjective task (RT on seen minus RT on unseen trials) and introduced them as covariates in the ANOVA.

Finally, we assessed functional connectivity between brain regions via the beta correlation method (Rissman et al. 2004), implemented on SPM 5 and custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition, and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. We calculated the beta correlation values across all participants, extracting the average correlation strength for each pair of ROIs for each voxel. These beta values were submitted to repeated-measures ANOVAs with the factors of Validity (valid vs. invalid trials) and Awareness (seen vs. unseen reports).

Results

Behavioral Results

Performance levels on the line orientation task (objective task) were used to determine whether participants were using the spatial information provided by the cue to effectively orient attention toward the cued location. A repeated-measures ANOVA with the factors of Session (behavioral and fMRI experiments), cue Validity (valid and invalid trials; i.e., with cues signaling or not the location of the upcoming target), and Awareness (seen and unseen targets; i.e., reported by participants as being or not consciously detected) revealed no main effect of validity, $F < 1$, but a reliable interaction between Awareness and Validity, $F_{1,17} = 5.36, P = 0.035$. Seen targets elicited faster RTs on valid than on invalid trials, $F_{1,17} = 8.05, P = 0.011$, whereas there was no reliable RT difference for unseen targets, $F_{1,17} = 1.23, P = 0.282$ (Fig. 2A). This is consistent with previous observations (see Chica, Lasaponara, et al. 2011, Experiment 1; Hsu et al. 2011), demonstrating that endogenous attention shortens RTs and/or improves discrimination accuracy for validly cued versus invalidly cued targets, but only when the stimuli are consciously perceived. In the analysis of mean accuracy for the objective task, no effects of validity were observed. There was an expected main effect of Awareness, $F_{1,17} = 195.69, P < 0.001$, showing that responses were at

Figure 2. (A) Mean RT in the objective task, for each condition of Validity and Awareness. (B) Mean target contrast values used to achieve 50% “seen” and “unseen” targets presented at valid and invalid locations.
chance for unseen reports ($M = 47\%$) and well above chance for seen reports ($M = 93\%$).

Our manipulation of the percentage of seen targets for valid and invalid trials was effective in producing the desired amount of seen targets per condition. Participants reported to have seen 50\% of the targets in the valid condition and 49\% in the invalid condition (these values did not differ statistically, $F_{1,17} = 1.46, P = 0.244$). In agreement with previous findings (see, e.g., Pestilli and Carrasco 2005; Liu et al. 2009), spatial orienting driven by the cues also improved target conscious detection rates. Target contrast fulfilling the fixed threshold of 50\% correct conscious detection (subjective task) proved lower for valid than for invalid trials, and this difference was larger for unseen targets than for seen targets (interaction between Validity and Awareness for target contrast values, $F_{1,17} = 43.88, P < 0.001$; Fig. 2B).

It should be noted that differences in target contrast values for valid and invalid trials might have affected RT results for the objective task. This might confound our interpretation because participants were expected to be faster to respond to high-contrast than to low-contrast stimuli. However, RTs were faster for consciously detected (seen) validly cued targets than for invalidly cued targets, even though target contrast was lower for the valid than for the invalid condition. This indicates that our RT result in the objective task reflects a genuine effect of attention, which accelerated target processing at the attended location.

**fMRI Results**

A whole-brain contrast ($P < 0.001$, FDR corrected for multiple comparisons) between the "Cue" versus the jitter fixation epochs revealed activations in brain regions typically involved in attentional orienting (Fig. 3 and Table 1), consistent with previous findings (Nobre 2001; Yantis et al. 2002; Corbetta et al. 2008; Natale et al. 2009). More precisely, increased activations occurred bilaterally in the superior parietal lobule (SPL) and extended to the right inferior parietal lobule (IPL) and the right angular gyrus (ANG). Frontal activations were observed bilaterally in the FEFs and the insula, extending into the left MFG and the right IFG. Temporoooccipital (TO) activations were present in the bilateral middle TO gyrus.

ROI analyses were conducted for the areas showing a significant modulation in the prior contrast and known to be part of the dorsal or the ventral frontoparietal attentional networks (Corbetta and Shulman 2002). The examination of the pattern of activations within these ROIs allowed us to test specific hypotheses about the activation of these regions during the orienting of attention for conscious and unconscious reports. For each region, we performed a repeated-measures ANOVA with Validity (valid and invalid trials) and Awareness (seen and unseen reports) as factors. $t$-tests were used to compare fMRI parameter estimates of each validity condition for targets reported as seen or unseen.

The bilateral TO and SPL, the right ANG, and the IPL in the left hemisphere showed a main effect of Awareness, which was independent of cue validity. More precisely, those regions were more strongly engaged for seen than for unseen reports, after both valid and invalid cues (see Fig. 3 and Table 2). In contrast, the left FEF and the right IPL showed a significant interaction between Validity and Awareness, being more strongly engaged for trials involving targets reported as seen than for unseen targets, but this time only when the cue correctly oriented attention toward the target location.

![Figure 3](https://academic.oup.com/cercor/article-abstract/23/6/1269/425706)
The observed patterns of dependence or independence from cue validity suggest the implication of 2 separate networks in supporting specific and differentiated roles during attentional orienting. On the one hand, a spatial attention-indepen- dent network, involving the bilateral TO and SPL, the right ANG, and the left IPL, is likely to support a general preparatory state for perception of subsequent targets, which correlates with conscious reports. On the other hand, a spatial attention-dependent network, involving the left FEF and the right IPL, seems to be encoding for the attended visual field; this network would facilitate the conscious detection of targets displayed at the cued location.

Previous studies have consistently demonstrated that right hemisphere structures such as the IFG and SMG are part of the ventral attentional network, important for reorienting attention to task-relevant events (Corbetta et al. 2008). We thus hypothesized that activity in this ventral attentional network may have triggered an attention reorienting response (Shulman et al. 2009) whenever participants did not perceive any target and consequently reoriented their attention elsewhere. A time course analysis (see Materials and Methods) was used to test this prediction. We performed an ANOVA with the factors of Region (right IFG and right SMG), Validity, Awareness, and Time (with 6 time points every 2 s after cue appearance) as between-participant factors. The RT indexes of validity and subjective task responses (see Materials and Methods, fMRI Data Analysis) were introduced as covariates in the ANOVA. Results demonstrated a significant interaction between those 4 main factors, $F_{3,35} = 3.08, P = 0.013$. As it can be observed in Figure 4, for both regions, responses were enhanced for unseen reports as compared with seen reports. For right IFG, this difference started 2 s after target onset and was sustained until 6 s post-target onset. For right SMG, the differential response for unseen as compared with seen reports started later, 6 s after target onset, and lasted until 8 s following target onset. Moreover, for right SMG, responses were enhanced for invalid as compared with valid seen trials, 2 and 4 s post-target onset. No significant differences between responses for valid and invalid trials were observed for unseen trials in right SMG (all $P > 0.05$). For right IFG, responses for valid and invalid trials did not statistically differ, neither for seen nor for unseen reports (all $P > 0.05$). Finally, the interaction between Region, Validity, Awareness, and Time was not affected by any of the 2 covariates indexes (all $P > 0.05$). This suggests that these results cannot be explained by differences in RTs between valid and invalid trials or between seen and unseen trials.

Additional analyses demonstrated that both seen and unseen stimuli elicited similar BOLD responses in the inferior occipital lobe in a period up to 6 s after target onset and that the response to unseen stimuli was larger between 8 and 10 s after onset, clearly demonstrating that unseen stimuli are activating early sensory areas (A general concern with the use of near-threshold stimuli is the fate of unreported stimuli, since ambiguity remains on whether unreported stimuli are having any impact in the brain or, alternatively, they are just not being processed at all. Nonetheless, our previous ERP data (Chica et al. 2010) strongly suggest that whereas evoked signals elicited by both seen and unseen targets were similar until~300 ms poststimulus onset, only seen targets elicited a P300 component distributed throughout frontoparietal electrodes [see also Sergent et al. 2005]. This suggests that visual processing of seen and unseen stimuli might be similar up to reaching extrastriate visual areas. As a consequence, in our paradigm, unseen targets were indeed visually computed at early stages of processing. In order to explore whether unseen stimuli were producing measurable neural effects in our current fMRI experiment, we created an anatomical ROI in the inferior occipital lobe. Based on recent experimental data [for a review, see Dehaene and Changeux 2011], we hypothesized that responses in this early perceptual region should be similar for seen and unseen targets. BOLD activity time series, averaged across all voxels in the occipital ROI, were extracted for each functional run. Mean time courses for each condition were then constructed by averaging together appropriate trial time courses, which were defined as 12 s windows of activity after each trial onset. These condition-averaged time courses were then averaged across functional sessions and across participants. These time course values were submitted to a repeated-measures ANOVA with the factors of Validity, Awareness, and Time [with 6 time points every 2 s
after cue onset]. The analysis demonstrated a significant interaction between Awareness and Time, $F_{8,85} = 8.33, P < 0.001$. Bonferroni post hoc tests demonstrated that seen responses were statistically similar to unseen responses until 6 s after target onset [all $P_s > 0.99$]. In the last 2 time bins (8 and 10 s after target onset), responses in the inferior occipital region were enhanced for unseen targets as compared with seen targets. This result clearly indicates that unseen stimuli were being processed in a similar way to seen stimuli in primary visual areas. The enhanced response for unseen as compared with seen stimuli at later time points might be related to responses in the ventral attentional network [right SMG and IFG], which also showed enhanced responses for unseen as compared with seen targets, and which has been recently shown to be coupled with visual occipital areas when reorienting is required [Indovina and Macaluso 2004]. Although speculative, this possibility could be explored in future research.

**Functional Connectivity Analysis**

To further examine the interactions between spatial attention and conscious perception networks, we conducted pairwise functional connectivity analyses, including the functional ROIs examined during the orienting of attention. We extracted the average beta correlation strength values for each possible pair of ROIs in each participant. These values were submitted to 2 separate repeated-measures ANOVAs with the factors of Validity and Awareness (Table 3).

A frontoparietal network involving the bilateral SPL and IPL (also including the right ANG), the left FEF and the right IFG, showed a significant interaction between Validity and Awareness (see Table 4). All these regions demonstrated a tighter coupling for seen reports than for unseen reports when the cues validly signaled the target location, and lower coupling strength for seen than for unseen reports when cues were spatially invalid. Hence, the regional coupling shown in Figure 5 is consistent with an effective orienting of spatial attention toward the cued location (Siegel et al. 2008). In other words, when cues were spatially valid, a stronger coupling was associated with subjective reports of targets as being seen; by contrast, when cues were invalid, a stronger coupling was associated with subjective reports of targets as being unseen. Table 4 and Figure 5 show that correlation values were higher
for seen than unseen targets in validly cued trials, while the effect reversed for invalidly cued trials. These results remained highly consistent for all the brain regions showing an interaction between Validity and Awareness. The left FEF and the right IPL were coupled, consistent with the ROI analyses presented above, showing an interaction between Validity and Awareness for these 2 regions.

Our results suggest that frontoparietal interactions are not only relevant for the conscious perception of near-threshold targets, as proposed by recent models (Dehaene and Naccache 2001; Dehaene et al. 2006; Lamme 2006); they also play a crucial role during attentional orienting, before target presentation, facilitating access to consciousness for attended targets.

Discussion

We used fMRI to unveil the neural correlates guiding the interactions between spatial attention and the conscious perception of near-threshold targets. Our main analyses focused on the processing of the spatial cue and the attentional orienting operations, which according to prior studies should be determinant for the subsequent access to consciousness (Chica et al. 2010, forthcoming; Chica, Lasaponara, et al. 2011; Chica and Bartolomeo 2012).

Spatial Attention–Independent Network

Our results revealed the functional correlates of 2 brain networks with particular bearing on visual consciousness. A corticocortical network (bilateral TO and SPL, the right ANG, and the left IPL) showed stronger activation for trials in which targets were reported as seen than unseen, independent of cue validity. This system could underlie a general pretarget onset preparatory state. Hence, its activation patterns are not influenced by cue-driven spatial orienting in space per se, while still contributing to facilitating the conscious access to near-threshold visual targets.

Forms of nonspatial pretarget preparation include attentional orientation to the time of target onset (temporal attention) and phasic alerting. Both may have contributed to the present results. The temporal attention account is consistent with fMRI evidence of substantial overlap between regions involved in orienting attention in time and in space.

<table>
<thead>
<tr>
<th>Valid</th>
<th>Invalid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seen</td>
<td>Unseen</td>
</tr>
<tr>
<td>L FEF-R IPL</td>
<td>0.10</td>
</tr>
<tr>
<td>R IFG-R ANG</td>
<td>0.19</td>
</tr>
<tr>
<td>R ANG-R SPL</td>
<td>0.51</td>
</tr>
<tr>
<td>L IPL-R SPL</td>
<td>0.36</td>
</tr>
<tr>
<td>R IPL-L SPL</td>
<td>0.11</td>
</tr>
<tr>
<td>R IPL-R SPL</td>
<td>0.35</td>
</tr>
</tbody>
</table>

Table 4. Beta correlation values for each experimental condition, for each pair of regions showing a significant interaction between Validity and Awareness (see also Fig. 5).
(Coull 2004; Nobre et al. 2007), as those emerging from our analysis. In support of the phasic alerting hypothesis, recent data from our laboratory suggest that conscious perception of near-threshold visual targets can be enhanced by nonspatially localized warning auditory signals (Kusnir et al. 2011). Furthermore, neuroimaging evidence shows that brain regions underlying alerting partially colocalize with those devoted to spatial orienting (Sturm and Willmes 2001).

Spatial Attention-Dependent Network
A distinct attention-dependent system (including the right IPL and the left FEF) was directly linked to facilitatory effects of spatial orienting on visual consciousness. In particular, the left FEF, a prefrontal node of the dorsal attentional network (Corbetta and Shulman 2002), emerged as a crucial area supporting the interaction between spatial attention and conscious perception, showing higher activity during the orienting period for validly cued targets reported as seen than for unseen targets. In addition to its contribution to the dorsal attention network, the FEF has well-known roles in the planning and execution of voluntary saccades (Schall 2002). Populations of FEF neurons have the ability to encode and maintain the spatial information provided by a cue during the cue-to-target delay period in nonsaccadic tasks, similar to ours (Armstrong et al. 2009). Both monkey and human studies have shown that the FEF can exert attention-dependent causal influences on occipital activity (Moore and Fallah 2001; Grosbras and Paus 2002, 2003; Moore and Armstrong 2003; Ruff et al. 2006; Taylor et al. 2007; Ekstrom et al. 2008) and by doing so ultimately modulate conscious visual processing.

Due to the complexity of our current design, a separate analysis for left- and right-sided targets was not possible. Such analysis could have eventually revealed a functional specialization of the left and right FEFs (Hilgetag et al. 2001; Grosbras and Paus 2003). Nonetheless, the left hemisphere activation patterns observed in our study are consistent with recent fMRI evidence (Szczepanski et al. 2010) demonstrating that although activations related to attentional orienting were generally larger in the right hemisphere than in the left hemisphere, and most of the frontoparietal regions explored preferentially responded to the contralateral visual field, left hemisphere FEF and IPS generated stronger signals than their right hemisphere counterparts. Thus, these left hemisphere regions might act to maintain a balanced distribution of attentional resources across the visual field. Also consistent with our results, Lau and Passingham (2006) equated participants’ objective performance while manipulating subjective visibility and detected an fMRI correlate of consciousness only in left prefrontal cortex. Moreover, verbalization of self-report in the subjective task (“I saw”/“I did not see”), as well as perceptual decisions, such as those presumably involved of the present study, are likely to preferentially rely on left hemisphere resources (see, e.g., Schluter et al. 2001).

The Role of the Attentional Reorienting Network
We explored the implication of the attention-reorienting network (including the right IFG and SMG) in conscious perception. When targets were consciously reported, activity in the right SMG was stronger following invalid than valid targets. This is consistent with many prior studies demonstrating this same pattern of results when responding to supra-threshold targets (for a review, see Corbetta et al. 2008). Furthermore, our results demonstrated for the first time that the right IFG and SMG were more active for unseen versus seen targets, which is consistent with our hypothesis that unseen events might require reorienting during the target period in order to further search for the target until the trial elapses. Moreover, the temporal dynamics of their activation indicated that the right IFG was engaged earlier for the unseen than seen modulation than the right SMG. The right IFG might indicate the need of reorienting when a target was not consciously detected. This hypothesis is consistent with recent evidence (Asplund et al. 2010) that the inferior frontal junction (located in the posterior aspect of the inferior frontal sulcus, parts of Brodmann areas 9, 44, and 6) not only contributes as a component of the ventral reorienting network but it is also recruited by the dorsal network during goal-directed behavior (He et al. 2007). In other words, the right IFG might be a key structure allowing the interaction between the dorsal and ventral frontoparietal networks (He et al. 2007).

Interactions between Spatial Attention and Consciousness: Reconciling Opposite Views
The attention-independent reportability effects found in our study in caudal regions, such as TO, could serve to reconcile opposite views standing for (Chica et al. 2010; Chica, Lasaponara, et al. 2011; Chica and Bartolomeo 2002) or against (Wyart and Tallon-Baudry 2008) the links between spatial attention and consciousness. Neither elsewhere (Wyart and Tallon-Baudry 2008) nor in the current study, interactions between spatial attention and conscious perception have been observed in visual areas, whether striate or extrastriate. The emerging evidence suggests instead that frontoparietal cortical areas embody the interactions between spatial attention and conscious perception, whereas posterior temporal and occipital regions may contribute to visual consciousness in a spatial attention–independent manner. These results are partially consistent with the “cumulative influence model”, recently advanced by Tallon-Baudry (2012) to account for the complex links between spatial attention and conscious perception. She proposed that spatial attention and conscious perception can produce independent effects at perceptual stages of processing. However, this information will be combined at a later decisional stage, leading to the final verbal report of the subject. Our data confirm that spatial attention and conscious perception produce independent effects at early stages of processing (see also Wyart and Tallon-Baudry 2008). However, interactions between spatial attention and conscious perception occurred in core regions of the attentional orienting network. This suggests that spatial attention gates the access of information to conscious reports, consistent with the view that spatial attention is an important modulator of our conscious experience.

Intra- and Interhemispheric Frontoparietal Coupling and Visual Consciousness
Our functional connectivity data further emphasized the role of frontoparietal networks in the orienting of spatial attention and in its influence on conscious perception. Some dorsal frontoparietal regions (including the bilateral SPL and IPL, the right ANG, the left FEF, and the right IFG) supported a significant interaction between spatial orienting and its...
power to modulate visual consciousness. This is in agreement with the observation that disruption of those very same systems, although largely lateralized to the right hemisphere, often induces signs of left visual neglect (Bartolomeo et al. 2006, 2007; Bartolomeo et al. 2007; He et al. 2007), a neurological condition characterized by the association of severe deficits in orienting attention to left-sided items, resulting in unawareness of visual stimuli.

These observations are consistent with current models of consciousness accessibility, postulating that conscious perception is not mediated by the activation of isolated cortical regions or unilateral networks but require a widespread bilateral reverberation of information throughout frontoparietal systems (Dehaene and Naccache 2001; Dehaene et al. 2006; Lamme 2006; see also Boly et al. 2011). The findings of the present study support and extend this model, by demonstrating that such unilateral and bilateral frontoparietal widespread activation patterns can benefit from attention being attracted by peripheral spatial cues, before target onset. Whether spatial attention is necessary for primary consciousness or it is only necessary for stabilizing perceptual representations and consequently allowing participants to access and report the attended information, remains an open question, which should be addressed in future research.

Conclusions

Our study provides novel evidence that spatial attention influences conscious perception and that such interactions are tightly associated to the activity of dorsal and ventral frontoparietal networks traditionally involved in attentional orienting. By uncoupling the neural basis supporting those interactions, the present results become relevant to theoretical models of access to consciousness (Dehaene and Naccache 2001; Dehaene et al. 2006; Lamme 2006). The depiction of spatial attention-dependent and attention-independent networks with bearing on visual consciousness can eventually contribute to reconcile opposite views on the relationships between spatial attention and consciousness. Finally, fMRI imaging has proven a great tool to identify the nodes of relevant networks distinctively involved in visual consciousness. Future studies using TMS will hopefully provide causal confirmation of neural contribution of accessible cortical regions to visual consciousness and define the likely temporal sequence of recruitment of the areas revealed by our study.

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Notes

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Goebel R, Muckli L, Zanella FE, Singer W, Stoerig P. 2001. Sustained activity patterns can benefit from attention being attracted by peripheral spatial cues, before target onset. Whether spatial attention is necessary for primary consciousness or it is only necessary for stabilizing perceptual representations and consequently allowing participants to access and report the attended information, remains an open question, which should be addressed in future research.


