Distinct Contributions of Nonpredictive and Predictive Peripheral Cues to Visual Conscious Perception: an MEG study

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Abstract

Do we need attention to become aware of an external event? We used magnetoencephalography (MEG) in human participants to assess the effects of nonpredictive and predictive supra-threshold peripheral visual cues on the conscious perception of near-threshold Gabor patches. Both nonpredictive and predictive valid cues increased the number of detected targets, and shifted the response criterion towards a more liberal decision. Predictive cues unexpectedly induced a greater sensitivity (*d'*) for invalid trials than for valid trials. With nonpredictive cues, seen targets were associated with right-lateralized frontoparietal feed-forward and feedback sweeps. For seen targets there was increased connectivity among visual regions, and between these areas and the inferior parietal lobes and the anterior insular cortices (AIC), bilaterally. Valid predictive cues interacted with conscious target detection, with greater activation of areas mostly located in the left hemisphere, especially in the frontoparietal network and temporoparietal junction, and induced an increased connectivity between the right AIC and areas of the visual ventral stream in the seen condition only. Thus, neural activity induced by nonpredictive and predictive spatial cues can enhance conscious visual perception through distinct mechanisms, mostly relying on frontoparietal activity in the right or left hemisphere, respectively. Connectivity involving the AIC participates in shaping the interaction between attention and conscious visual perception.

Significance Statement

Do we need to pay attention to external objects in order to become aware of them? Characterizing the spatiotemporal dynamics of attentional effects on visual perception is critical to understand how humans process information coming from relevant aspects of their environment. Participants detected near-threshold visual targets preceded by supra-threshold spatial cues with varying degrees of predictivity, while their brain activity was recorded using

magnetoencephalography. Results demonstrated that spatial cues, especially when predictive, biased participants' conscious perception through an early recruitment of frontoparietal regions. This work highlights an interactive pattern between spatial attention and consciousness, as shown by the effects of attention-related regions on visual sensory cortices bilaterally, consistent with the hypothesis that attention is a pathway to conscious perception.

Introduction

The relationship between attention and consciousness remains debated. Some argue that conscious perception cannot occur without attention (Posner, 1994; Dehaene et al., 2006; Mashour et al., 2020); others propose that attention and consciousness are dissociable processes (Wyart and Tallon-Baudry, 2008; Tallon-Baudry, 2012). In spite of the growing effort devoted to characterizing the neural substrates supporting visual conscious perception, this quest is still open, possibly because attention is a heterogeneous psychological construct consisting of independent but interactive functions, which may differentially influence conscious visual perception.

Studies investigating how attention modulates conscious perception mainly focused on visuospatial orienting, which enhances the processing of stimuli appearing in a specific region of the visual field (Posner, 1980). Nonpredictive visual cues, which are not informative about the future location of the target, exogenously capture attention (Fan et al., 2002; Funes et al., 2007; Chica et al., 2013b; Spagna et al., 2015). For short stimulus-onset asynchronies (SOAs) a benefit in performance often occurs when the cue and the target appear on the same side (so-called “valid” trials), compared to when they occur on opposite sides (“invalid” trials). More endogenous, or goal-driven forms of orienting occur with predictive cues that correctly indicate the location of the upcoming target in most trials. Neuroimaging studies have shown partially distinct neural processes underlying exogenous and endogenous orienting (Corbetta and Shulman, 2002; Fan et al., 2005; Chica et al., 2013b; Xuan et al., 2016), but the spatiotemporal dynamics of these mechanisms remain unclear, possibly due to insufficient temporal resolution.

Longstanding evidence indicates that nonpredictive orienting cues improve conscious perception (Chica et al., 2011b; Sergent et al., 2013). However, the effects of endogenous orienting remain more controversial (Ling and Carrasco, 2006; Koch and Tsuchiya, 2007;

Kentridge et al., 2008; Liu et al., 2009; Van Boxtel et al., 2010; Tsuchiya and Koch, 2014, 2016; Botta et al., 2017; Vernet et al., 2019). Peripheral predictive cues engage a mix of exogenous and endogenous orienting mechanisms, because they initially capture attention exogenously, but as time passes attention is endogenously kept at the cued location. This endogenous persistence is apparently strategic, because it is more likely that the target appears at the cued location (but see Bartolomeo et al., 2007). A series of studies (Chica et al., 2011b; Chica et al., 2013b; Botta et al., 2017) showed that exogenous attention affects perceptual consciousness, and that the maximal attentional effect on conscious perception is observed when attention is first exogenously captured, and then endogenously maintained at the target location. Characterizing the spatial and temporal dynamics of the neural substrates supporting possible interactions between attentional orienting and visual conscious processing could reduce the tension between competing, but not necessarily mutually exclusive, theoretical frameworks.

Here, we addressed two questions: (1) What are the spatiotemporal dynamics of the effects of peripheral cues on visual conscious processing? (2) How does cue predictivity modulate these effects? We recorded magnetoencephalography, capitalizing on its unique capacity to characterize a wide range of neural dynamics (Baillet, 2017), while participants performed a version of a Posner-type cueing paradigm (Chica et al., 2014b) with supra-threshold peripheral cues and near-threshold Gabor targets. In different experiments, spatial cues were either nonpredictive or predictive of the site of occurrence of targets. This setting enabled us to examine the effects of cues on conscious visual perception, in terms of behavioral effects, neural activity, and brain connectivity.

The gateway hypothesis would be supported by findings of increased reportability of the target stimuli under conditions of increased attention (i.e., valid cues) (Posner, 1994), perhaps with larger effects for predictive than for nonpredictive cues (Chica et al., 2011b),

and a possible involvement of frontoparietal attention networks in the interaction between attention and consciousness (Chica et al., 2013c). The absence of cue validity effects on conscious perception would instead favor the cumulative influence hypothesis (Wyart and Tallon-Baudry, 2008; Tallon-Baudry, 2012), together with an absence of interaction between attention and consciousness in frontoparietal activations.

Materials and Methods

Participants. To estimate the sample size required to detect a difference in *d'* for valid and invalid cue trials, we conducted a statistical power analysis using the parameters estimated in our previous study (Chica et al., 2011b). With alpha = 0.05, an expected power of 0.80 and an effect size of 0.81, the projected sample size needed was of n = 15 (two-tailed). We also conducted a statistical power analysis to estimate the sample size required to detect a difference in *criterion* for valid and invalid cue trials in the experiment with predictive cues. With alpha = 0.05, an expected power of 0.80, and the effect size of 1.53 as shown in previous research (Chica et al., 2011b), the projected sample size needed was of n = 6 (two-tailed).

In total, 37 participants were recruited across two experiments. Eighteen participants completed the experiment with nonpredictive cues (age = 24 ± 3.13 years; age range = 22-33 years; 6M), and nineteen participants completed the experiment with predictive cues (age = 24 ± 3.79 years; age range = 20-32 years; 7M). Five participants had to be excluded from data analysis of the predictive cue experiment, due to issues in the data quality of MEG recordings. All participants reported normal or corrected-to-normal vision, and gave written informed consent before participation. The study was approved by the INSERM and by the Institutional Review Boards of Paris Ile de France (CPP 1).

Stimuli and Procedure. The tasks were compiled and run using E-Prime software (RRID: SCR_009567; Psychology Software Tools, Pittsburgh, PA) on a Windows XP desktop

computer. All stimuli were presented on a gray background at the center of a black projection screen using a PROPixx projector (resolution, 1050 × 1400 pixels; refresh rate, 60 Hz) located outside the shielded recording room. **Fig 1a.** shows a schematic representation of the sequence of events in an invalid trial. **Fig 1b.** illustrates size of the stimuli used in our tasks. The display consisted of three black boxes (3.6° × 4.9° of visual angle) presented on a gray background; the central one was presented at the center of the screen and contained a fixation point (a black cross) at its center. The other two boxes were located 6° of visual angle to the left and right side and 4° of visual angle below the central box, respectively, a setting created to maximize MEG responses from early visual areas (Portin et al., 1999).

Participants sat in the MEG recording room, with the screen being positioned approximately 80 cm away from their eyes, and performed two tasks sequentially: 1) a discrimination task, which required to identify the orientation of a Gabor patch (spatial frequency: 5 cycles per degree of visual angle; diameter: 2.5° of visual angle; orientation: chosen among 12 equally spaced between 0 and 180°, vertical and horizontal orientations being excluded) that was presented for 16ms in either the box to the left or to the right side of the display. After a 484ms delay, participants were asked to press a button on a response box with 3 vertical buttons to indicate the orientation of the grating among two possibilities presented vertically on the screen, distant by 3° from each other. Participants pressed the upper response button with their index finger to choose the upper orientation or the middle response button with their middle finger to choose the lower orientation. The location of the correct orientation was randomized. After the participants' response, or after 3s without response, 2) a detection task was presented, which required to press one of the three buttons of the response box to indicate whether the target was absent, or whether it had been presented in the left or right box. Two arrow-like stimuli (>>>>>> or <<<<<<) were presented above and below the fixation cross, their respective position being randomized

across trial, and the word “absent” presented under the arrow-like stimuli. For trials in which participants reported to have seen a stimulus, they then pressed the upper or lower response button (with their index or middle finger, respectively) to indicate the visual hemifield of the target presentation. For trials in which participants reported to have not seen the stimulus, they pressed the lower response button with their ring finger. After the participants’ response, or after 3s without response, the next trial began after a variable delay of 1 to 1.5 s.

Before the recording session, participants were briefly instructed about the goal of the study and were then shown instructions on the screen. Each participant underwent a calibration session (mean duration, 6 min), during which the target contrast was manipulated in order to estimate the individual threshold for which the percentage of consciously perceived target was 50%. The calibration session consisted of two randomly inter-leaved psychophysical staircases (one-up / one-down), theoretically converging toward a detection rate of 50%. During the calibration session, participants were engaged in the same paradigm as described previously, except that the contrast of the stimuli was varied from trial to trial depending on their previous seen – unseen report in the corresponding staircase. Threshold contrasts were estimated separately for the valid and invalid locations. The calibration session was followed by eight recording sessions (mean duration, 8 min per session).

Each trial started with a fixation display, whose duration varied randomly between 1,000ms and 1,500ms. In the target-present trials, a cue occurred 300ms before targets, in the form of a black dot with a 1° diameter, and presented for 50ms near the external upper corner of one of the two peripheral boxes. Such a small cue was used in order to avoid possible phenomena of perceptual interference with the subsequent, near-threshold target.

Experimental designs and statistical analyses. In the nonpredictive cue experiment, each of the eight MEG recording sessions consisted of 110 trials, including 88 stimulus-present trials (in which stimuli at threshold contrast were presented either in the left or right

lower visual quadrants) and 22 stimulus-absent trials (in which no stimulus was presented). The total number of trials was 880, with 50% valid cue trials (352 trials), 50% invalid cue trials (352 trials), and 176 catch trials. Fifty percent of the targets were presented at the cued location (valid cue condition); the other 50% was presented at the uncued location (invalid cue condition) (**Fig. 1c**). Trials within a recording session were presented in a different randomized order for each subject.

In the experiment with predictive cues, parameters of stimulus size and timing of presentation were the same as those used in the nonpredictive cue experiment, except that the total number of trials on each of the eight MEG recording sessions consisted of 784 trials, with 67% valid cue trials (448 trials), 33% invalid cue trials (224 trials), and 112 catch trials (**Fig. 1d**).

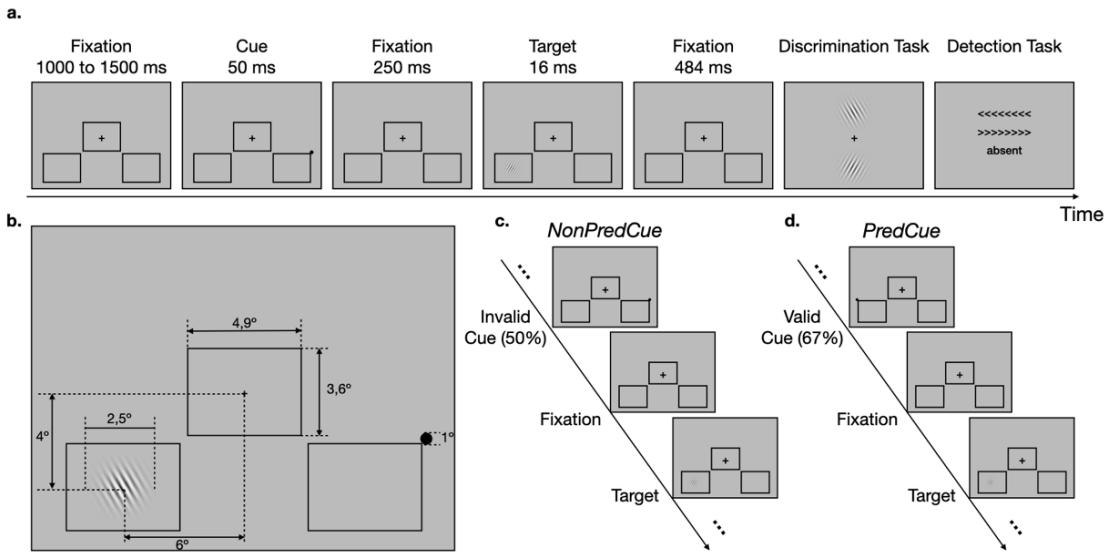

Figure 1 a. Schematic representation of the sequence of events in an invalid-cue trial. **b.** Size of the stimuli and exact location of presentation on the screen. The experiment with nonpredictive cues (*NonPredCue*) and the experiment with predictive cues (*PredCue*) shared the same sequence of event and size of stimuli; **c.** in the *NonPredCue* experiment 50% of cues were valid and 50% were invalid; **d.** in the *PredCue* experiment 67% of cues were valid and 33% were invalid.

MEG recordings. Continuous MEG recordings were conducted at the CENIR (http://www.cenir.org) with an ELEKTA Neuromag TRIUX® machine (204 planar gradiometers and 102 magnetometers) located in a magnetically shielded room with a sampling frequency rate of 1kHz and a bandwidth ranging from of 0.01 to 300 Hz. The recordings were then MaxFiltered (v2.2) (Taulu and Simola, 2006) to attenuate environmental noise, Signal Space Separation (SSS) was then implemented, automatic detection of bad channels was conducted, data were filtered (1 to 250 Hz), and resampled at a rate of 250Hz, and then converted in the Fieldtrip structure (RRID: SCR_004849; http://www.fieldtriptoolbox.org/) (Oostenveld et al., 2011) to conduct further preprocessing and analytic steps. Cardiac activity (electrocardiogram – ECG), vertical and horizontal EOG signals were also recorded together with the electrophysiological data. The exact timing of the presentation of the stimuli onset was corrected in accordance to the signal received from a photodiode located in the MEG room, in order to adjust to the delay produced by the refresh rate of the projector.

Preprocessing and Artifact Rejection. Additional preprocessing steps were conducted using Fieldtrip and included an initial visual inspection of the recordings conducted by two of the authors (D.J.B. and Z.R.) to exclude segments with artifacts and ensure data quality control. Electroculogram (EOG) recordings from both vertical and horizontal sensors were then used to reject trials in which eye movements (beyond 3º) occurred. Rejection thresholds for both horizontal and vertical EOG traces was set to ± .66V, corresponding to a deviation greater than 3º of visual angle (and with the target at 6º of visual angle). Trials with excessive eye movements and eye blinks (~10.52% of trials) were rejected offline from the MEG traces according to the 3º threshold mentioned above. Signal from the photodiode was used to discard 1) trials with a delay between the trigger and the photodiode greater than 300ms; 2) trials with a delay between the cue and the target greater than 827ms; 3) trials in which the

delay between the trigger of the cue and the photodiode was greater than 40ms or smaller than 30ms, for a total of ~1% of the trials. Last, trials contaminated by muscular activity (jump or movement) were rejected manually upon visual inspection (~15%). For the nonpredictive cue experiment, out of the 15,840 trials acquired, 8517 trials were analyzed (*right visual field*: seen invalid = 1033; seen valid = 1284; unseen invalid = 1056; unseen valid = 882; *left visual field*: seen invalid = 1191; seen valid 1176; unseen invalid = 956; unseen valid = 939). For the predictive cue experiment, out of the 10,796 trials acquired in total, 7454 trials were analyzed (*right visual field*: seen invalid = 396; seen valid = 1588; unseen invalid = 812; unseen valid = 1379; *left visual field*: seen invalid = 639; seen valid 1144; unseen invalid = 576; unseen valid = 1379) (see **Table S1** for a subject-by-subject breakdown of the number of trials in each condition remaining after artifact rejection).

Event-Related Magnetic Fields. Data from 102 neuromag channels was analyzed in this study. A Matlab® script was used to separate the MEG continuous recordings into 2300ms-long epochs (ranging from -1000 before the cue and 1300ms after the cue), and epochs from the eight experimental conditions from each participant were then imported into Brainstorm (Tadel et al., 2011). For each condition, event-related magnetic fields were then averaged (weighted) along their entire length (2300ms).

Source reconstruction. Signal amplitude from the 15,000 cortical elemental dipoles underlying the signals measured by the sensors were then estimated from the epochs using the weighted minimum norm estimation (wMNE) imaging method as implemented in Brainstorm (Tadel et al., 2011), which first identifies a current source density image fitting the data through the forward model, and then favors solutions that are of minimum energy by using source covariance as a prior. To use this method, a noise covariance matrix was estimated for each subject from the recordings using the pre-stimulus interval (-1,000 to -2ms before the presentation of the cue), while constrained source covariance model was used to model one

dipole, oriented normally to the surface. Further processing conducted on the sources per participant consisted of z-score transformation of the signal with reference to the baseline (from -1,000 to -2ms). A spatial smoothing kernel (FWHM = 3mm) was then applied on the sources, that were then re-interpolated (projected) on a common template (default anatomy).

MRI recordings. High-resolution T1-weighted structural MRI images (MPRAGE sequence, flip-angle, 9; Repetition Time, 2300ms; Echo Time, 4.18ms; voxel size: $1 \times 1 \times 1$ mm) were acquired for each participant using a 3-T Siemens, TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) located at the CENIR MRI center (Salpetriere Hospital, Paris, France). After acquisition, images were then segmented using the FreeSurfer "recon-all" pipeline (Fischl, 2012), and imported in Brainstorm (Tadel et al., 2011) for co-registration purposes. MEG sensors and structural MRI images were first manually aligned using the nasion/left ear/right ear (NAS/LPA/RPA) fiducial points recorded in the MEG file and in the MRI MNI coordinates. Co-registration was then further refined using the "refine using head points" option on Brainstorm, which uses an iterative closest point algorithm to fit the head shape and the digitized scalp points. Additional details about the MRI-MEG co-registration steps as done in Brainstorm can be found here (Tadel et al., 2019).

Behavioral Data Analysis. Response times (RTs) below 150ms (anticipated responses) and above 1,800ms (delayed responses) were excluded from subsequent analyses (below 2% of total number of trials). Independent sample *t*-tests were used to assess potential differences in the thresholds sampled during the calibration sessions separately for invalid and valid cue trials. Analysis of Variance (ANOVA) and Signal Detection Theory (SDT) analyses were conducted to examine whether and how nonpredictive and predictive cues modulated visual conscious perception. The Kolmogorov-Smirnov and the Shapiro Wilk test for normality were conducted to examine whether the data on accuracy was normally distributed. For both RT and Accuracy (in percentage), a 2 (seen, unseen) $\times$ 2 (valid, invalid) repeated measures

ANOVA was conducted on correctly discriminated responses. These analyses were conducted to examine behavioral differences between trials reported as seen or unseen under the valid and invalid cue conditions. SDT was conducted to estimate changes in the signal to noise ratio as a function of cue validity condition (*d'*), and to investigate whether the presence of a cue could bias the observer towards a more liberal reporting threshold (*criterion*). For the *d'*, participants' performance was estimated using the standardized difference between target-present (Hits: z(H)) and target-absent (false alarms: z(F)) trials, by diving the percentage of correctly detected trials by the number of false alarms (FA: trials in which participants reported having seen the stimulus); zero false alarm rates (n = 12) were corrected using the following formula (FA = (FA + 0,5) / (FA + CR + 1,0)) (Snodgrass and Corwin, 1988). The greater the value of *d'*, the higher the quantity between the noise and the signal distribution (i.e., the signal/noise ratio). The *criterion (C)* summarizes the distance of the threshold relative to the noise distribution *B* from the threshold of an ideal observer (*-0.5 * ([z(H) + z(F)]))*. A negative value of *C* represents a more liberal threshold, while a positive value of *C* represents a more conservative threshold. Both *d'* and *C* were estimated separately for valid and invalid trials, and paired sample *t*-test was used to assess differences in *d'* and *criterion* between these two conditions.

MEG data analysis. In parallel with the behavioral analyses, 2 (seen, unseen) × 2 (valid, invalid) × 2 (left, right) repeated-measures ANOVAs were conducted on individuals' estimated activity (z-scores) of reconstructed source images to examine how neuronal activity induced by nonpredictive cues can enhance conscious perception. Spatiotemporal cluster-based permutation tests (Maris and Oostenveld, 2007) were used for comparing main effects and interactions between brain activations in the time window between 0 and 800ms (locked to cue onset), with the number of permutations set to 1000 and the alpha threshold level set to 0.05 for all tests.

Connectivity Analysis. To examine the modulation in connectivity between brain areas as a result of the experimental conditions, we estimated leakage-controlled (orthogonalized) high-gamma (60 to 90 Hz) amplitude envelope correlation (AEC) (Brookes et al., 2012; Colclough et al., 2015) of eighteen regions of interest (ROIs). Analyses were conducted solely on the high-gamma frequency band because of the extensive knowledge on the role of the oscillatory synchronization in this frequency band in spatial attention and its modulation of visual areas (Tallon-Baudry et al., 2005; Magazzini and Singh, 2018; Fiebelkorn and Kastner, 2019). ROIs were selected on the basis of previous results (Corbetta and Shulman, 2002; Fan et al., 2005; Tallon-Baudry et al., 2005; Bressler et al., 2008; Chica et al., 2013c; Chica et al., 2016b; Xuan et al., 2016), showing their involvement in attention-related processes. In addition, areas of the ventral visual stream were also added to the ROI analyses to examine potential frontoparietal modulation of activity in early and late visual areas. The ROIs were created using Brainstorm (Tadel et al., 2011), seed vertices and area (in cm^2) of the ROIs are listed in **Table 1** (in MNI coordinates). Paired sample *t*-tests ($p < .05$, FDR corrected) were used to compare the AEC estimates across experimental conditions.

Results

Does the validity of nonpredictive cues affect participants' response to visual Gabor targets? To answer this question, we examined behavioral responses to seen and unseen targets separately for valid and invalid nonpredictive cues. Valid cues, compared to invalid cues, lowered the response criterion (mean ± SD valid: 0.85 ± 0.28; invalid: 1.03 ± 0.27; $t(17) = -2.82$; $p < .05$), and increased the percentage of detected targets (mean ± SD valid: 0.57 ± 0.09; invalid: 0.52 ± 0.11; $t(17) = -3.08$; $p < .01$). However, sensitivity (*d'*) was similar for valid and invalid trials (valid: 2.30 ± 0.57; invalid: 2.29 ± 0.47; $t(17) < 1$) (see **Fig 2**). These results did not depend on different perceptual thresholds resulting from the calibration session, because these thresholds were similar for valid trials (43.98%) and for invalid trials

(43.99%; $t < 1$). Left- and right-sided targets evoked a similar number of correct responses (sum of the total number of correctly discriminated targets presented to the left visual field: 3,489; mean ± SD: 194.83 ± 37.05; sum of the total number of correctly discriminated targets presented to the right visual field: 3,507; mean ± SD: 194.83 ± 33.6; Wilcoxon signed-rank test = 76; $p = .70$; Bayesian Wilcoxon signed-rank test $BF_{10} = 0.56$, with median posterior δ = -0.079, 95% CI [-1.07, 0.91]).

As expected, participants were more accurate in discriminating the orientation of *Seen* targets (79.2 ± 14.0%) than that of *Unseen* targets (50.2 ± 7.0%) [ANOVA with *Consciousness* (seen, unseen), *Visual Field* (left, right), and *Validity* (valid, invalid) as factors, $F_{(1,17)} = 85.60$; $p < .0001$; $\eta^2 = .84$] (**Fig 2a)**. No other factors or interactions reached statistical significance.

A similar ANOVA conducted on RTs (see **Fig 2b**) revealed a main effect of *Consciousness* ($F_{(1,17)} = 102.65$; $p < .0001$; $\eta^2 = .86$), because participants were slower for *Seen* targets (1034 ± 115ms) than for *Unseen* targets (601 ± 190ms). No other factors or interactions reached significance.

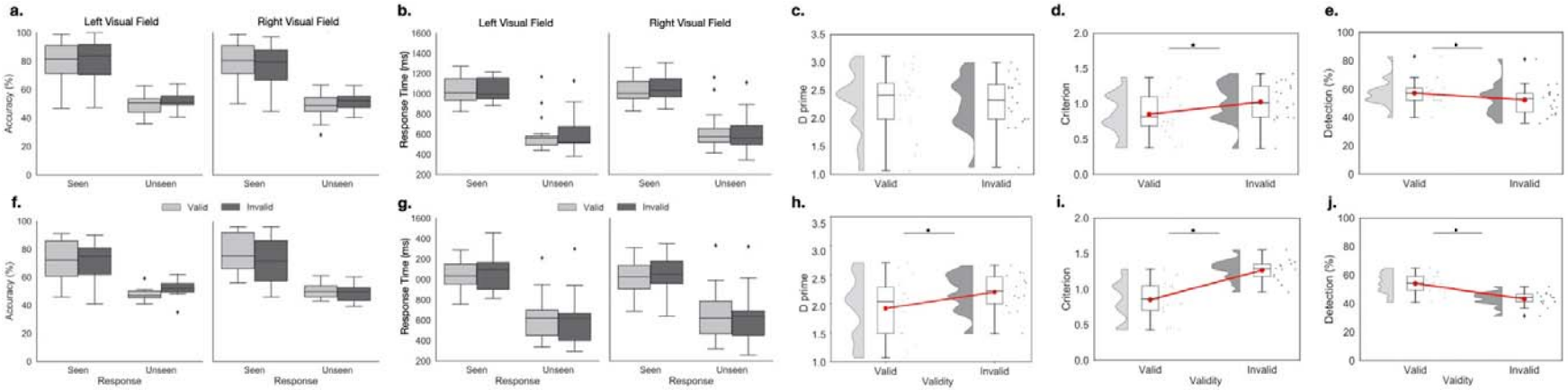

Figure 2. Results of the behavioral analyses conducted on performance with nonpredictive cues (a.-e.) and with predictive cues (f.-j.). **a.** and **b.** report result of the ANOVA conducted on Accuracy (in percentage) and RTs (in ms), respectively, while **c.**, **d.**, and **e** report result of the Signal Detection Theory analysis for d', criterion, and detection (in percentage). **f.** and **g.** report result of the ANOVA conducted on Accuracy (in percentage) and RT (in ms), respectively, while **h.**, **i.**, and **j.** report results of the SDT analysis for d prime, criterion, and detection (in percentage).

Does the validity of nonpredictive cues affect neural responses associated with the conscious report of visual Gabor targets? We addressed this question by examining brain responses to seen and unseen targets separately for valid and invalid nonpredictive cues. Source analysis of the MEG signal revealed that conscious perception was associated with right-lateralized frontoparietal feed-forward and feedback sweeps. Two clusters exceeding the threshold of randomization distribution under H0 emerged for the seen *vs* unseen comparison (both *p*s < 0.001) in the time window of 400 - 800ms after cue onset. The first cluster was in the right hemisphere, the second in the left hemisphere. Both clusters started in the occipital cortex and afterwards extended to the frontoparietal network and temporal regions, bilaterally (see **Fig 3**). The differences for the main effects of *Validity* (valid, invalid), for the main effect of *Visual Field* (left, right), and for the interactions did not reach statistical significance. Control analyses showed that there was no significant difference between the number of MEG trials for left- and right-sided targets (left visual field, mean ± SD: 235.39 ± 32.49; right visual field, 235.5 ± 30.02; Wilcoxon signed-rank test = 85; p = 1; Bayesian Wilcoxon signed-rank test BF_{10} = 0.57, with median posterior δ = -0.05, 95% CI [-1.09, 0.96]).

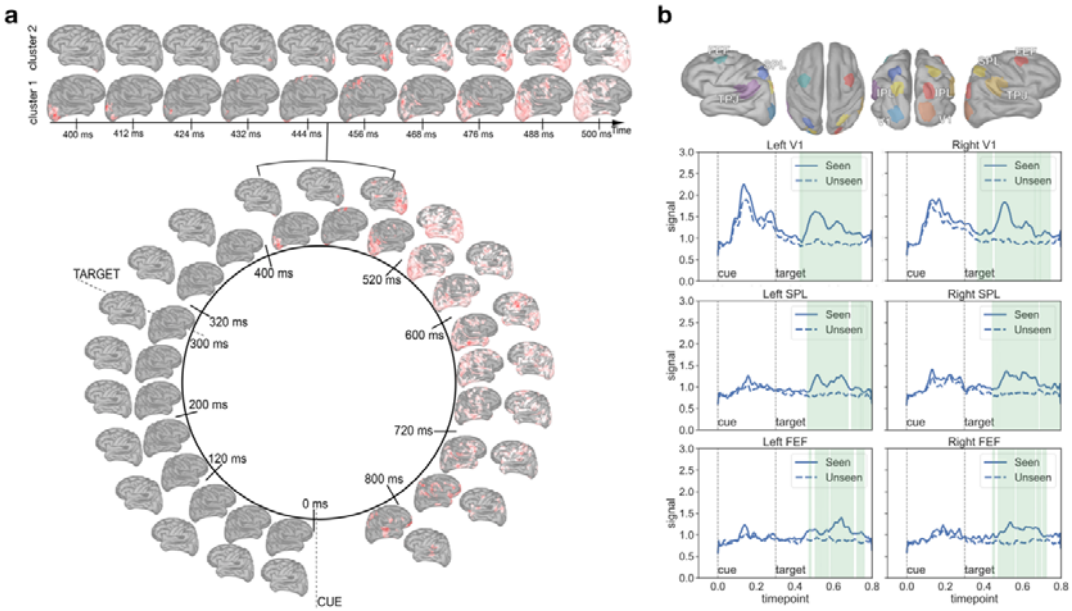

Figure 3. a. When preceded by nonpredictive cues, seen targets evoked two clusters of brain activity compared to unseen targets. Cluster 1 occurred in the 400 - 800ms time window after cue onset, was lateralized to the right hemisphere, and encompassed a frontoparietal *feed-forward* and *feedback sweeps* (around 456ms), with subsequent diffusion to widespread bilateral activation. Cluster 2 occurred also in the 400 - 800ms time window after cue onset, but was lateralized to the left hemisphere, and encompassed a widespread brain activation. **b.** Average signal changes in the ROIs separately for the Seen (solid line) and Unseen (dashed line) condition. The area in green highlights the time interval in which cluster-corrected analysis showed a significant difference between the two signals.

Does the validity of nonpredictive cues modulate the connectivity between ROIs associated with the conscious report of visual Gabor targets? To answer this question, we examined functional connectivity associated to seen and unseen targets separately for valid and invalid nonpredictive cues. Whole-trial (0 – 800ms) high-gamma band (60 - 90Hz) amplitude envelope correlation analyses conducted among attention-related ROIs (see **Table 1**) revealed a strong connectivity within visual ventral areas and between these areas and the anterior insular cortex (AIC), bilaterally for *Seen* compared to *Unseen* trials ($p < .001$, FDR corrected; **Fig 4a**). There was no evidence for a difference in connectivity between *Valid* and *Invalid* trials. Differences (ps $< .005$, FDR corrected; **Fig 4b** and **c**) emerged in the connectivity between *Seen Valid* and *Unseen Valid* trials across areas within the visual ventral stream as well as with the right inferior parietal lobule (IPL) and with the right AIC. There was also increased connectivity of the right AIC with areas in the visual ventral cortical stream and in *Seen Invalid* trials than *Unseen Invalid* trials.

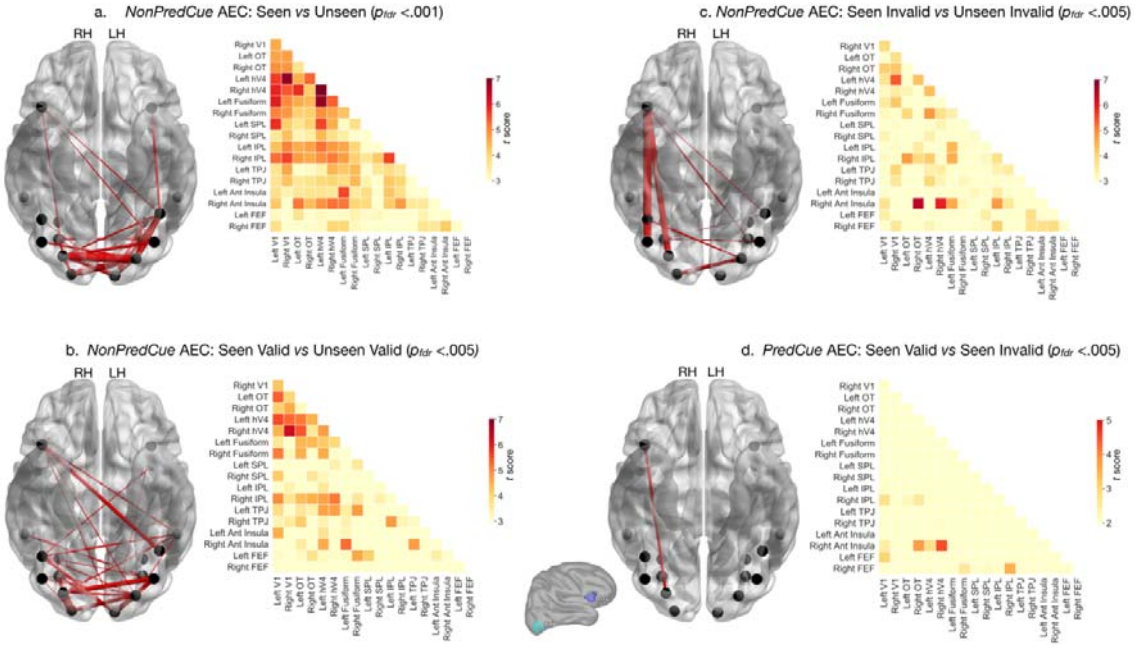

Figure 4. Pairwise functional connectivity (estimated using amplitude envelope correlation, AEC, of the whole duration of the trials – 0 to 800ms) between ROIs, with weighted edges denoting significant *t*-score values (overall *ps* < .005, FDR corrected) obtained from the contrast between the conditions of interest. **a.** difference in AEC between *Seen* and *Unseen* trials in the nonpredictive cue (*NonPredCue*) experiment; **b.** difference in the AEC between *Seen Valid* and *Unseen Valid* in the *NonPredCue* experiment; **c.** difference in the AEC *Seen Invalid* and *Unseen Invalid* in the *NonPredCue* experiment; **d.** difference in the AEC *Seen Valid* and *Seen Invalid* in the predictive cue (*PredCue*) experiment.

Thus, the validity of nonpredictive cues modulated participants' conscious reports of visual Gabors for both behavioral performance and MEG connectivity measures. Differences also emerged between seen and unseen trials that were not confined to the occipital lobe, but were quickly followed by frontoparietal activity (approximately 150ms after the target and 50ms after the occipital activation), and subsequently by a widespread activity that lasted to the end of the trial, and resembled the pattern described as the Global Neuronal Workspace (Mashour et al., 2020).

Does the validity of predictive cues affect participants' response to visual Gabor targets? To address this issue, we examined behavioral responses to seen and unseen targets separately for valid and invalid predictive cues. As did nonpredictive cues, also valid predictive cues, compared to invalid predictive cues, lowered the response criterion (mean ± SD valid: (0.85 ± 0.28; 1.26 ± 0.15; ($t(13) = -6.37$; $p < .001$), because participants adopted a more liberal response threshold in the valid cue condition, and increased the percentage of detected targets (mean ± SD valid: 54.11 % ± 7.13%; invalid: 43.33 ± 5.14%; $t(13) = 8.06$; $p < .001$). However, *sensitivity* (*d'*) was greater for invalid trials (2.20 ± 0.33) than for valid trials (1.91 ± 0.54) ($t(13) = -2.29$; $p < .05$) (see **Fig 2**). These results did not depend on possible differences between the thresholds established separately for valid and invalid trials cue trials during the calibration session (valid trials: 59.21; invalid trials: 60.79; $t<1$). Unexpectedly, right-sided targets evoked more correct responses that left-sided ones (right visual field, mean ± SD: 220.21 ± 35.42; left visual field, 194.72 ± 21.89; Wilcoxon signed-rank test = 6.00; $p < .01$; Bayesian Wilcoxon signed-rank test $BF_{10} = 4.06$, with median posterior $\delta = -1.19$, 95% CI [-2.51, 0.01]).

Results of the ANOVA conducted on Accuracy percentages to the discrimination task (after ensuring that these percentages followed a normal distribution by using the Kolmogorov-Smirnov and the Shapiro Wilk tests for normality) are shown in **Fig 2f**. There was a main effect of the factor *Consciousness* ($F_{(1,13)} = 31.62$; $p < .0001$; $\eta^2 = .71$), because participants were more accurate for *Seen* trials (72.87 ± 15.2%) than for *Unseen* (49.71 ± 5.9%) trials. No other effect or interaction reached significance, except for the interactions between *Consciousness* and *Validity* ($F_{(1,13)} = 11.9$; $p < .01$; $\eta^2 = .48$) and between *Visual Field* and *Validity* ($F_{(1,13)} = 8.89$; $p < .05$; $\eta^2 = .41$). Pairwise comparisons showed that the difference between valid and invalid trials was significant for the seen trials (valid: 74.88 ± 14.41%; invalid: 70.86 ± 16.14%; $p < .01$), but not for the unseen trials (valid: 48.91 ± 5.13%;

invalid 50.51 ± 6.52%; $p = .14$). Participants detected more validly cued targets than invalidly cued targets in the right visual field (valid: 64.24 ± 9.92%, invalid: 60.08 ± 12.26%, $p < .01$), but not in the left visual field (valid: 59.56 ± 9.62%; invalid: 61.29 ± 10.04% $p = .21$).

Results of the ANOVA conducted on the RTs (see **Fig 2g**) showed that participants responded slower to *Seen* targets (1048 ± 171ms) than to *Unseen* ones (640 ± 259ms; $F_{(1,13)} = 28.91$; $p < .0001$; $\eta^2 = .69$). The main effects of *Visual Field* and *Validity* did not reach significance (both Fs < 1). *Consciousness* interacted with *Visual Field* ($F_{(1,13)} = 5.08$; $p < .05$; $\eta^2 = .28$), because the seen/unseen difference was greater for left-sided targets (seen: 1,055 ± 168ms; unseen: 624 ± 249ms; $p < .001$) than for right-sided targets (seen: 1,040 ± 177; unseen: 656 ± 272; $p < .001$).

Does the validity of predictive cues affect neural responses associated with the conscious report of visual Gabor targets? We addressed this question by examining brain responses to seen and unseen targets separately for valid and invalid predictive cues. Similar to the experiment with nonpredictive cues, two clusters exceeding the threshold of randomization distribution under H0 emerged for the seen *vs* unseen comparison (*ps* < 0.001), both in the time window of 460 - 760ms after cue onset. The first cluster was lateralized to the right hemisphere, the second was lateralized to the left hemisphere. Both started in the occipital cortex and then spread to the parieto-temporal regions, without any evidence of involvement of prefrontal regions. *Consciousness* interacted with *Validity*. Four clusters exceeding the threshold of randomization distribution under H0 were found for the interaction term ((seen valid *minus* unseen valid) *minus* (seen invalid *minus* unseen invalid)). The first cluster ($p < 0.001$) occurred in the 100 - 150ms time window after cue onset, and was lateralized to the left visual cortex; the second cluster ($p < 0.05$), was also lateralized to the left visual cortex and left IPL, in the 300 - 380ms time window after cue onset; the third cluster ($p < 0.05$) occurred in the inferior temporal lobe of the right hemisphere and spanned across the time

window of 550 and 600ms after cue onset; the forth cluster ($p < 0.05$) was localized in the left precuneus, extending into the left posterior cingulate cortex and spanned across the time window of 580 and 600ms after cue onset. **Fig 5** displays the follow-up analysis conducted in the valid *vs* invalid comparison for the seen condition only (seen valid *minus* seen invalid). Three clusters exceeded the threshold of randomization distribution under H0. A first cluster ($p < 0.001$) was lateralized to the left hemisphere and occurred in the 50 - 400ms time window after cue onset, spanning across visual cortex, to the parietal cortex (around 100ms post-cue), prefrontal cortex (around 150ms post-cue), and temporoparietal cortex. A second cluster ($p < 0.05$), occurred later, as a right-hemisphere occipito-parietal activation around 200ms post-cue, and then substantially resembled the activity found in the first cluster, spanning across the frontoparietal cortex (around 240ms post-cue), and temporoparietal cortex (around 280ms post-cue). The third cluster ($p < 0.05$) was lateralized to the left visual cortex and included middle- and infero-temporal areas, the inferior frontal gyrus (around 470ms post-cue), the left frontal eye fields (524ms post-cue) and then temporoparietal, inferior parietal, and inferior temporal areas.

Control analyses showed that there was no significant difference between the number of MEG trials for left- and right-sided targets (left visual field mean ± SD: 265.43 ± 21.16; right visual field; mean ± SD: 266.79 ± 26.91; Wilcoxon signed-rank test = 48.5; $p = 0.83$; Bayesian Wilcoxon signed-rank test $BF_{10} = 0.58$, with median posterior $\delta = -0.073$, 95% CI [-1.11, 0.94]).

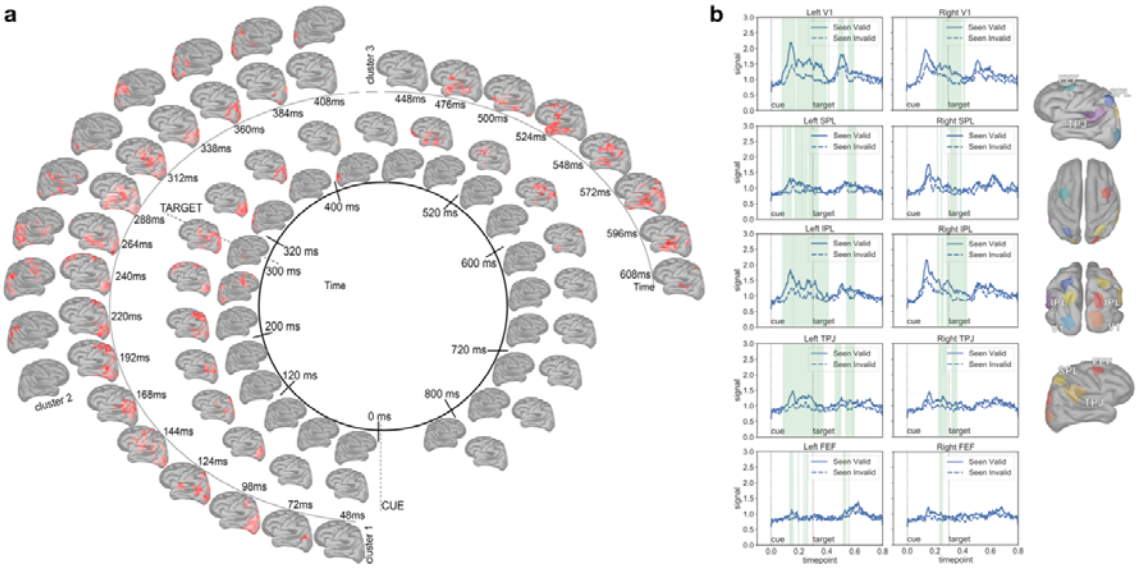

Figure 5. When preceded by valid predictive cues, seen targets evoked three clusters of brain activity, compared to invalidly cued targets. **a**) Cluster 1 occurred in the 50-400ms time window after cue onset and was lateralized to the left hemisphere ($p < 0.001$); Cluster 2 occurred in 200ms time-window after cue onset and was lateralized to the right hemisphere ($p < 0.05$); Cluster 3: occurred 470ms after cue onset and lateralized to the left hemisphere. The same valid-invalid comparison for unseen targets did not reveal any significant cluster. **b)** average signal changes in the ROIs separately for the Seen Valid (solid line) and Seen Invalid (dashed line) condition. The area in green highlights the time interval in which cluster-corrected analysis showed a significant difference between the two signals.

Does the validity of predictive cues modulate the connectivity between ROIs associated with the conscious report of visual Gabor targets? We examined functional connectivity associated to seen and unseen targets separately for valid and invalid predictive cues. High-gamma band (60 - 90Hz) amplitude envelope correlation analyses conducted on the ROIs revealed increased connectivity between the right AIC and the right temporo-occipital area for *Seen Valid vs Seen Invalid* trials (see Fig 4d). The comparisons between connectivity patterns in the *Seen Valid vs Unseen Valid* and the comparison between connectivity patterns in the *Seen Invalid vs Unseen Invalid* did not yield statistically significant results.

Thus, similar to nonpredictive cues, also the validity of predictive cues modulated participants' conscious reports of visual Gabors for both behavioral performance and neural activity measures. Differences between seen and unseen trials with predictive cues emerged in the post-target time period, but these were delayed in time compared to the same contrast with nonpredictive cues. Bilateral activity started in the visual cortex, around 160ms after the target, and was followed by mainly temporo-parietal activity, with prefrontal activity arising only later in time (almost 300ms after the target). The interaction between attention and consciousness showed four clusters of activation located in occipito-temporal regions that spanned across both the cue-target and the post-target periods, possibly showing the *site* of attentional modulation (Posner and Driver, 1992) rather than the *source* of it (Bressler et al., 2008; Liu et al., 2016). The modulation produced by predictive cues on visual awareness was also evident in the contrast between the functional connectivity patterns in valid and invalid trials for seen targets, which again showed correlated activity in AIC and areas in the ventral visual stream, bilaterally.

Cross-experiment comparison: different effects of nonpredictive and predictive cues on visual conscious perception.

Did nonpredictive and predictive cues produce different effects on brain activity and connectivity? Seen targets preceded by a nonpredictive cue evoked a significant cluster (Fig 6), occurring in the 210 - 300ms time window after cue onset, lateralized to the right hemisphere, and encompassing an early activation in the middle and inferior frontal gyri, the superior frontal gyrus and the temporoparietal junction (mainly located in the angular gyrus), with subsequent diffusion to occipitotemporal regions (cluster-corrected Welch's t test conducted in the cue-target period (0 – 300 ms), $p < .02$).

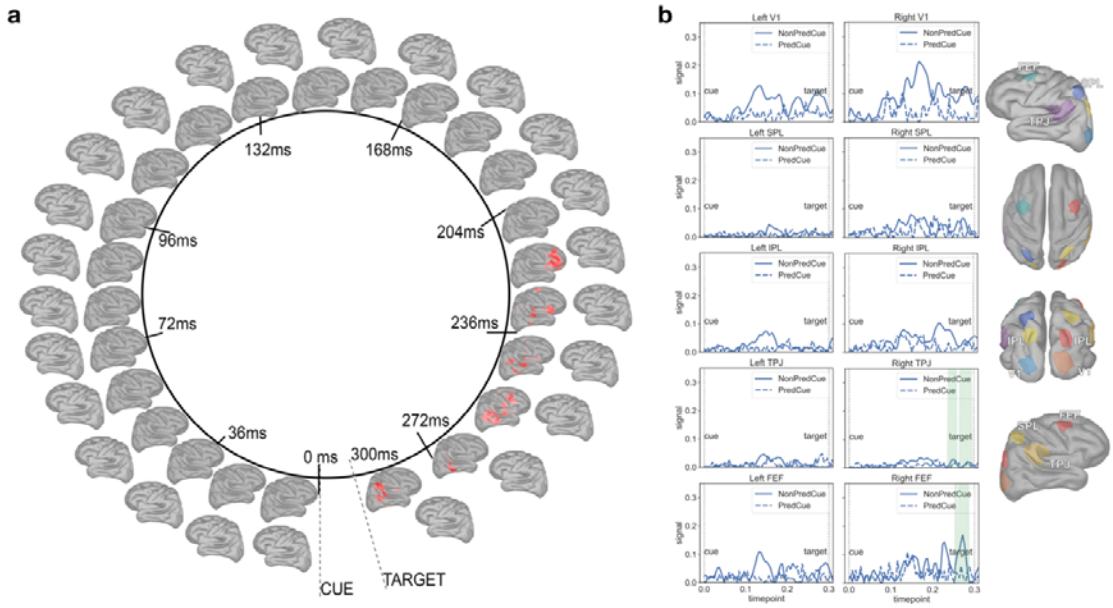

Figure 6. MEG activity evoked by nonpredictive vs. predictive cues for Seen vs. Unseen targets in the cue-target period (0 – 300 ms). **a.** One right-hemispheric cluster emerged in the 210-300ms time window, and included the temporoparietal junction and the prefrontal cortex. **b.** Average signal changes in the ROIs separately for the experiments with nonpredictive cue (solid line) and with predictive cues (dashed line). The area in green highlights the time interval in which cluster-corrected analysis showed a significant difference between the two signals.

Whole-trial (0 – 800ms) high-gamma band (60-90Hz) pairwise functional connectivity analyses conducted among attention-related ROIs (see Table 1) revealed a stronger connectivity between the left TPJ and right fusiform gyrus ($p < .01$), the left anterior insular cortex (AIC) and the left fusiform gyrus ($p < .05$), and between the left superior parietal lobe (SPL) and the right IPL ($p < .05$) for the seen minus unseen contrast with nonpredictive cues, as compared to same contrast with predictive cues.

Discussion

Our results establish the existence of interaction patterns between spatial attention and consciousness that vary based on the predictivity of the cue, and specify how attention modulates conscious perception. Altogether, the contributions of nonpredictive and predictive cues in improving target detection indicate that distinct spatiotemporal dynamics support the flexible allocation of attentional resources for near-threshold visual information to reach a conscious level of processing.

Valid spatial cues influence conscious reports. Both predictive and nonpredictive valid cues increased the proportion of correctly detected targets. These results align with behavioral evidence showing the modulation of orienting cues in increasing visual awareness (Ling and Carrasco, 2006; Liu et al., 2009; Chica et al., 2011b; Sergent et al., 2013; Botta et al., 2017; Vernet et al., 2019). However, only predictive cues improved performance on the discrimination task, while Chica et al. (2011b) found effects of both nonpredictive and predictive cues in a similar task. One important methodological difference between our study and the Chica et al. (2011b) study is that in the current experiments two supra-threshold Gabor patches were presented 500ms after the target to collect the discrimination response. This screen could have increased the perceptual difficulty of the task and therefore reduced or abolished the effects of nonpredictive cues (Kerzel et al., 2009). Unexpectedly, valid predictive cues decreased perceptual sensitivity. This result is at odds with previous observations of increased perceptual sensitivity (Chica et al., 2011b) and contrast sensitivity (Carrasco, 2018) at attended locations with predictive cues. Possible masking effects caused by the post-target display might explain our finding. Validly cued targets might have suffered interference from the preceding cue and the subsequent response Gabors, while invalid targets were only masked by the response Gabors. Facilitatory effects induced by peripheral cues are typically much larger for discrimination than for detection tasks (Lupiáñez et al., 1997; Lupiáñez et al., 2001; Chica et al., 2006). Consequently, the possible increased difficulty of

detecting a near-threshold target, might have reduced the behavioral effects of spatial attention. Peripheral cues (whether nonpredictive or predictive) produced a shift in the response criterion towards a more liberal response in valid compared to invalid trials, indicating that orienting cues modulated decision-related processes in our setting.

Distinct neural processes elicited by nonpredictive and predictive cues. MEG results indicated distinct spatiotemporal dynamics across tasks, both at the source level and in the functional connectivity patterns. Nonpredictive cues elicited a greater activation of the right TPJ and right prefrontal cortex in the seen *minus* unseen contrast compared to predictive cues. This network is connected by the ventral branch of the superior longitudinal fasciculus (SLF III) (Thiebaut De Schotten et al., 2011), and involved in exogenous attention (Corbetta and Shulman, 2002; Chica et al., 2011a). Interestingly, comparison of brain activity elicited by nonpredictive *versus* predictive cues (irrespective of participants' responses), showed a right-hemispheric TPJ-prefrontal cluster. The reduced TPJ activity for predictive cues compared to nonpredictive cues is consistent with evidence of TPJ deactivation during endogenous orienting (Shulman et al., 2007; Doricchi et al., 2010). Moreover, the combination of spatial and temporal resolution of MEG results demonstrated that this reduced TPJ activation for predictive as compared to nonpredictive cue was preceded by deactivation of the prefrontal nodes of the SLF III network in the middle and inferior frontal gyri. The statistically higher frequency of valid trials in the predictive cue experiment than in the nonpredictive cue experiment might explain the occurrence of different preparatory states after cue presentation between the two experiments. This possibility may account for the absence of such effects in the task with nonpredictive cues, which did not induce any probabilistic expectations. Together with the behavioral validity effect occurring with predictive cues, this result suggests that cue predictivity enhances attentional modulation. Interestingly, while the occipital activation was bilateral, the IPL-TPJ activations lasted longer (by around 100ms)

only in the right hemisphere, in line with abundant evidence on anatomical and functional asymmetries in frontoparietal attention networks favoring the right hemisphere (reviewed in Bartolomeo and Malkinson, 2019; see also Spagna et al., 2020b), and specifically with the role of the right TPJ in attentional orienting (Doricchi et al., 2010; Chica et al., 2014a), and in the processing of behaviorally relevant stimuli (Macaluso and Doricchi, 2013).

Frontoparietal networks and visual awareness. Dysfunction of SLF II and III networks in the right hemisphere is a typical finding in brain-damaged patients with left visual neglect, who have impaired awareness of left-sided events (Bartolomeo et al., 2012). The frontoparietal activity found with nonpredictive cues seems consistent with the *forward* and *backward sweeps* associated with the awareness of a visual target (Lamme, 2006), and suggests a role for exogenous attention in this process. The relationship of these forward/backward sweeps with behavioral changes in criterion, but not in sensitivity, might be consistent with the known role of frontoparietal networks in the activation of general processes, such as the alerting system (Périn et al., 2010; Chica et al., 2016a; Baria et al., 2017; Petersen et al., 2017; Podvalny et al., 2019). An interaction of nonpredictive cues with alerting is also supported by the functional connectivity analysis, which showed a role of the right AIC in differentiating seen *vs.* unseen trials separately for valid and invalid trials (see **Fig 6**). This result is consistent with evidence showing the critical role of the AIC in the production and maintenance of alertness, both in terms of BOLD response and of functional connectivity (Cai et al., 2014; Sadaghiani and D'Esposito, 2015; Chica et al., 2016a; Coste and Kleinschmidt, 2016; Han et al., 2019; Haupt et al., 2019). As a node of the SLF III network, the AIC may have an important role in signaling behaviorally relevant stimuli (Uddin, 2015).

In conclusion, four results of this study are broadly consistent with the gateway hypothesis (Posner, 1994), and demonstrate how the interaction between attention and visual

conscious processing heavily depends on the specific attentional component manipulated. First, both predictive and nonpredictive visual cues modulated behavioral performance in the form of a shift towards a more liberal response criterion. Second, peripheral predictive cues were able to modulate visual conscious processing, as shown by the interaction with response accuracy, in line with previous evidence (Chica et al., 2013a). Third, predictive cues also interacted with consciousness at the neural level, and induced increased activity in visual areas, possibly related to the site of attentional modulation. Last, high-gamma band functional connectivity patterns involving the AIC and the visual areas for seen trials differed across task conditions, with valid cues inducing greater modulation of the visual areas compared to invalid cues.

It remains possible that attention is required for conscious processing only when there is some competition between the stimuli to be resolved (Tsuchiya and Koch, 2014; Davidson et al., 2018), which was the case in our setting with two possible target locations. Alternatively, even an isolated stimulus might need some attentional capture to be consciously processed. Evidence from visual mental imagery studies, showing the implication of frontoparietal attention networks within the conscious imagination of an object in its absence, and thus without any competition (Spagna et al., 2020a), might support this possibility, which needs to be empirically assessed. Altogether, the comparison of the spatiotemporal dynamics underlying the interaction between nonpredictive and predictive attention with consciousness shown here confirmed that these distinct contributions span across behavioral, neural, and connectivity measures, and underlines the role of the right AIC in visual awareness.

Author Contributions

D.B., A.B.C., and P.B. designed the experiments; A.S., D.B., and Z.R. analyzed the data. All authors discussed the results and contributed to writing up the report. Behavioral data and the code to reproduce the figures (built using Python on Spyder) can be found on the GitHub page of A.S. We thank Fabrizio Doricchi, Isabella Elaine Rosario, and Catherine Tallon-Baudry for providing extensive comments on this manuscript.

Conflict of Interest Statement

The authors report no conflict of interest.

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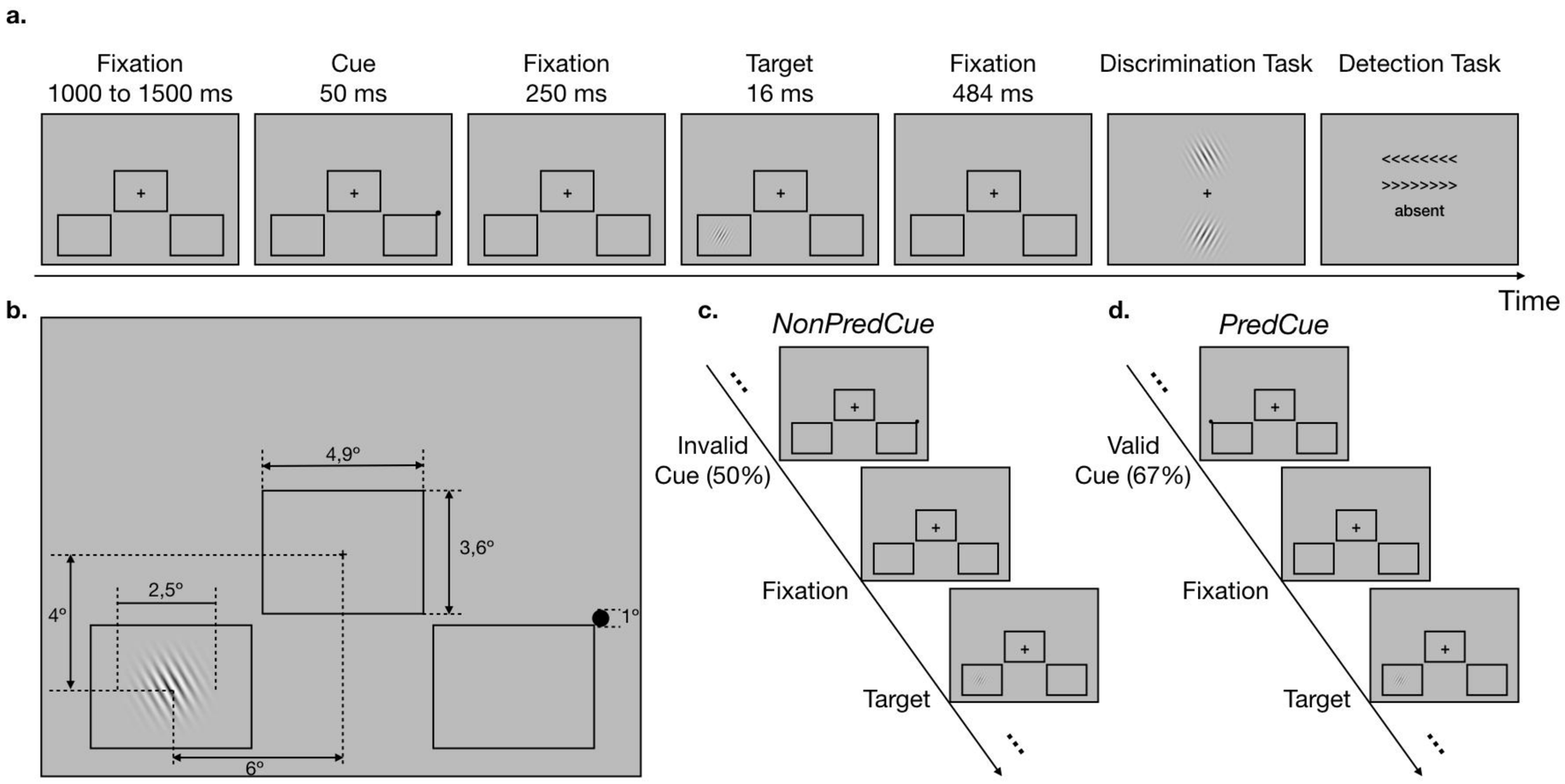
Tables

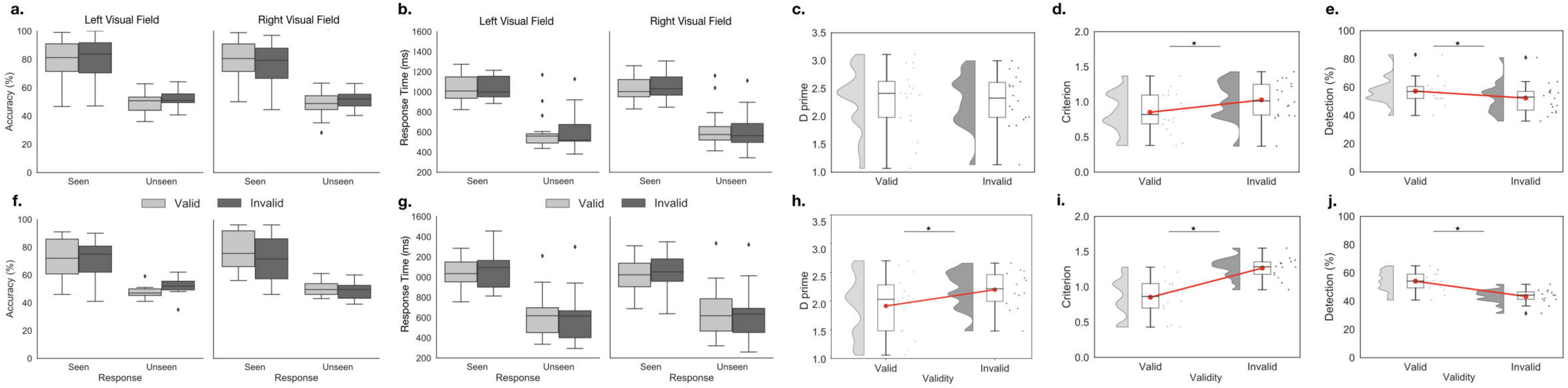
Table 1. MNI Coordinates and size of the area (in cm^2) used in the connectivity analyses.

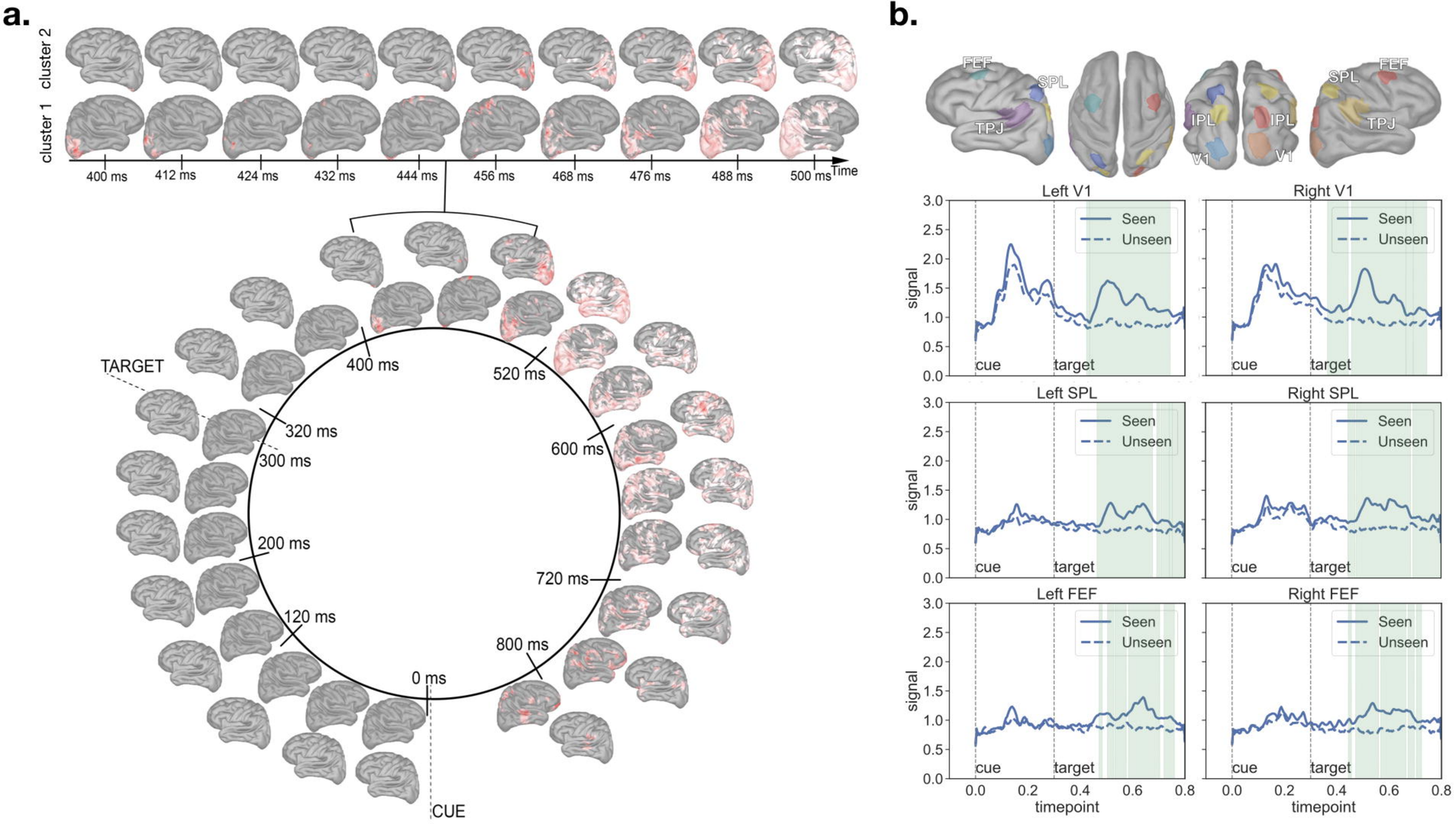
ROI	x	y	z	area
Left V1	-26	-99	7	12.63
Right V1	25	99	9	17.03
Left OT	-45	-88	-10	12.69
Right OT	45	-80	-17	12.67
Left hV4	-25	-95	-20	10.78
Right hV4	16	-95	-16	7.62
Left Fusiform	-34	-50	-21	9.82
Right Fusiform	34	-50	-21	9.59
Left SPL	-28	-60	57	16.64
Right SPL	21	-39	62	16.17
Left IPL	-27	-82	45	16.65
Right IPL	31	-82	43	16.96
Left TPJ	-62	-55	17	42.86
Right TPJ	67	-38	20	34.75
Left Ant Insula	-35	21	3	13.5
Right Ant Insula	35	21	3	13.82
Left FEF	-47	14	52	14.17
Right FEF	47	14	53	12.28

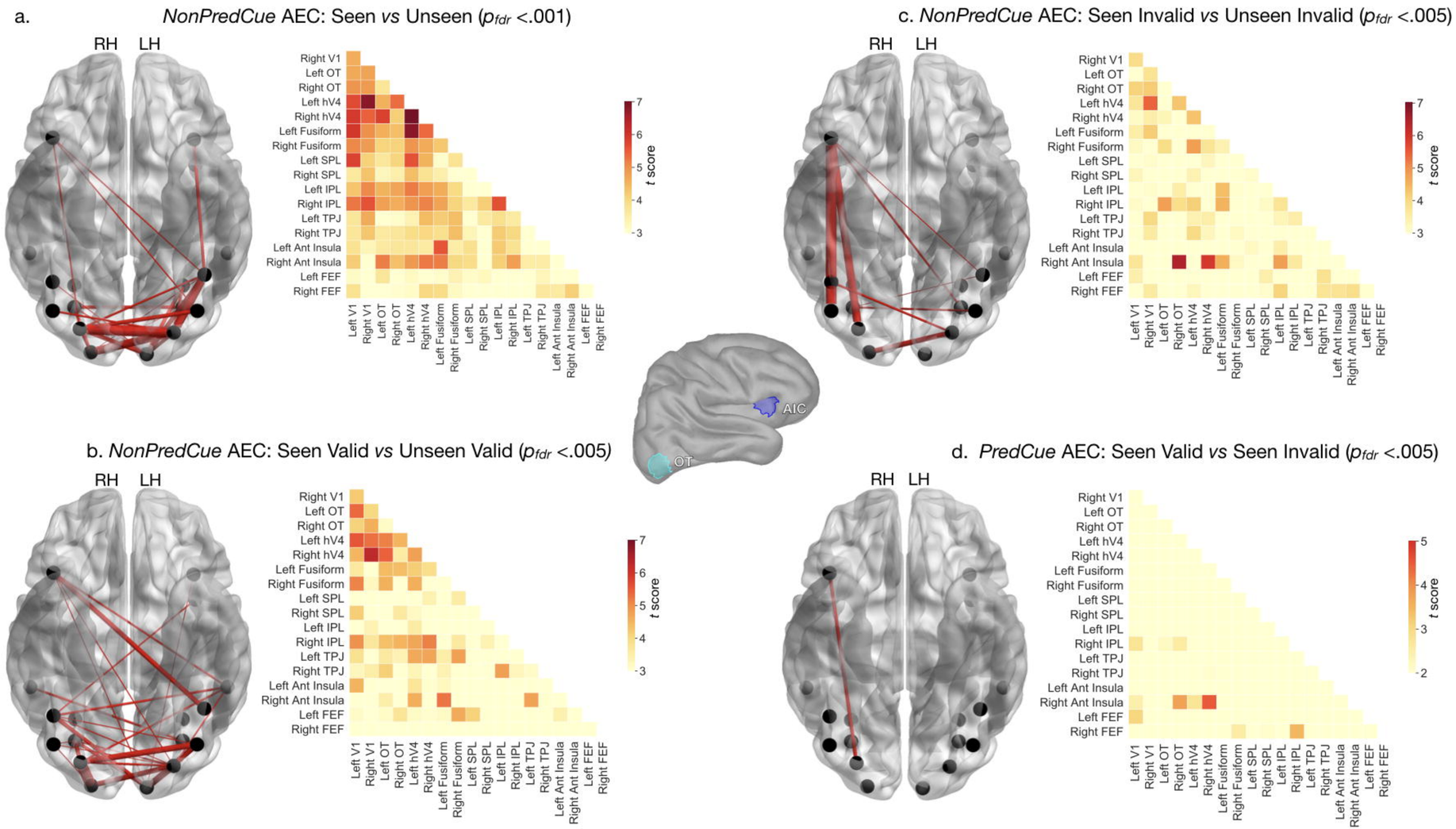
Note: ROIs were selected based on results from previous studies (Corbetta and Shulman, 2002; Fan et al., 2005; Tallon-Baudry et al., 2005; Bressler et al., 2008; Chica et al., 2013c; Chica et al., 2016b; Xuan et al., 2016) showing the involvement of these areas in attention-related processes. In addition, areas of the ventral visual stream were also added to the ROI analyses to examine the potential modulation of the activity in attention network regions on

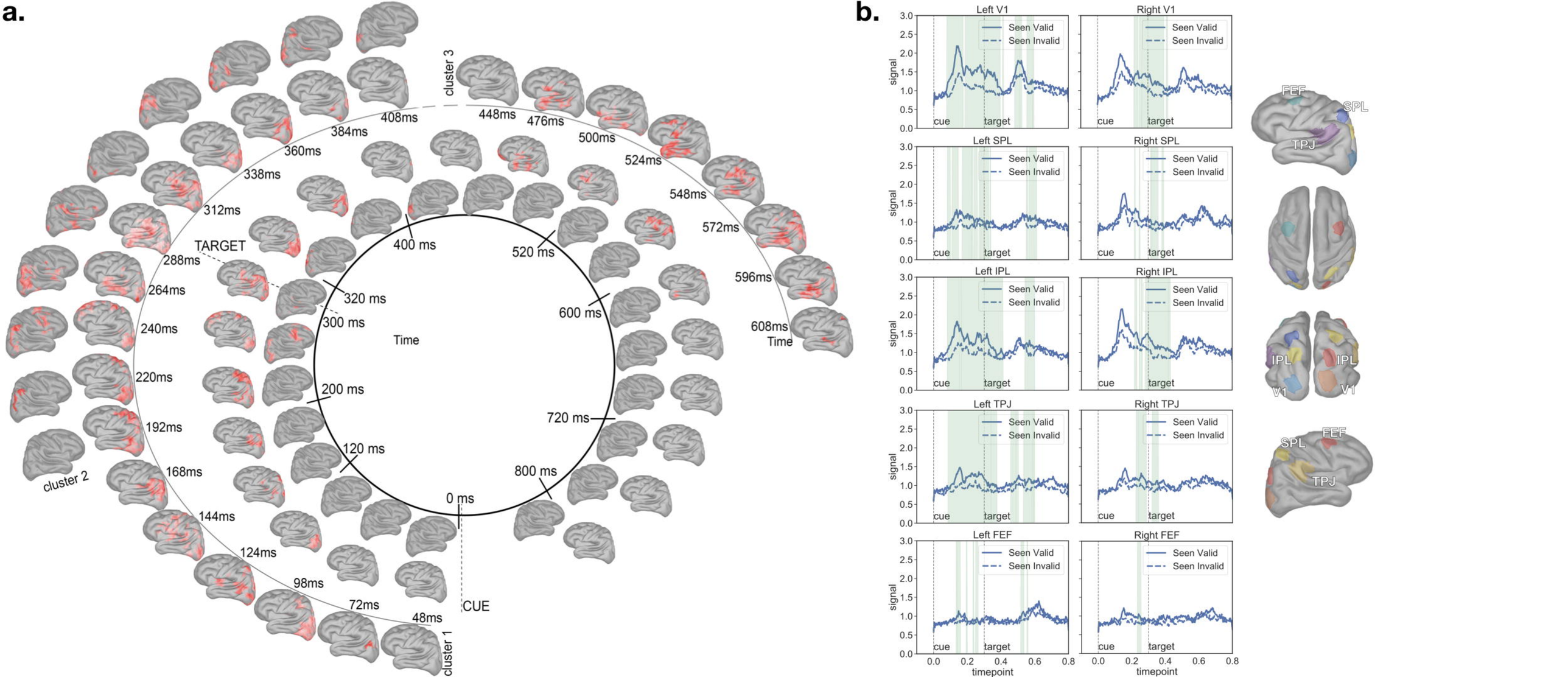
early and late visual areas. Seed vertices of the ROIs are reported in MNI coordinates, and the area of the ROI is reported in cm^2.

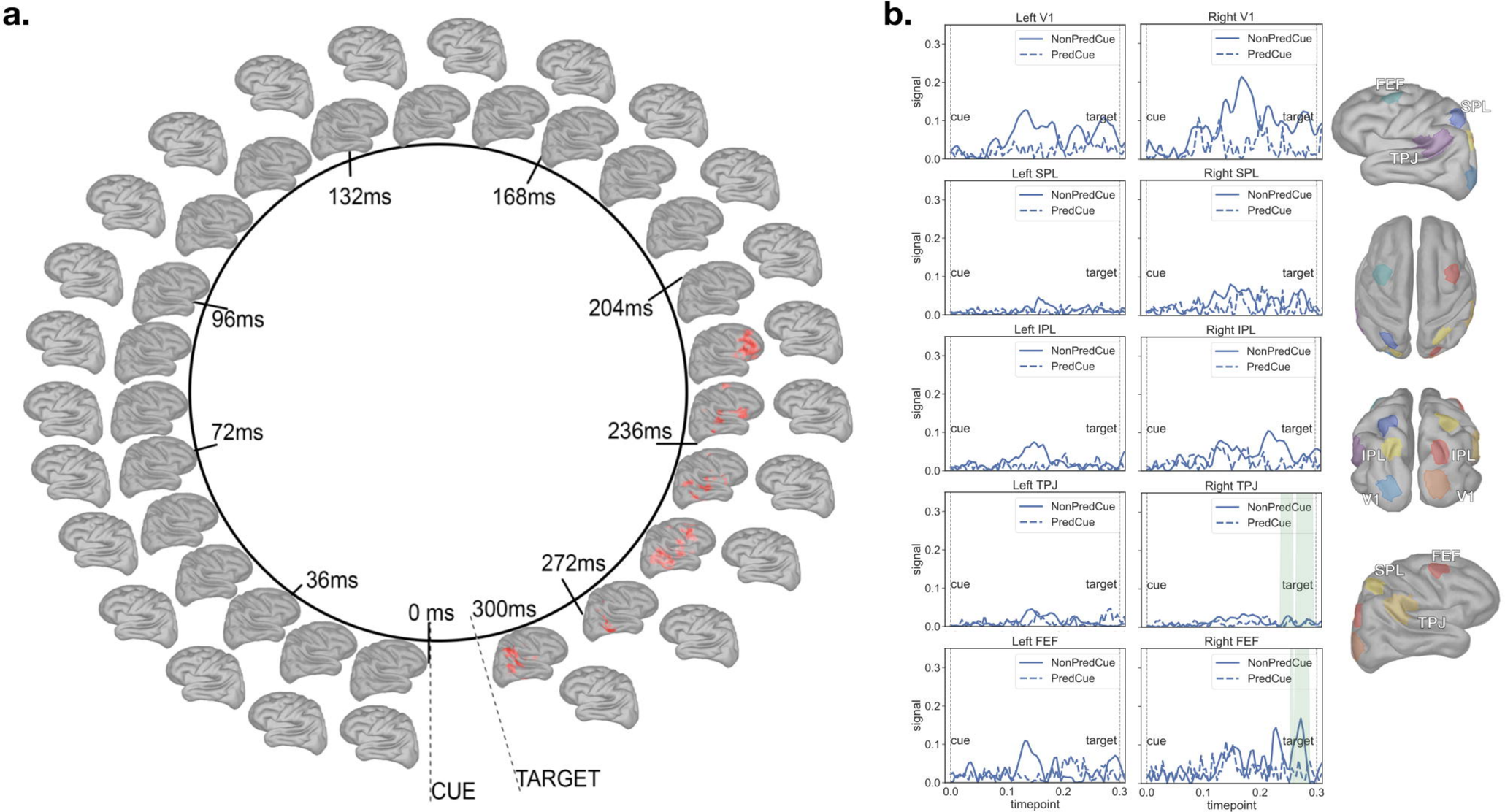

a.
Fixation
1000 to 1500 ms
Cue
50 ms
Fixation
250 ms
Target
16 ms
Fixation
484 ms
Discrimination Task
Detection Task
<<<<<<<<
>>>>>>>>
absent
Time
b.
4,9°
3,6°
2,5°
4°
1°
6°
c.
NonPredCue
Invalid
Cue (50%)
Fixation
Target
d.
PredCue
Valid
Cue (67%)
Fixation
Target


a.
Left Visual Field
Right Visual Field
Accuracy (%)
Seen
Unseen
b.
Response Time (ms)
c.
D prime
Valid
Invalid
d.
Criterion
e.
Detection (%)
f.
Valid
Invalid
Response
g.
h.
Validity
i.
j.


a.
cluster 2
cluster 1
400 ms
412 ms
424 ms
432 ms
444 ms
456 ms
468 ms
476 ms
488 ms
500 ms
Time
TARGET
400 ms
520 ms
320 ms
300 ms
600 ms
200 ms
720 ms
120 ms
800 ms
0 ms
CUE
b.
FEF
SPL
TPJ
IPL
V1
Left V1
Right V1
Left SPL
Right SPL
Left FEF
Right FEF
Seen
Unseen
signal
cue
target
timepoint


a. NonPredCue AEC: Seen vs Unseen (p_{fdr} <.001)
b. NonPredCue AEC: Seen Valid vs Unseen Valid (p_{fdr} <.005)
c. NonPredCue AEC: Seen Invalid vs Unseen Invalid (p_{fdr} <.005)
d. PredCue AEC: Seen Valid vs Seen Invalid (p_{fdr} <.005)
RH
LH
AIC
OT
Right V1
Left OT
Right OT
Left hV4
Right hV4
Left Fusiform
Right Fusiform
Left SPL
Right SPL
Left IPL
Right IPL
Left TPJ
Right TPJ
Left Ant Insula
Right Ant Insula
Left FEF
Right FEF
t score


a.
cluster 3
cluster 2
cluster 1
TARGET
CUE
Time
0 ms
120 ms
200 ms
300 ms
320 ms
400 ms
520 ms
600 ms
720 ms
800 ms
48ms
72ms
98ms
124ms
144ms
168ms
192ms
220ms
240ms
264ms
288ms
312ms
338ms
360ms
384ms
408ms
448ms
476ms
500ms
524ms
548ms
572ms
596ms
608ms
b.
Left V1
Right V1
Left SPL
Right SPL
Left IPL
Right IPL
Left TPJ
Right TPJ
Left FEF
Right FEF
Seen Valid
Seen Invalid
signal
cue
target
timepoint
FEF
SPL
TPJ
IPL
V1


a.
132ms
168ms
96ms
204ms
72ms
236ms
36ms
272ms
0 ms
300ms
CUE
TARGET
b.
Left V1
Right V1
Left SPL
Right SPL
Left IPL
Right IPL
Left TPJ
Right TPJ
Left FEF
Right FEF
NonPredCue
PredCue
cue
target
signal
timepoint
FEF
SPL
TPJ
IPL
V1