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## **Distinct Contributions of Nonpredictive and Predictive Peripheral Cues to Visual Conscious Perception: an MEG study** — [Source link](#)

Alfredo Spagna, Alfredo Spagna, Dimitri J. Bayle, Zaira Romeo ...+3 more authors

**Institutions:** Columbia University, Allen Institute for Brain Science, Paris West University Nanterre La Défense, University of Padua ...+2 more institutions

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### Abstract

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Do we need attention to become aware of an external event? We used

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magnetoencephalography (MEG) in human participants to assess the effects of nonpredictive

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and predictive supra-threshold peripheral visual cues on the conscious perception of near-

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threshold Gabor patches. Both nonpredictive and predictive valid cues increased the number

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of detected targets, and shifted the response criterion towards a more liberal decision.

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Predictive cues unexpectedly induced a greater sensitivity ( $d'$ ) for invalid trials than for valid

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trials. With nonpredictive cues, seen targets were associated with right-lateralized

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frontoparietal feed-forward and feedback sweeps. For seen targets there was increased

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connectivity among visual regions, and between these areas and the inferior parietal lobes and

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the anterior insular cortices (AIC), bilaterally. Valid predictive cues interacted with conscious

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target detection, with greater activation of areas mostly located in the left hemisphere,

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especially in the frontoparietal network and temporoparietal junction, and induced an

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increased connectivity between the right AIC and areas of the visual ventral stream in the

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seen condition only. Thus, neural activity induced by nonpredictive and predictive spatial

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cues can enhance conscious visual perception through distinct mechanisms, mostly relying on

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frontoparietal activity in the right or left hemisphere, respectively. Connectivity involving the

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AIC participates in shaping the interaction between attention and conscious visual perception.

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### Significance Statement

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Do we need to pay attention to external objects in order to become aware of them?

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Characterizing the spatiotemporal dynamics of attentional effects on visual perception is

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critical to understand how humans process information coming from relevant aspects of their

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environment. Participants detected near-threshold visual targets preceded by supra-threshold

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spatial cues with varying degrees of predictivity, while their brain activity was recorded using

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

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## 62 **Introduction**

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

71           Studies investigating how attention modulates conscious perception mainly focused on  
72 visuospatial orienting, which enhances the processing of stimuli appearing in a specific region  
73 of the visual field (Posner, 1980). Nonpredictive visual cues, which are not informative about  
74 the future location of the target, exogenously capture attention (Fan et al., 2002; Funes et al.,  
75 2007; Chica et al., 2013b; Spagna et al., 2015). For short stimulus-onset asynchronies (SOAs)  
76 a benefit in performance often occurs when the cue and the target appear on the same side  
77 (so-called “valid” trials), compared to when they occur on opposite sides (“invalid” trials).  
78 More endogenous, or goal-driven forms of orienting occur with predictive cues that correctly  
79 indicate the location of the upcoming target in most trials. Neuroimaging studies have shown  
80 partially distinct neural processes underlying exogenous and endogenous orienting (Corbetta  
81 and Shulman, 2002; Fan et al., 2005; Chica et al., 2013b; Xuan et al., 2016), but the  
82 spatiotemporal dynamics of these mechanisms remain unclear, possibly due to insufficient  
83 temporal resolution.

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

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87 Kentridge et al., 2008; Liu et al., 2009; Van Boxtel et al., 2010; Tsuchiya and Koch, 2014,  
88 2016; Botta et al., 2017; Vernet et al., 2019). Peripheral predictive cues engage a mix of  
89 exogenous and endogenous orienting mechanisms, because they initially capture attention  
90 exogenously, but as time passes attention is endogenously kept at the cued location. This  
91 endogenous persistence is apparently strategic, because it is more likely that the target appears  
92 at the cued location (but see Bartolomeo et al., 2007). A series of studies (Chica et al., 2011b;  
93 Chica et al., 2013b; Botta et al., 2017) showed that exogenous attention affects perceptual  
94 consciousness, and that the maximal attentional effect on conscious perception is observed  
95 when attention is first exogenously captured, and then endogenously maintained at the target  
96 location. Characterizing the spatial and temporal dynamics of the neural substrates supporting  
97 possible interactions between attentional orienting and visual conscious processing could  
98 reduce the tension between competing, but not necessarily mutually exclusive, theoretical  
99 frameworks.

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

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

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

## 117 **Materials and Methods**

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

127 In total, 37 participants were recruited across two experiments. Eighteen participants  
128 completed the experiment with nonpredictive cues (age =  $24 \pm 3.13$  years; age range = 22-33  
129 years; 6M), and nineteen participants completed the experiment with predictive cues (age =  
130  $24 \pm 3.79$  years; age range = 20-32 years; 7M). Five participants had to be excluded from data  
131 analysis of the predictive cue experiment, due to issues in the data quality of MEG recordings.  
132 All participants reported normal or corrected-to-normal vision, and gave written informed  
133 consent before participation. The study was approved by the INSERM and by the Institutional  
134 Review Boards of Paris Ile de France (CPP 1).

135 *Stimuli and Procedure.* The tasks were compiled and run using E-Prime software (RRID:  
136 SCR\_009567; Psychology Software Tools, Pittsburgh, PA) on a Windows XP desktop



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

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

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

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

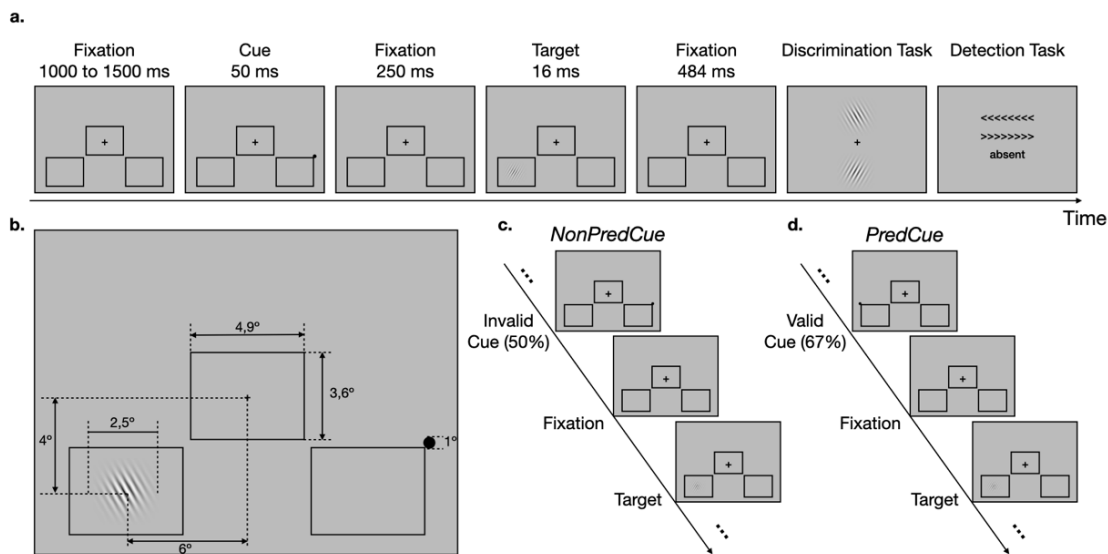
179 Each trial started with a fixation display, whose duration varied randomly between  
180 1,000ms and 1,500ms. In the target-present trials, a cue occurred 300ms before targets, in the  
181 form of a black dot with a 1° diameter, and presented for 50ms near the external upper corner  
182 of one of the two peripheral boxes. Such a small cue was used in order to avoid possible  
183 phenomena of perceptual interference with the subsequent, near-threshold target.

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

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

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



198  
199 **Figure 1 a.** Schematic representation of the sequence of events in an invalid-cue trial. **b.** Size of the stimuli and  
200 exact location of presentation on the screen. The experiment with nonpredictive cues (*NonPredCue*) and the  
201 experiment with predictive cues (*PredCue*) shared the same sequence of event and size of stimuli; **c.** in the  
202 *NonPredCue* experiment 50% of cues were valid and 50% were invalid; **d.** in the *PredCue* experiment 67% of  
203 cues were valid and 33% were invalid.

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204 *MEG recordings.* Continuous MEG recordings were conducted at the CENIR  
205 (<http://www.cenir.org>) with an ELEKTA Neuromag TRIUX<sup>®</sup> machine (204 planar  
206 gradiometers and 102 magnetometers) located in a magnetically shielded room with a  
207 sampling frequency rate of 1kHz and a bandwidth ranging from 0.01 to 300 Hz. The  
208 recordings were then MaxFiltered (v2.2) (Taulu and Simola, 2006) to attenuate environmental  
209 noise, Signal Space Separation (SSS) was then implemented, automatic detection of bad  
210 channels was conducted, data were filtered (1 to 250 Hz), and resampled at a rate of 250Hz,  
211 and then converted in the Fieldtrip structure (RRID: SCR\_004849;  
212 <http://www.fieldtriptoolbox.org/>) (Oostenveld et al., 2011) to conduct further preprocessing  
213 and analytic steps. Cardiac activity (electrocardiogram – ECG), vertical and horizontal EOG  
214 signals were also recorded together with the electrophysiological data. The exact timing of the  
215 presentation of the stimuli onset was corrected in accordance to the signal received from a  
216 photodiode located in the MEG room, in order to adjust to the delay produced by the refresh  
217 rate of the projector.

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

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229 delay between the trigger of the cue and the photodiode was greater than 40ms or smaller than  
230 30ms, for a total of ~1% of the trials. Last, trials contaminated by muscular activity (jump or  
231 movement) were rejected manually upon visual inspection (~15%). For the nonpredictive cue  
232 experiment, out of the 15,840 trials acquired, 8517 trials were analyzed (*right visual field*:  
233 seen invalid = 1033; seen valid = 1284; unseen invalid = 1056; unseen valid = 882; *left visual*  
234 *field*: seen invalid = 1191; seen valid 1176; unseen invalid = 956; unseen valid = 939). For the  
235 predictive cue experiment, out of the 10,796 trials acquired in total, 7454 trials were analyzed  
236 (*right visual field*: seen invalid = 396; seen valid = 1588; unseen invalid = 812; unseen valid =  
237 1379; *left visual field*: seen invalid = 639; seen valid 1144; unseen invalid = 576; unseen valid  
238 = 1379) (see **Table S1** for a subject-by-subject breakdown of the number of trials in each  
239 condition remaining after artifact rejection).

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

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

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254 dipole, oriented normally to the surface. Further processing conducted on the sources per  
255 participant consisted of z-score transformation of the signal with reference to the baseline  
256 (from -1,000 to -2ms). A spatial smoothing kernel (FWHM = 3mm) was then applied on the  
257 sources, that were then re-interpolated (projected) on a common template (default anatomy).  
258 *MRI recordings.* High-resolution T1-weighted structural MRI images (MPRAGE sequence,  
259 flip-angle, 9; Repetition Time, 2300ms; Echo Time, 4.18ms; voxel size: 1 × 1 × 1 mm) were  
260 acquired for each participant using a 3-T Siemens, TRIO whole-body MRI scanner (Siemens  
261 Medical Solutions, Erlangen, Germany) located at the CENIR MRI center (Salpêtrière  
262 Hospital, Paris, France). After acquisition, images were then segmented using the FreeSurfer  
263 “recon-all” pipeline (Fischl, 2012), and imported in Brainstorm (Tadel et al., 2011) for co-  
264 registration purposes. MEG sensors and structural MRI images were first manually aligned  
265 using the nasion/left ear/right ear (NAS/LPA/RPA) fiducial points recorded in the MEG file  
266 and in the MRI MNI coordinates. Co-registration was then further refined using the “refine  
267 using head points” option on Brainstorm, which uses an iterative closest point algorithm to fit  
268 the head shape and the digitized scalp points. Additional details about the MRI-MEG co-  
269 registration steps as done in Brainstorm can be found here (Tadel et al., 2019).  
270 *Behavioral Data Analysis.* Response times (RTs) below 150ms (anticipated responses) and  
271 above 1,800ms (delayed responses) were excluded from subsequent analyses (below 2% of  
272 total number of trials). Independent sample *t*-tests were used to assess potential differences in  
273 the thresholds sampled during the calibration sessions separately for invalid and valid cue  
274 trials. Analysis of Variance (ANOVA) and Signal Detection Theory (SDT) analyses were  
275 conducted to examine whether and how nonpredictive and predictive cues modulated visual  
276 conscious perception. The Kolmogorov-Smirnov and the Shapiro Wilk test for normality were  
277 conducted to examine whether the data on accuracy was normally distributed. For both RT  
278 and Accuracy (in percentage), a 2 (seen, unseen) × 2 (valid, invalid) repeated measures

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

296 *MEG data analysis.* In parallel with the behavioral analyses,  $2$  (seen, unseen)  $\times$   $2$  (valid,  
297 invalid)  $\times$   $2$  (left, right) repeated-measures ANOVAs were conducted on individuals'  
298 estimated activity (z-scores) of reconstructed source images to examine how neuronal activity  
299 induced by nonpredictive cues can enhance conscious perception. Spatiotemporal cluster-  
300 based permutation tests (Maris and Oostenveld, 2007) were used for comparing main effects  
301 and interactions between brain activations in the time window between 0 and 800ms (locked  
302 to cue onset), with the number of permutations set to 1000 and the alpha threshold level set to  
303 0.05 for all tests.

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304 *Connectivity Analysis.* To examine the modulation in connectivity between brain areas as a  
305 result of the experimental conditions, we estimated leakage-controlled (orthogonalized) high-  
306 gamma (60 to 90 Hz) amplitude envelope correlation (AEC) (Brookes et al., 2012; Colclough  
307 et al., 2015) of eighteen regions of interest (ROIs). Analyses were conducted solely on the  
308 high-gamma frequency band because of the extensive knowledge on the role of the oscillatory  
309 synchronization in this frequency band in spatial attention and its modulation of visual areas  
310 (Tallon-Baudry et al., 2005; Magazzini and Singh, 2018; Fiebelkorn and Kastner, 2019).  
311 ROIs were selected on the basis of previous results (Corbetta and Shulman, 2002; Fan et al.,  
312 2005; Tallon-Baudry et al., 2005; Bressler et al., 2008; Chica et al., 2013c; Chica et al.,  
313 2016b; Xuan et al., 2016), showing their involvement in attention-related processes. In  
314 addition, areas of the ventral visual stream were also added to the ROI analyses to examine  
315 potential frontoparietal modulation of activity in early and late visual areas. The ROIs were  
316 created using Brainstorm (Tadel et al., 2011), seed vertices and area (in cm<sup>2</sup>) of the ROIs are  
317 listed in **Table 1** (in MNI coordinates). Paired sample *t*-tests ( $p < .05$ , FDR corrected) were  
318 used to compare the AEC estimates across experimental conditions.

319 **Results**

320 *Does the validity of nonpredictive cues affect participants' response to visual Gabor*  
321 *targets?* To answer this question, we examined behavioral responses to seen and unseen  
322 targets separately for valid and invalid nonpredictive cues. Valid cues, compared to invalid  
323 cues, lowered the response criterion (mean  $\pm$  SD valid:  $0.85 \pm 0.28$ ; invalid:  $1.03 \pm 0.27$ ;  $t(17)$   
324  $= -2.82$ ;  $p < .05$ ), and increased the percentage of detected targets (mean  $\pm$  SD valid:  $0.57 \pm$   
325  $0.09$ ; invalid:  $0.52 \pm 0.11$ ;  $t(17) = -3.08$ ;  $p < .01$ ). However, sensitivity ( $d'$ ) was similar for  
326 valid and invalid trials (valid:  $2.30 \pm 0.57$ ; invalid:  $2.29 \pm 0.47$ ;  $t(17) < 1$ ) (see **Fig 2**). These  
327 results did not depend on different perceptual thresholds resulting from the calibration  
328 session, because these thresholds were similar for valid trials (43.98%) and for invalid trials



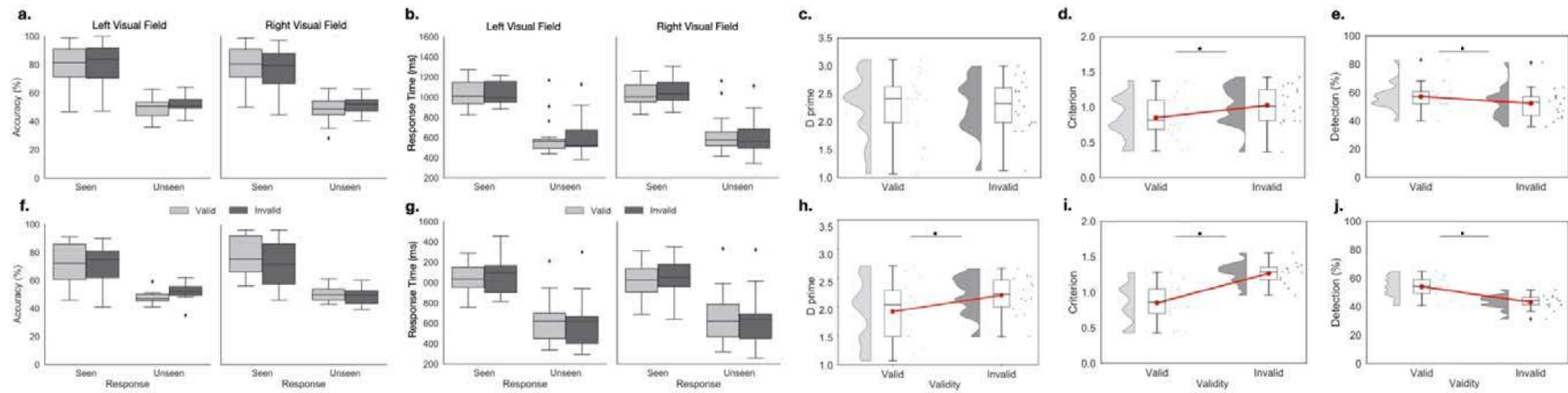
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329 (43.99%;  $t < 1$ ). Left- and right-sided targets evoked a similar number of correct responses  
330 (sum of the total number of correctly discriminated targets presented to the left visual field:  
331 3,489; mean  $\pm$  SD:  $194.83 \pm 37.05$ ; sum of the total number of correctly discriminated targets  
332 presented to the right visual field: 3,507; mean  $\pm$  SD:  $194.83 \pm 33.6$ ; Wilcoxon signed-rank  
333 test = 76;  $p = .70$ ; Bayesian Wilcoxon signed-rank test  $BF_{10} = 0.56$ , with median posterior  $\delta =$   
334  $-0.079$ , 95% CI  $[-1.07, 0.91]$ ).

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

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

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344

345 **Figure 2.** Results of the behavioral analyses conducted on performance with nonpredictive cues (a.-e.) and with predictive cues (f.-j.). **a.** and **b.**

346 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

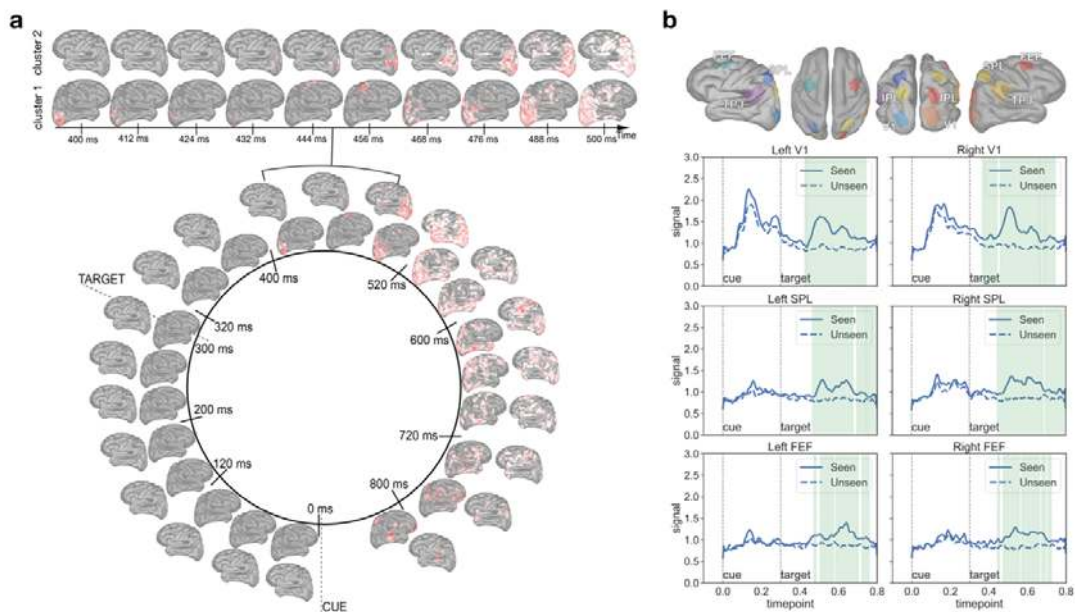
347 Detection Theory analysis for  $d'$ , criterion, and detection (in percentage). **f.** and **g.** report result of the ANOVA conducted on Accuracy (in

348 percentage) and RT (in ms), respectively, while **h.**, **i.**, and **j.** report results of the SDT analysis for  $d'$  prime, criterion, and detection (in

349 percentage).

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350 ***Does the validity of nonpredictive cues affect neural responses associated with the***  
351 ***conscious report of visual Gabor targets?*** We addressed this question by examining brain  
352 responses to seen and unseen targets separately for valid and invalid nonpredictive cues.  
353 Source analysis of the MEG signal revealed that conscious perception was associated with  
354 right-lateralized frontoparietal feed-forward and feedback sweeps. Two clusters exceeding the  
355 threshold of randomization distribution under H<sub>0</sub> emerged for the seen vs unseen comparison  
356 (both  $p_s < 0.001$ ) in the time window of 400 - 800ms after cue onset. The first cluster was in  
357 the right hemisphere, the second in the left hemisphere. Both clusters started in the occipital  
358 cortex and afterwards extended to the frontoparietal network and temporal regions, bilaterally  
359 (see **Fig 3**). The differences for the main effects of *Validity* (valid, invalid), for the main effect  
360 of *Visual Field* (left, right), and for the interactions did not reach statistical significance.  
361 Control analyses showed that there was no significant difference between the number of MEG  
362 trials for left- and right-sided targets (left visual field, mean  $\pm$  SD: 235.39  $\pm$  32.49; right  
363 visual field, 235.5  $\pm$  30.02; Wilcoxon signed-rank test = 85;  $p = 1$ ; Bayesian Wilcoxon  
364 signed-rank test  $BF_{10} = 0.57$ , with median posterior  $\delta = -0.05$ , 95% CI [-1.09, 0.96]).



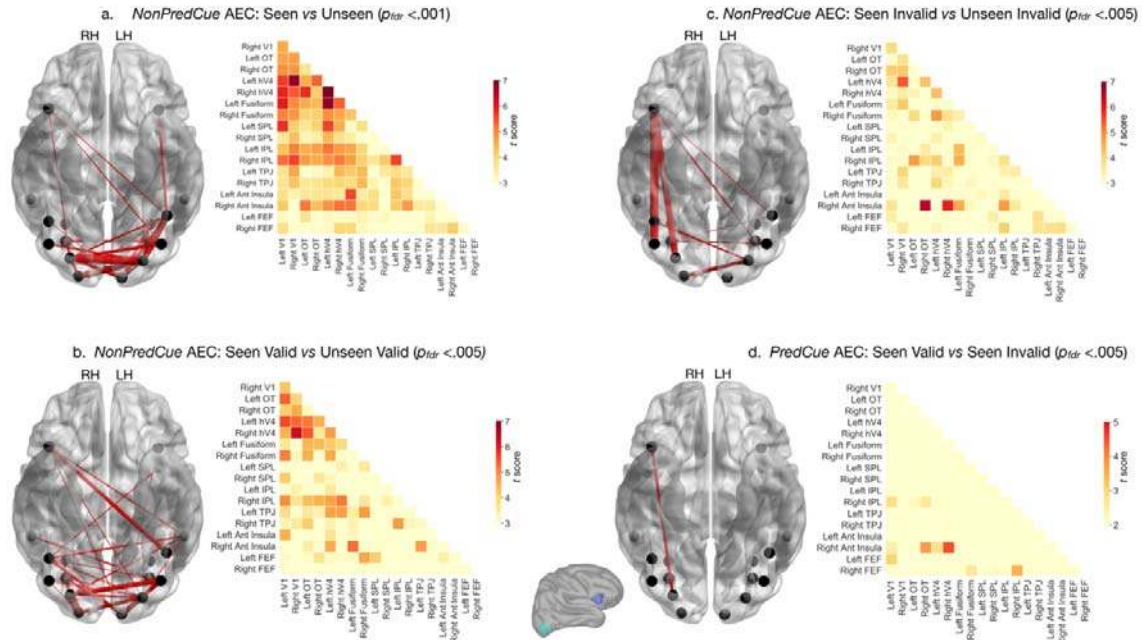
365

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

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

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388

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

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

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404 ***Does the validity of predictive cues affect participants' response to visual Gabor targets?*** To  
405 address this issue, we examined behavioral responses to seen and unseen targets separately for  
406 valid and invalid predictive cues. As did nonpredictive cues, also valid predictive cues,  
407 compared to invalid predictive cues, lowered the response criterion (mean  $\pm$  SD valid:  $(0.85 \pm$   
408  $0.28; 1.26 \pm 0.15; (t(13) = -6.37; p < .001)$ , because participants adopted a more liberal  
409 response threshold in the valid cue condition, and increased the percentage of detected targets  
410 (mean  $\pm$  SD valid:  $54.11 \% \pm 7.13\%$ ; invalid:  $43.33 \pm 5.14\%$ ;  $t(13) = 8.06; p < .001$ ).  
411 However, *sensitivity* ( $d'$ ) was greater for invalid trials ( $2.20 \pm 0.33$ ) than for valid trials ( $1.91$   
412  $\pm 0.54$ ) ( $t(13) = -2.29; p < .05$ ) (see **Fig 2**). These results did not depend on possible  
413 differences between the thresholds established separately for valid and invalid trials cue trials  
414 during the calibration session (valid trials:  $59.21$ ; invalid trials:  $60.79; t < 1$ ). Unexpectedly,  
415 right-sided targets evoked more correct responses than left-sided ones (right visual field, mean  
416  $\pm$  SD:  $220.21 \pm 35.42$ ; left visual field,  $194.72 \pm 21.89$ ; Wilcoxon signed-rank test =  $6.00; p <$   
417  $.01$ ; Bayesian Wilcoxon signed-rank test  $BF_{10} = 4.06$ , with median posterior  $\delta = -1.19$ , 95%  
418 CI  $[-2.51, 0.01]$ ).

419 Results of the ANOVA conducted on Accuracy percentages to the discrimination task  
420 (after ensuring that these percentages followed a normal distribution by using the  
421 Kolmogorov-Smirnov and the Shapiro Wilk tests for normality) are shown in **Fig 2f**. There  
422 was a main effect of the factor *Consciousness* ( $F_{(1,13)} = 31.62; p < .0001; \eta^2 = .71$ ), because  
423 participants were more accurate for *Seen* trials ( $72.87 \pm 15.2\%$ ) than for *Unseen* ( $49.71 \pm$   
424  $5.9\%$ ) trials. No other effect or interaction reached significance, except for the interactions  
425 between *Consciousness* and *Validity* ( $F_{(1,13)} = 11.9; p < .01; \eta^2 = .48$ ) and between *Visual*  
426 *Field* and *Validity* ( $F_{(1,13)} = 8.89; p < .05; \eta^2 = .41$ ). Pairwise comparisons showed that the  
427 difference between valid and invalid trials was significant for the seen trials (valid:  $74.88 \pm$   
428  $14.41\%$ ; invalid:  $70.86 \pm 16.14\%$ ;  $p < .01$ ), but not for the unseen trials (valid:  $48.91 \pm 5.13\%$ ;



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

432 Results of the ANOVA conducted on the RTs (see **Fig 2g**) showed that participants  
433 responded slower to *Seen* targets ( $1048 \pm 171$ ms) than to *Unseen* ones ( $640 \pm 259$ ms;  $F_{(1,13)} =$   
434  $28.91$ ;  $p < .0001$ ;  $\eta^2 = .69$ ). The main effects of *Visual Field* and *Validity* did not reach  
435 significance (both  $F_s < 1$ ). *Consciousness* interacted with *Visual Field* ( $F_{(1,13)} = 5.08$ ;  $p < .05$ ;  
436  $\eta^2 = .28$ ), because the seen/unseen difference was greater for left-sided targets (seen:  $1,055 \pm$   
437  $168$ ms; unseen:  $624 \pm 249$ ms;  $p < .001$ ) than for right-sided targets (seen:  $1,040 \pm 177$ ;  
438 unseen:  $656 \pm 272$ ;  $p < .001$ ).

439 ***Does the validity of predictive cues affect neural responses associated with the conscious***  
440 ***report of visual Gabor targets?*** We addressed this question by examining brain responses to  
441 seen and unseen targets separately for valid and invalid predictive cues. Similar to the  
442 experiment with nonpredictive cues, two clusters exceeding the threshold of randomization  
443 distribution under  $H_0$  emerged for the seen vs unseen comparison ( $ps < 0.001$ ), both in the  
444 time window of 460 - 760ms after cue onset. The first cluster was lateralized to the right  
445 hemisphere, the second was lateralized to the left hemisphere. Both started in the occipital  
446 cortex and then spread to the parieto-temporal regions, without any evidence of involvement  
447 of prefrontal regions. *Consciousness* interacted with *Validity*. Four clusters exceeding the  
448 threshold of randomization distribution under  $H_0$  were found for the interaction term ((seen  
449 valid *minus* unseen valid) *minus* (seen invalid *minus* unseen invalid)). The first cluster ( $p <$   
450  $0.001$ ) occurred in the 100 - 150ms time window after cue onset, and was lateralized to the  
451 left visual cortex; the second cluster ( $p < 0.05$ ), was also lateralized to the left visual cortex  
452 and left IPL, in the 300 - 380ms time window after cue onset; the third cluster ( $p < 0.05$ )  
453 occurred in the inferior temporal lobe of the right hemisphere and spanned across the time

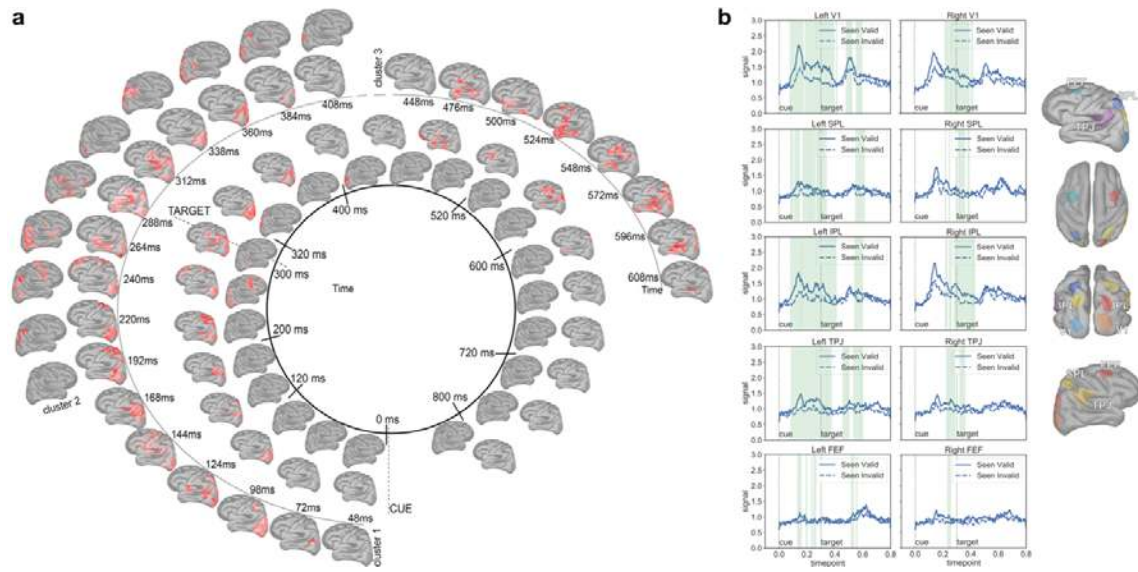
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454 window of 550 and 600ms after cue onset; the forth cluster ( $p < 0.05$ ) was localized in the left  
455 precuneus, extending into the left posterior cingulate cortex and spanned across the time  
456 window of 580 and 600ms after cue onset. **Fig 5** displays the follow-up analysis conducted in  
457 the valid *vs* invalid comparison for the seen condition only (seen valid *minus* seen invalid).  
458 Three clusters exceeded the threshold of randomization distribution under H0. A first cluster  
459 ( $p < 0.001$ ) was lateralized to the left hemisphere and occurred in the 50 - 400ms time  
460 window after cue onset, spanning across visual cortex, to the parietal cortex (around 100ms  
461 post-cue), prefrontal cortex (around 150ms post-cue), and temporoparietal cortex. A second  
462 cluster ( $p < 0.05$ ), occurred later, as a right-hemisphere occipito-parietal activation around  
463 200ms post-cue, and then substantially resembled the activity found in the first cluster,  
464 spanning across the frontoparietal cortex (around 240ms post-cue), and temporoparietal  
465 cortex (around 280ms post-cue). The third cluster ( $p < 0.05$ ) was lateralized to the left visual  
466 cortex and included middle- and infero-temporal areas, the inferior frontal gyrus (around  
467 470ms post-cue), the left frontal eye fields (524ms post-cue) and then temporoparietal,  
468 inferior parietal, and inferior temporal areas.

469 Control analyses showed that there was no significant difference between the number  
470 of MEG trials for left- and right-sided targets (left visual field mean  $\pm$  SD:  $265.43 \pm 21.16$ ;  
471 right visual field; mean  $\pm$  SD:  $266.79 \pm 26.91$ ; Wilcoxon signed-rank test = 48.5;  $p = 0.83$ ;  
472 Bayesian Wilcoxon signed-rank test  $BF_{10} = 0.58$ , with median posterior  $\delta = -0.073$ , 95% CI [-  
473 1.11, 0.94]).



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474

475 **Figure 5.** When preceded by valid predictive cues, seen targets evoked three clusters of brain  
476 activity, compared to invalidly cued targets. **a)** Cluster 1 occurred in the 50-400ms time  
477 window after cue onset and was lateralized to the left hemisphere ( $p < 0.001$ ); Cluster 2  
478 occurred in 200ms time-window after cue onset and was lateralized to the right hemisphere ( $p$   
479  $< 0.05$ ); Cluster 3: occurred 470ms after cue onset and lateralized to the left hemisphere. The  
480 same valid-invalid comparison for unseen targets did not reveal any significant cluster. **b)**  
481 average signal changes in the ROIs separately for the Seen Valid (solid line) and Seen Invalid  
482 (dashed line) condition. The area in green highlights the time interval in which cluster-  
483 corrected analysis showed a significant difference between the two signals.

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

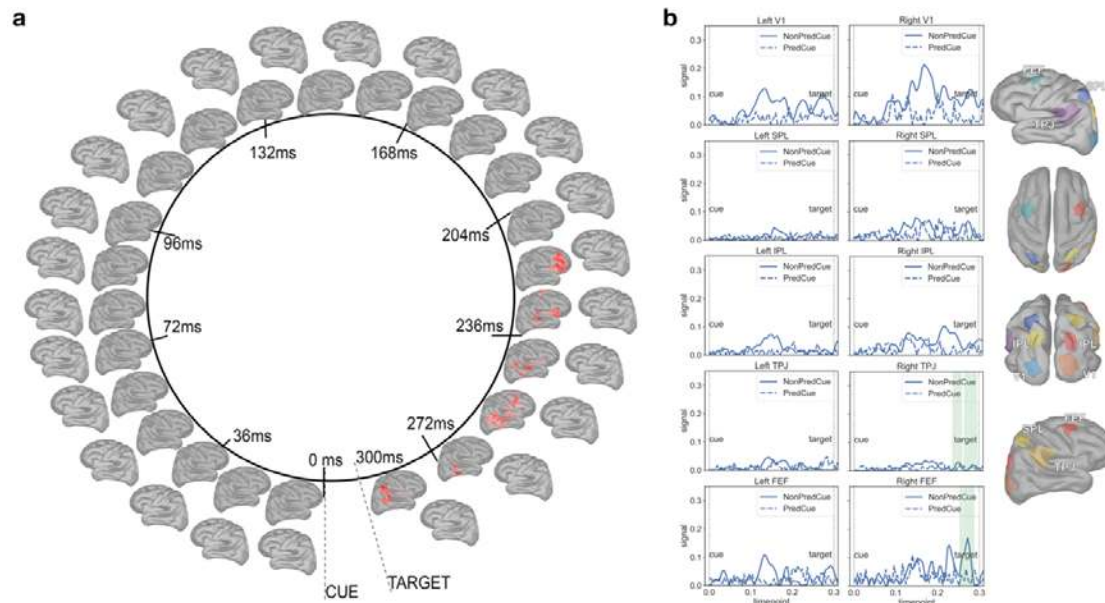
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492 Thus, similar to nonpredictive cues, also the validity of predictive cues modulated  
493 participants' conscious reports of visual Gabors for both behavioral performance and neural  
494 activity measures. Differences between seen and unseen trials with predictive cues emerged in  
495 the post-target time period, but these were delayed in time compared to the same contrast with  
496 nonpredictive cues. Bilateral activity started in the visual cortex, around 160ms after the  
497 target, and was followed by mainly temporo-parietal activity, with prefrontal activity arising  
498 only later in time (almost 300ms after the target). The interaction between attention and  
499 consciousness showed four clusters of activation located in occipito-temporal regions that  
500 spanned across both the cue-target and the post-target periods, possibly showing the *site* of  
501 attentional modulation (Posner and Driver, 1992) rather than the *source* of it (Bressler et al.,  
502 2008; Liu et al., 2016). The modulation produced by predictive cues on visual awareness was  
503 also evident in the contrast between the functional connectivity patterns in valid and invalid  
504 trials for seen targets, which again showed correlated activity in AIC and areas in the ventral  
505 visual stream, bilaterally.

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

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

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515

516 **Figure 6.** MEG activity evoked by nonpredictive vs. predictive cues for Seen vs. Unseen  
517 targets in the cue-target period (0 – 300 ms). **a.** One right-hemispheric cluster emerged in the  
518 210-300ms time window, and included the temporoparietal junction and the prefrontal cortex.  
519 **b.** Average signal changes in the ROIs separately for the experiments with nonpredictive cue  
520 (solid line) and with predictive cues (dashed line). The area in green highlights the time  
521 interval in which cluster-corrected analysis showed a significant difference between the two  
522 signals.

523

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

530 **Discussion**

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

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

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

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

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

586 *Frontoparietal networks and visual awareness.* Dysfunction of SLF II and III  
587 networks in the right hemisphere is a typical finding in brain-damaged patients with left visual  
588 neglect, who have impaired awareness of left-sided events (Bartolomeo et al., 2012). The  
589 frontoparietal activity found with nonpredictive cues seems consistent with the *forward* and  
590 *backward sweeps* associated with the awareness of a visual target (Lamme, 2006), and  
591 suggests a role for exogenous attention in this process. The relationship of these  
592 forward/backward sweeps with behavioral changes in criterion, but not in sensitivity, might  
593 be consistent with the known role of frontoparietal networks in the activation of general  
594 processes, such as the alerting system (Périn et al., 2010; Chica et al., 2016a; Baria et al.,  
595 2017; Petersen et al., 2017; Podvalny et al., 2019). An interaction of nonpredictive cues with  
596 alerting is also supported by the functional connectivity analysis, which showed a role of the  
597 right AIC in differentiating seen vs. unseen trials separately for valid and invalid trials (see  
598 **Fig 6**). This result is consistent with evidence showing the critical role of the AIC in the  
599 production and maintenance of alertness, both in terms of BOLD response and of functional  
600 connectivity (Cai et al., 2014; Sadaghiani and D'Esposito, 2015; Chica et al., 2016a; Coste  
601 and Kleinschmidt, 2016; Han et al., 2019; Haupt et al., 2019). As a node of the SLF III  
602 network, the AIC may have an important role in signaling behaviorally relevant stimuli  
603 (Uddin, 2015).

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



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

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

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629

### **Author Contributions**

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

635



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636

### **Conflict of Interest Statement**

637 The authors report no conflict of interest.

638

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639

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640

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**Tables**

**Table 1.** MNI Coordinates and size of the area (in cm<sup>2</sup>) used in the connectivity analyses.

<b>ROI</b>	<b>x</b>	<b>y</b>	<b>z</b>	<b>area</b>
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

824 Note: ROIs were selected based on results from previous studies (Corbetta and Shulman,  
825 2002; Fan et al., 2005; Tallon-Baudry et al., 2005; Bressler et al., 2008; Chica et al., 2013c;  
826 Chica et al., 2016b; Xuan et al., 2016) showing the involvement of these areas in attention-  
827 related processes. In addition, areas of the ventral visual stream were also added to the ROI  
828 analyses to examine the potential modulation of the activity in attention network regions on

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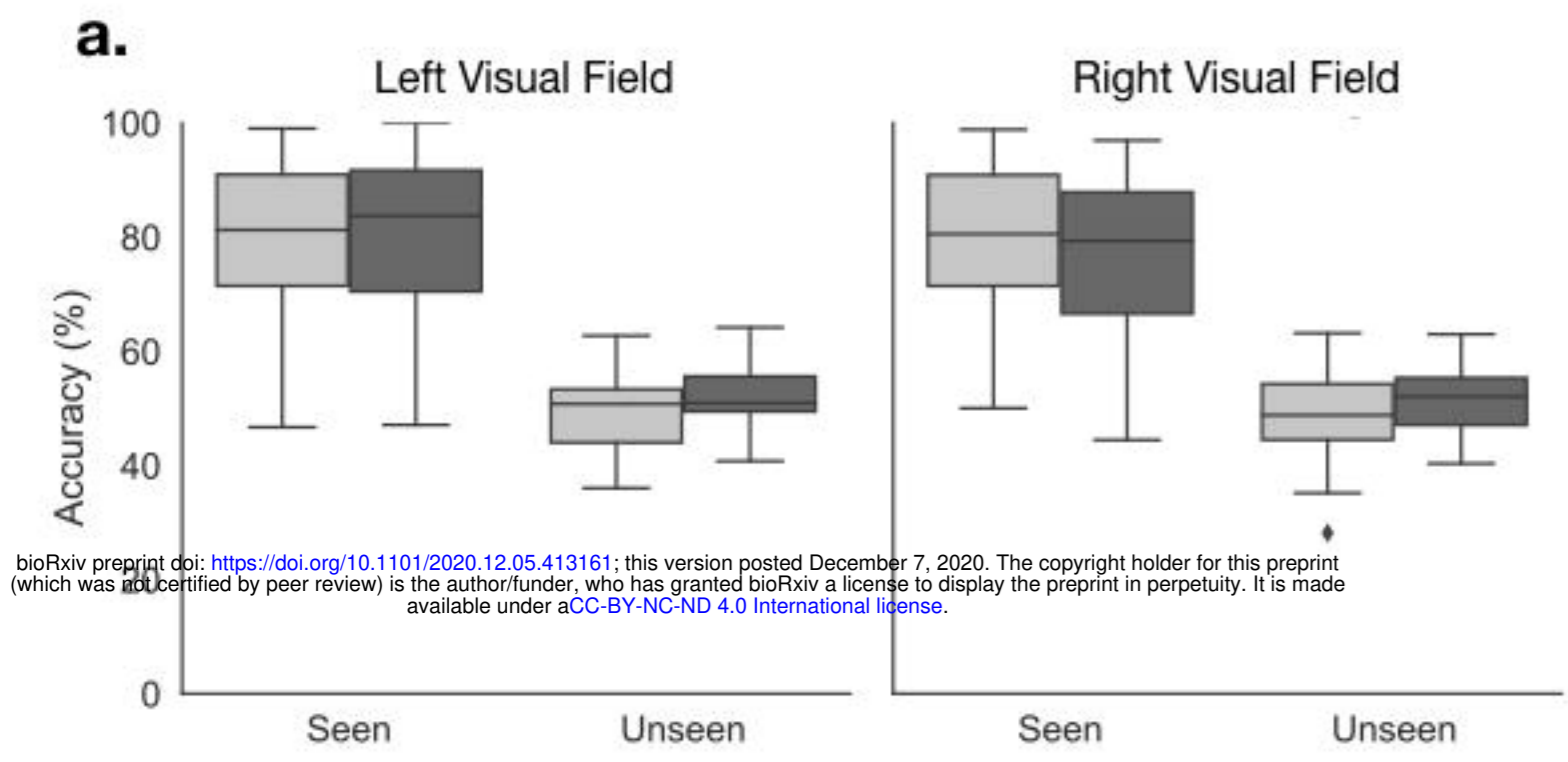
829 early and late visual areas. Seed vertices of the ROIs are reported in MNI coordinates, and the

830 area of the ROI is reported in cm<sup>2</sup>.

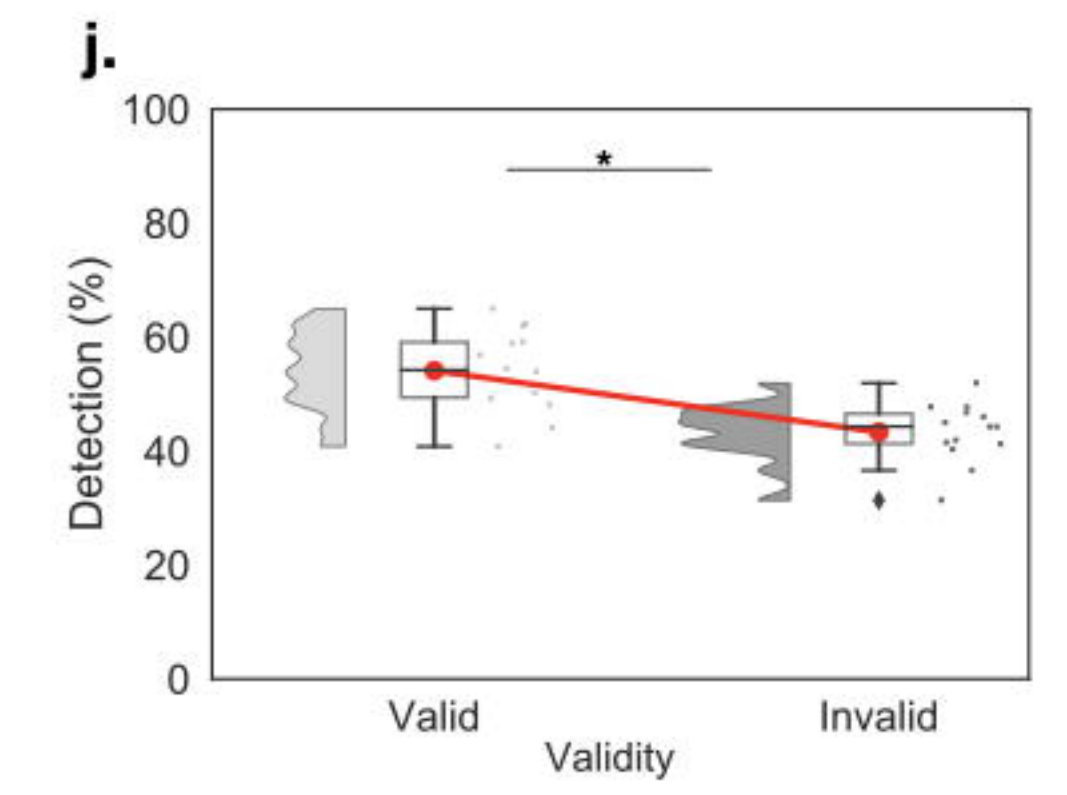
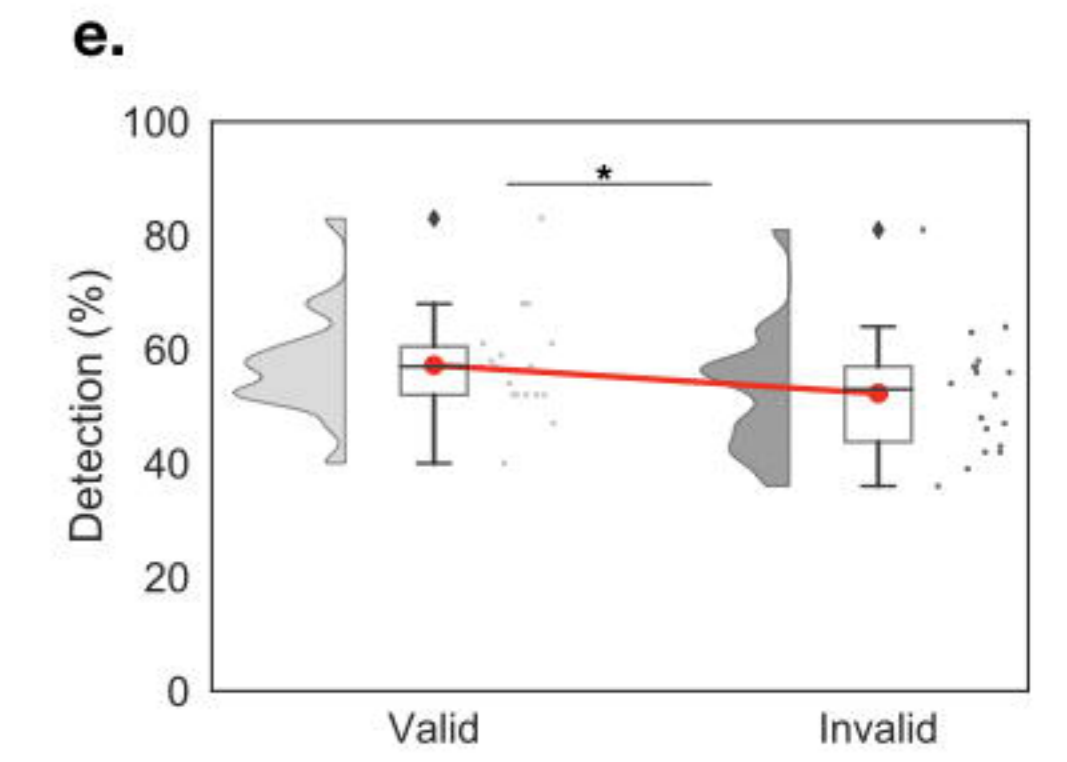
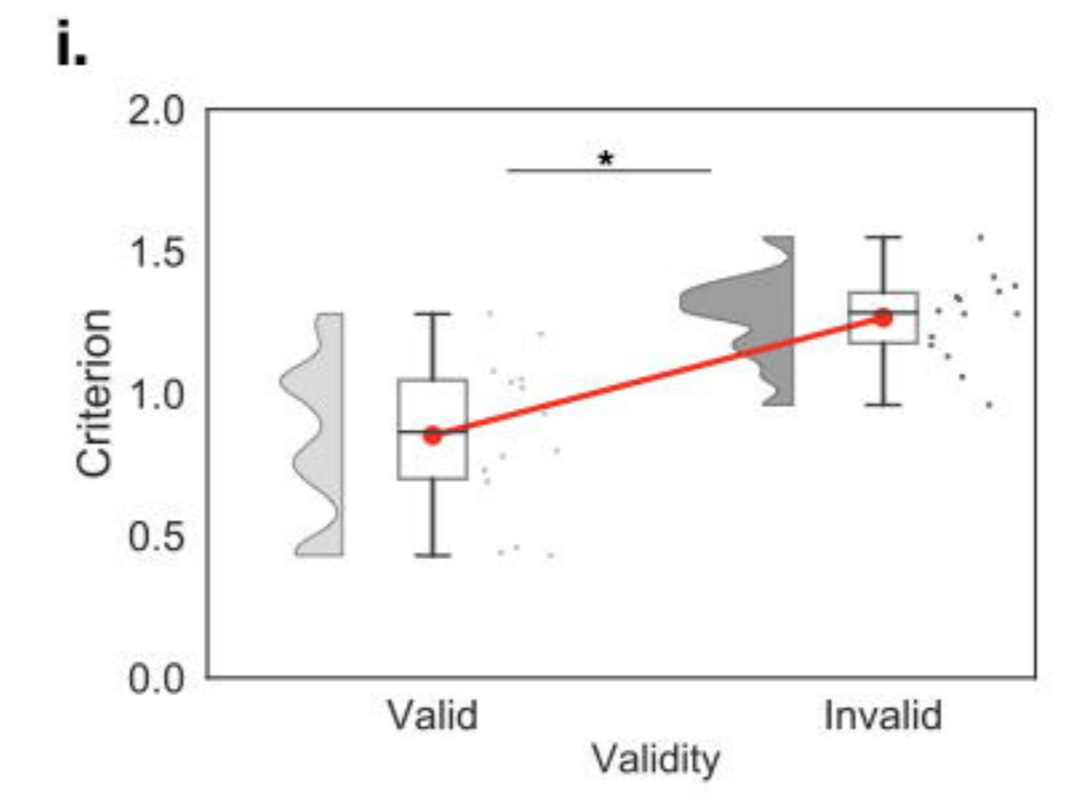
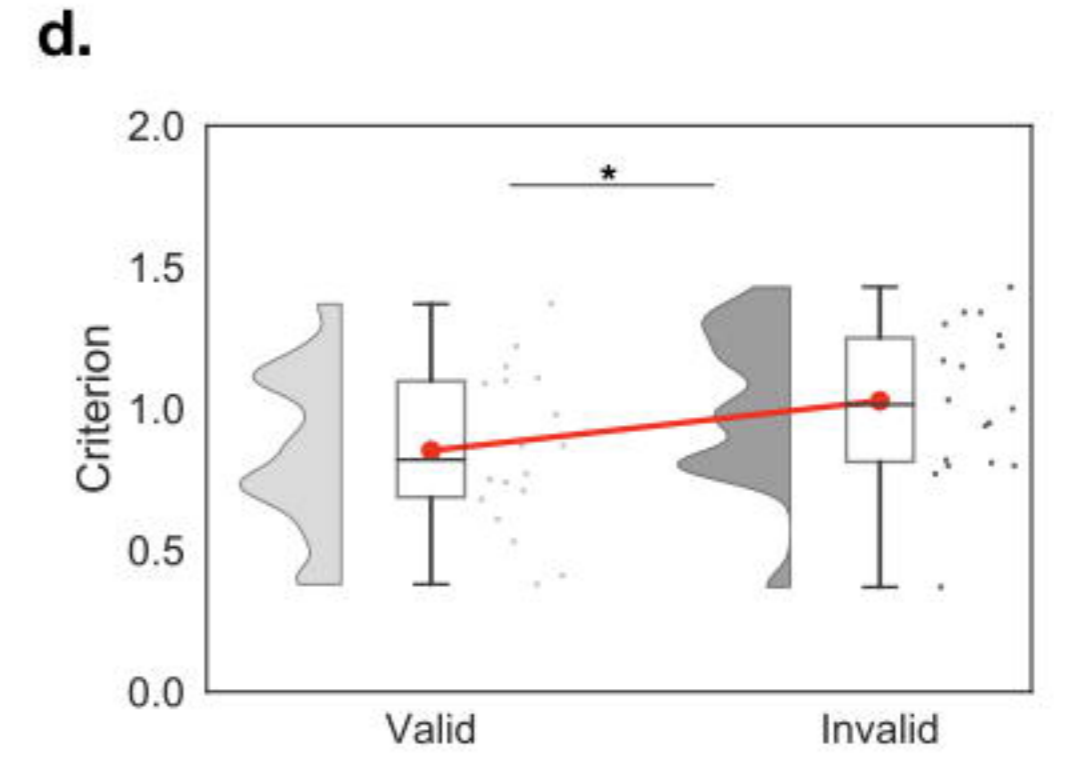
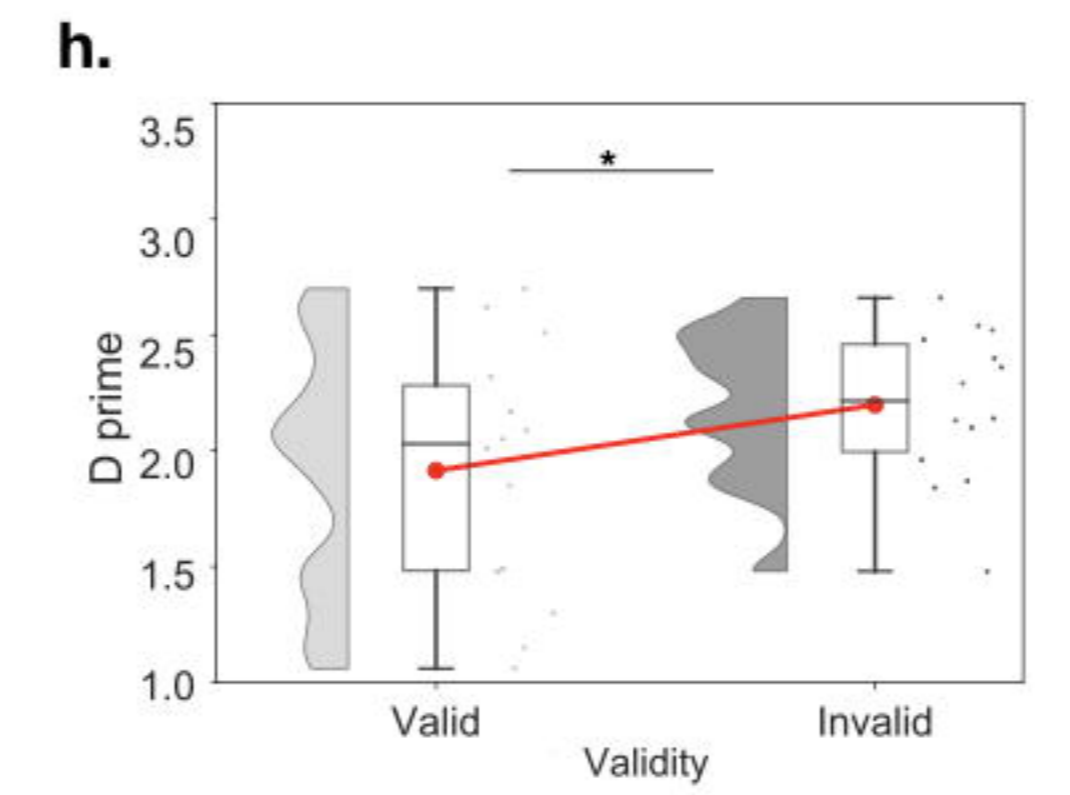
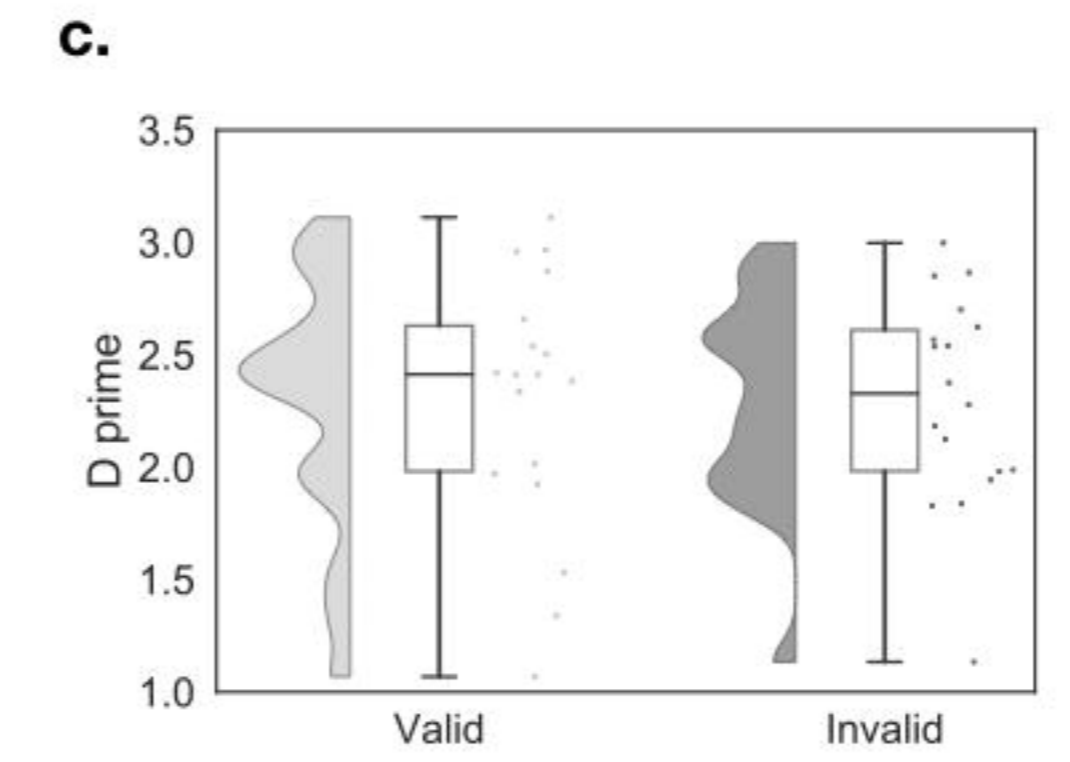
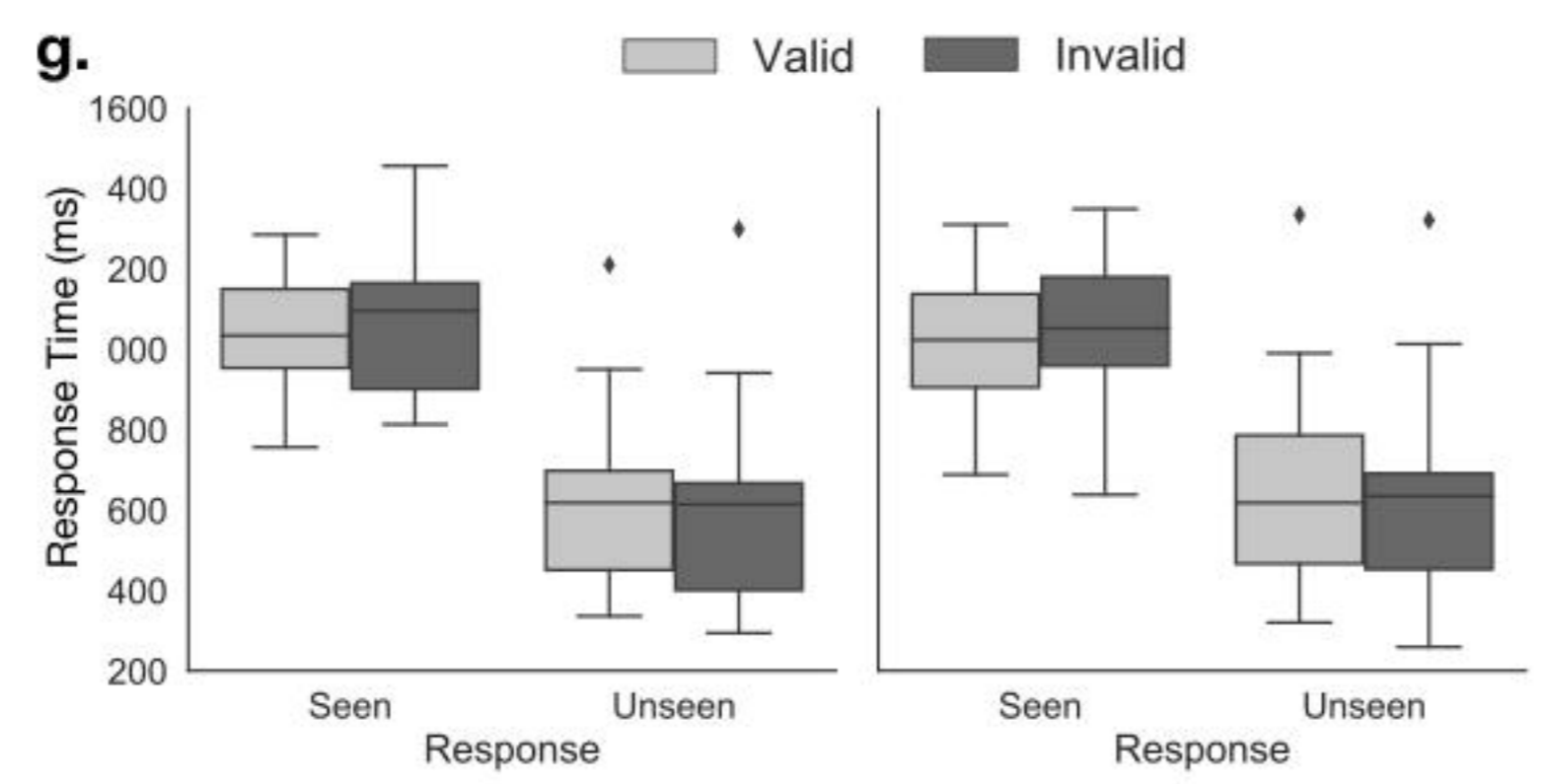
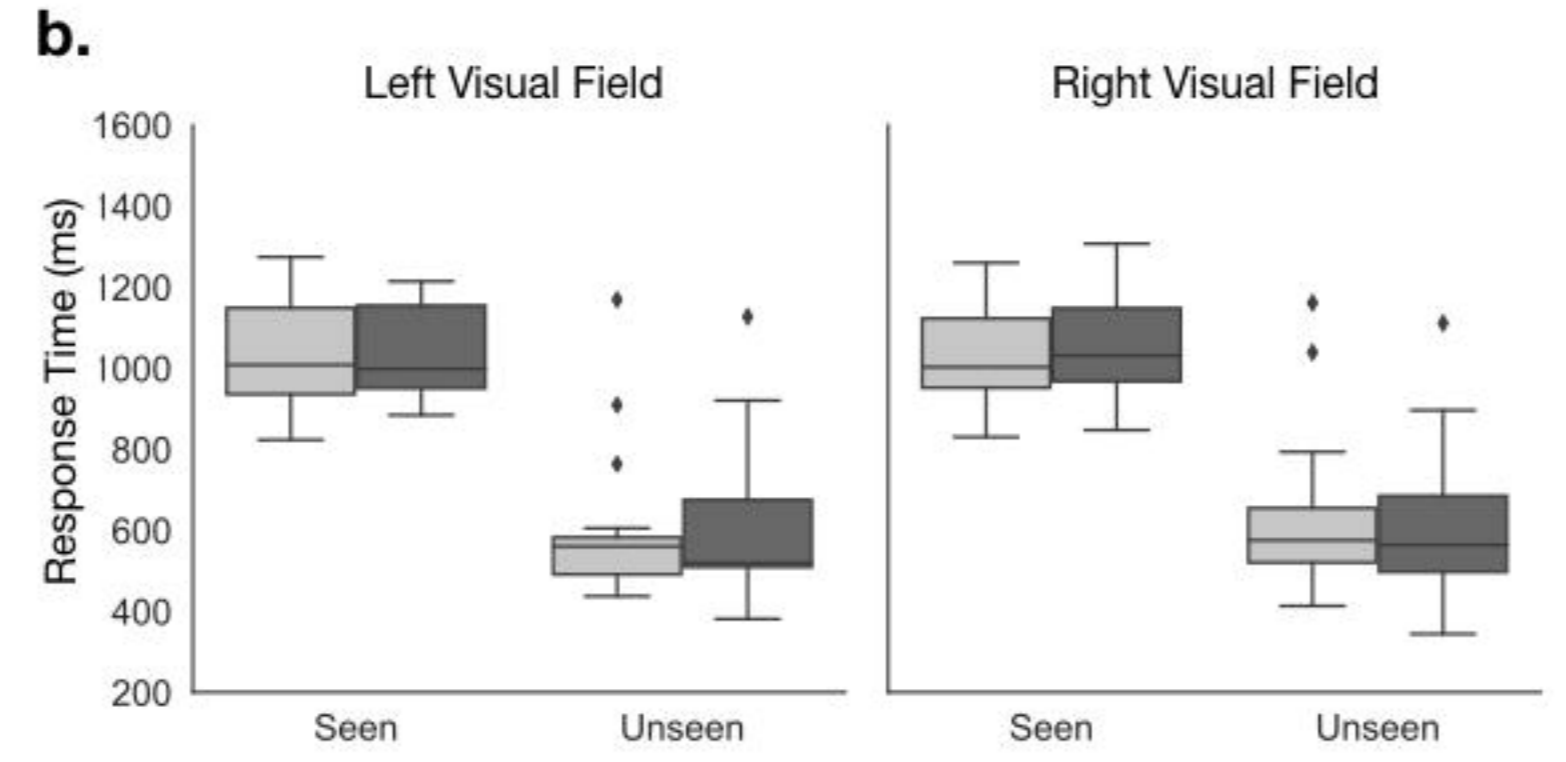
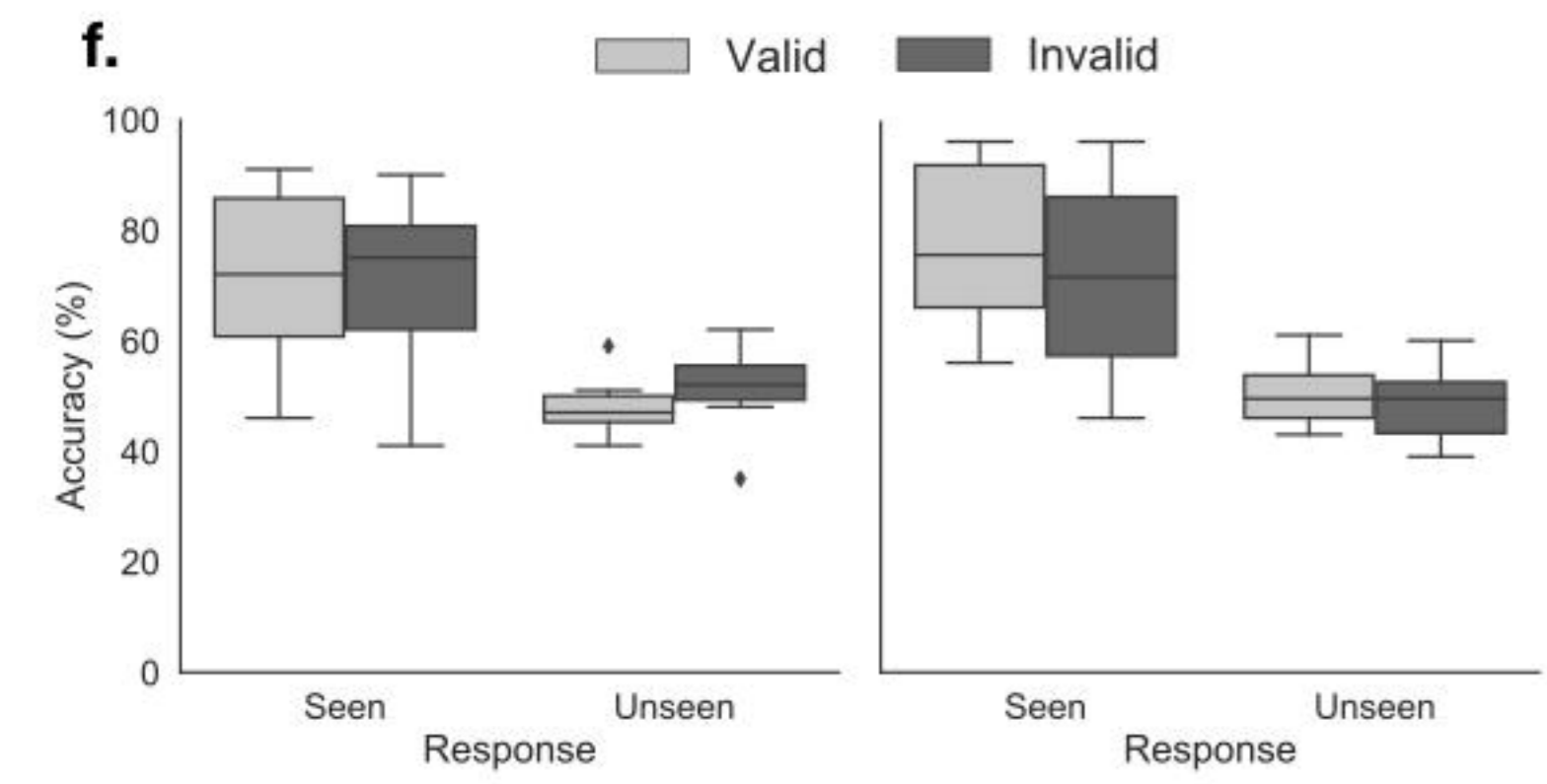
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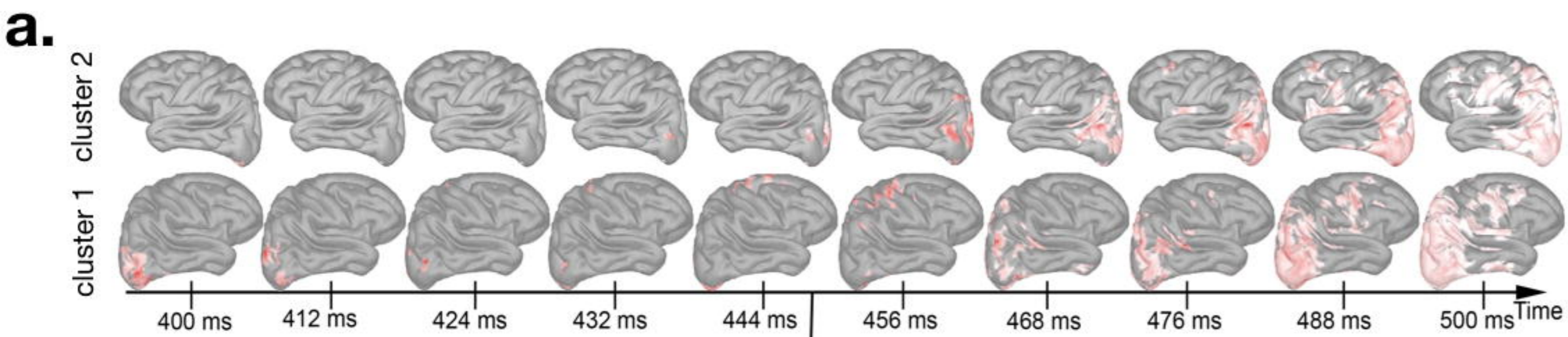




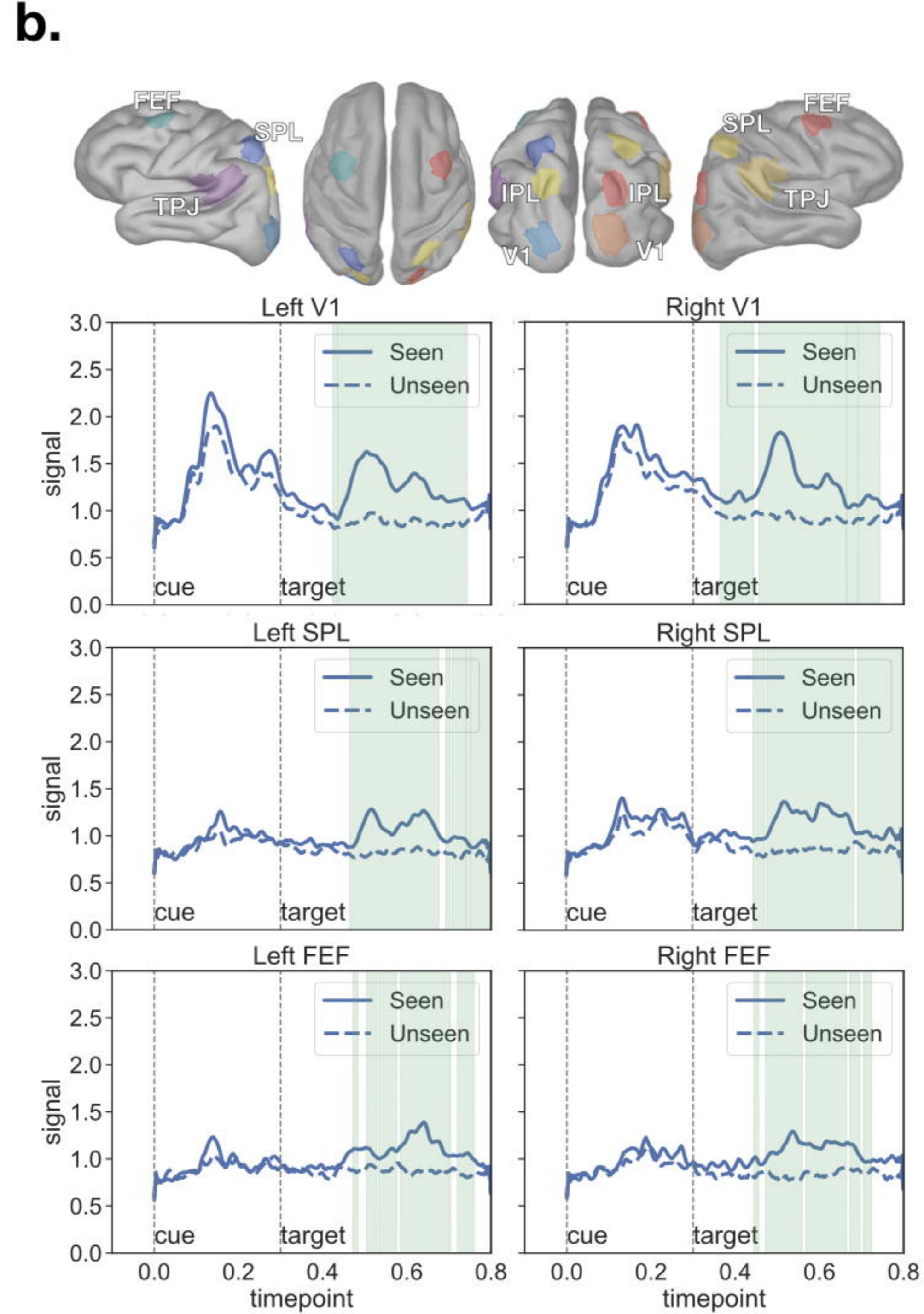
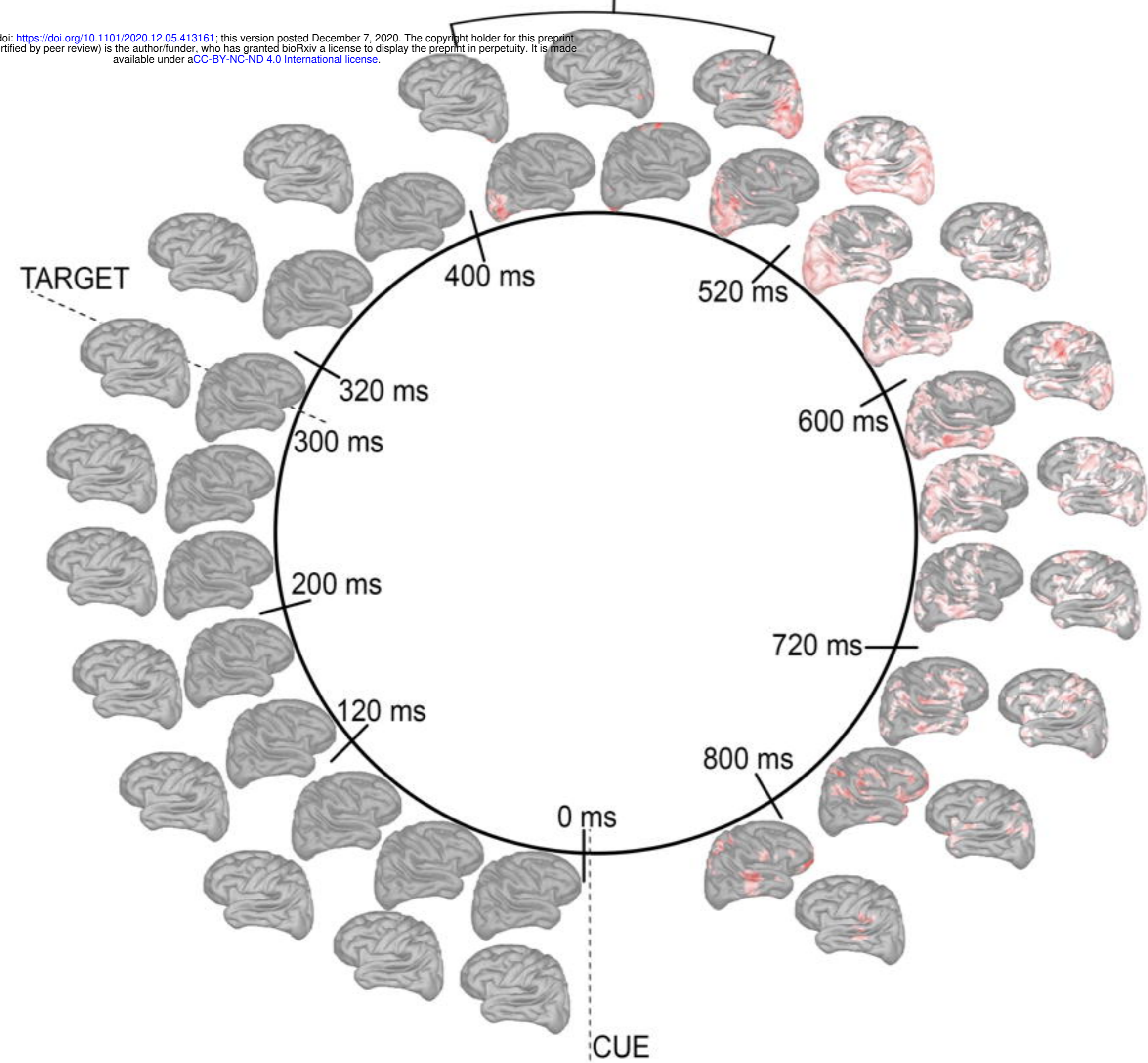
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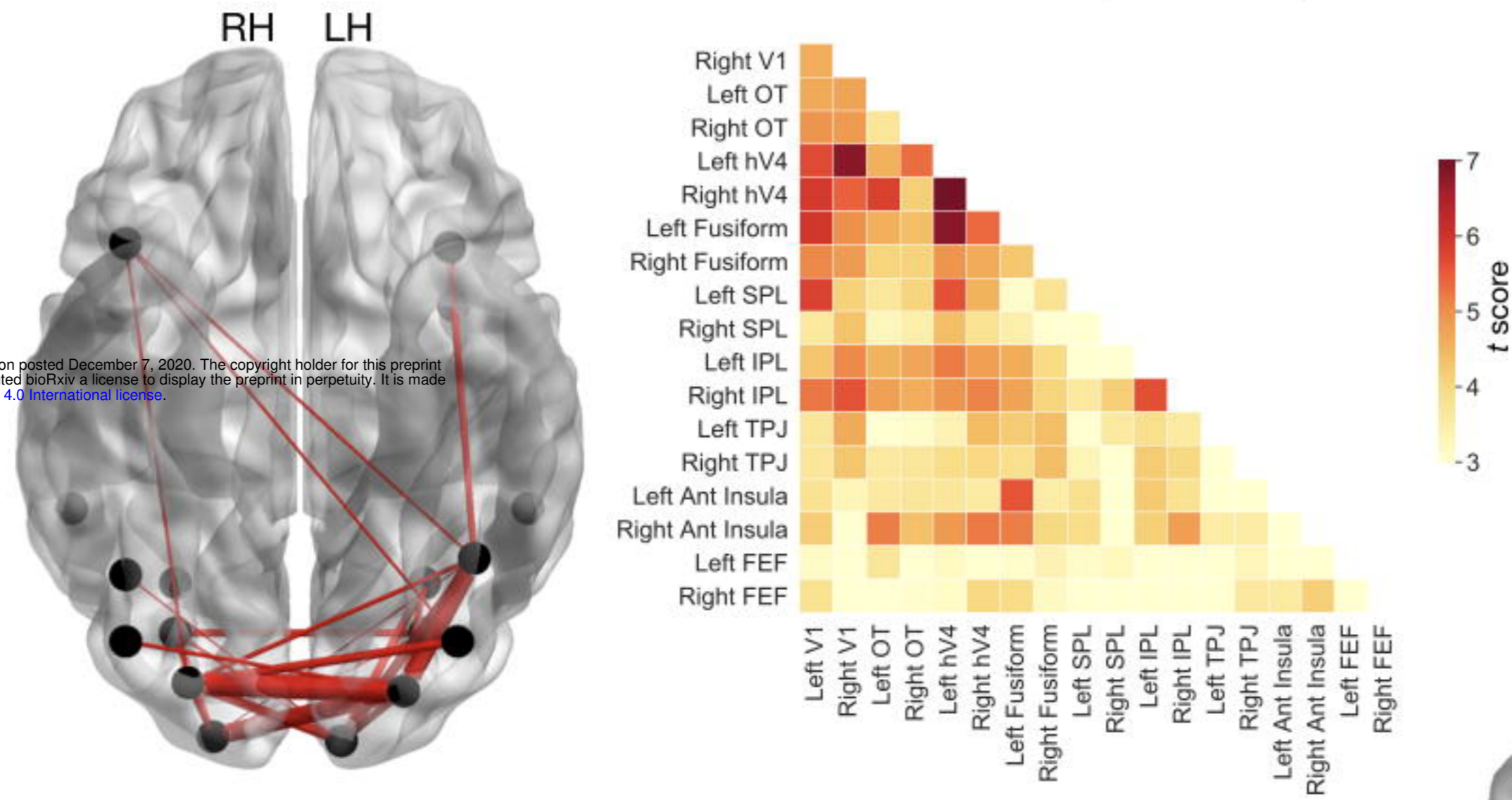


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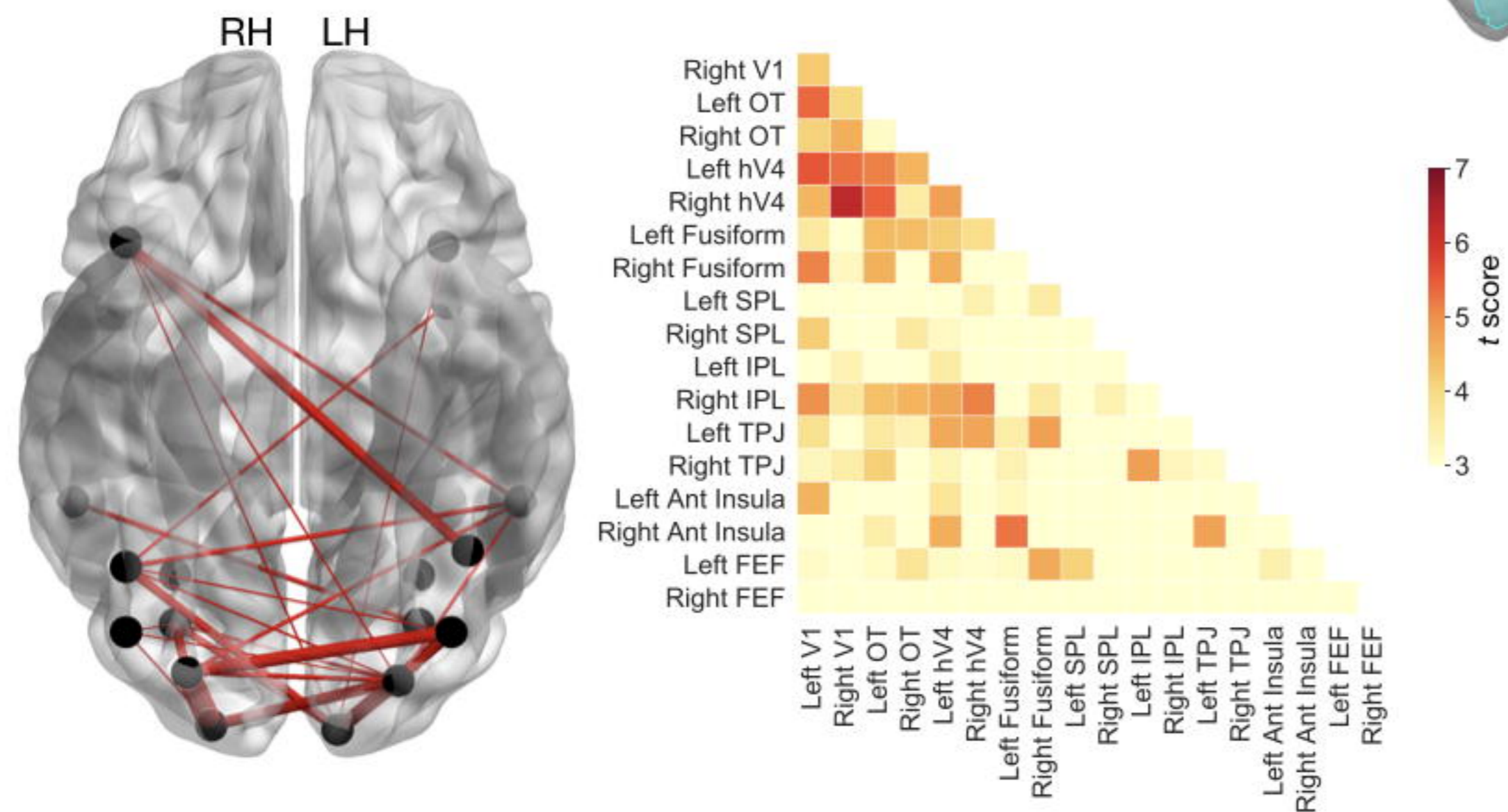




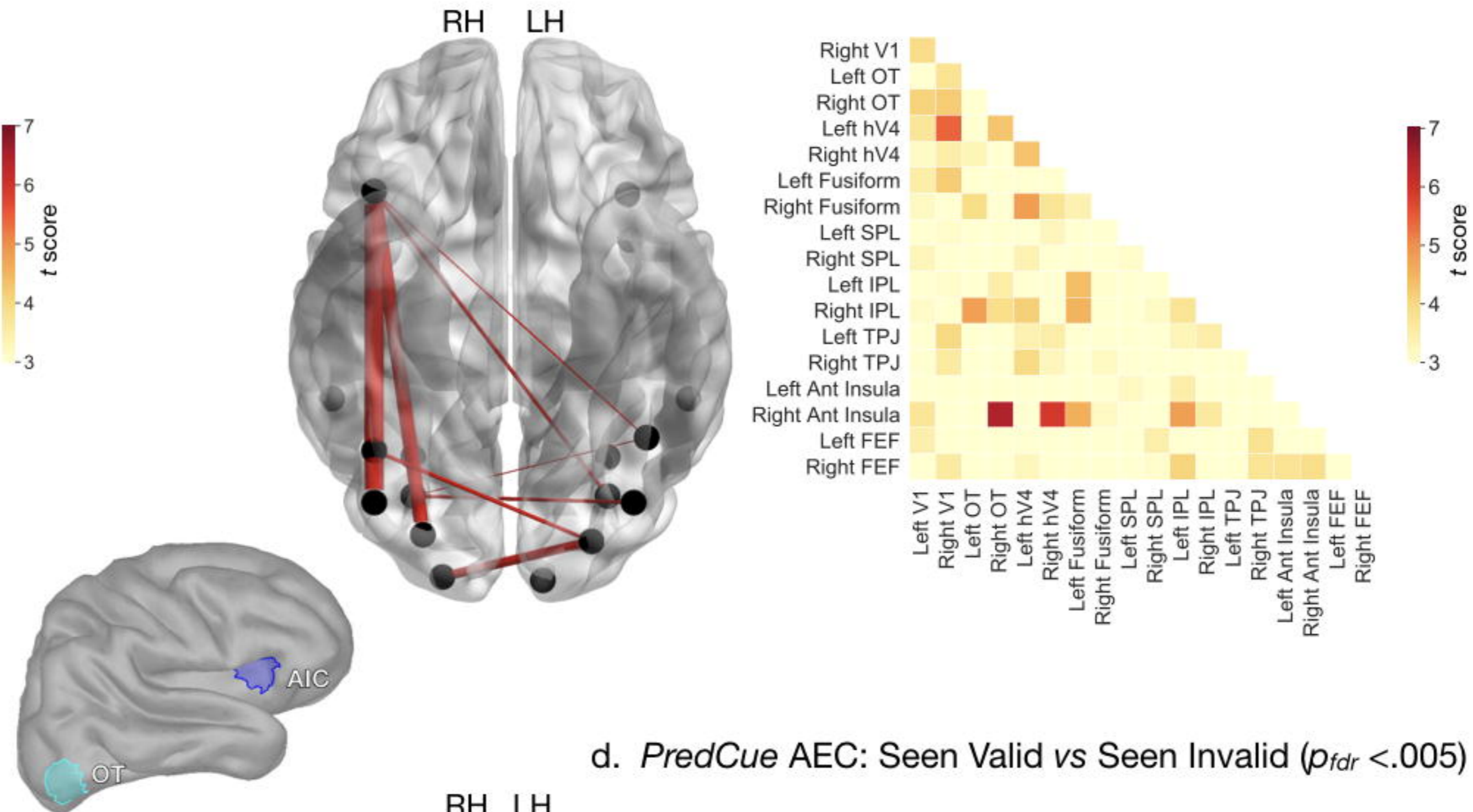
a. *NonPredCue* AEC: Seen vs Unseen ( $p_{fdr} < .001$ )



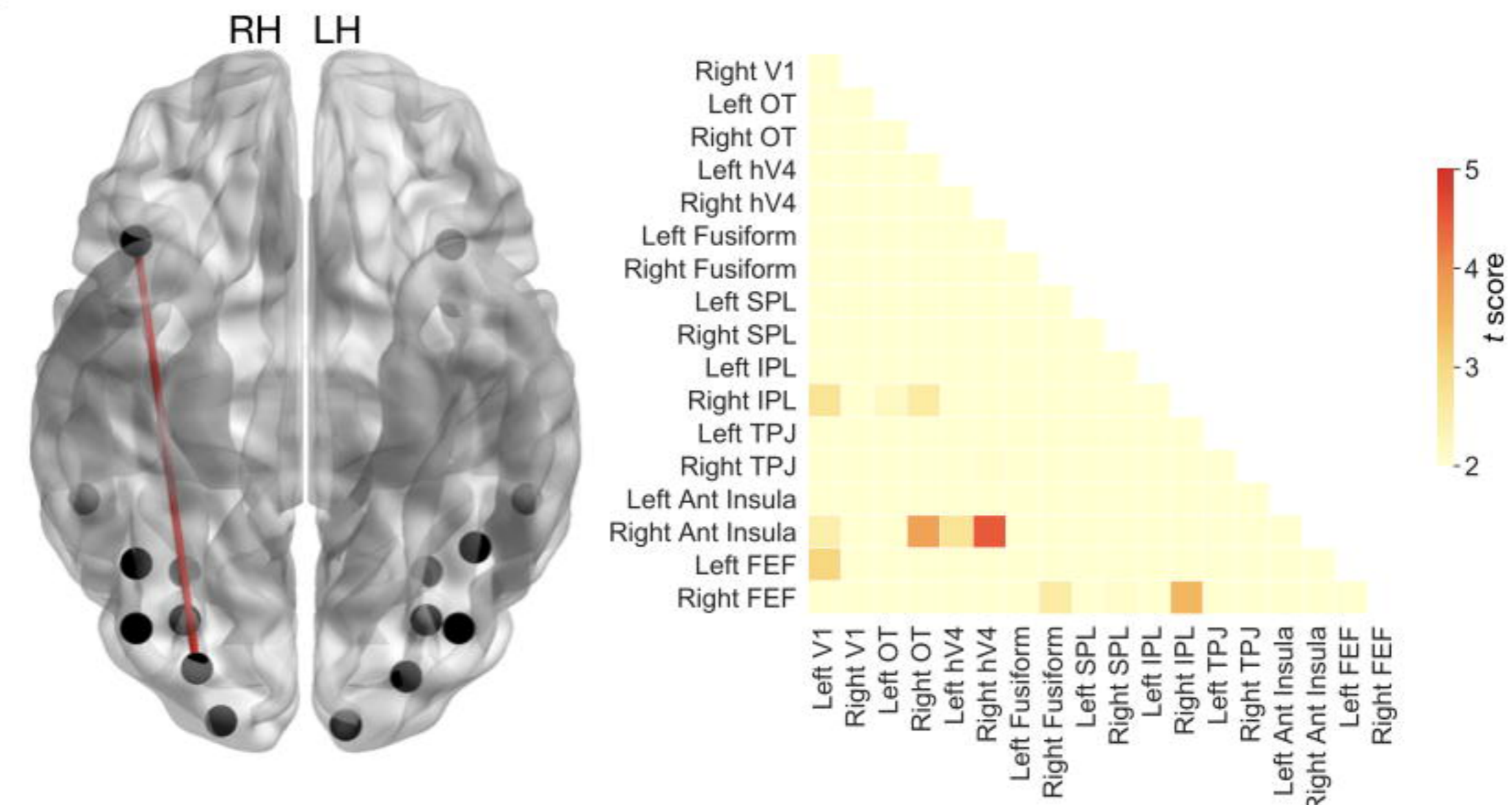
b. *NonPredCue* AEC: Seen Valid vs Unseen Valid ( $p_{fdr} < .005$ )



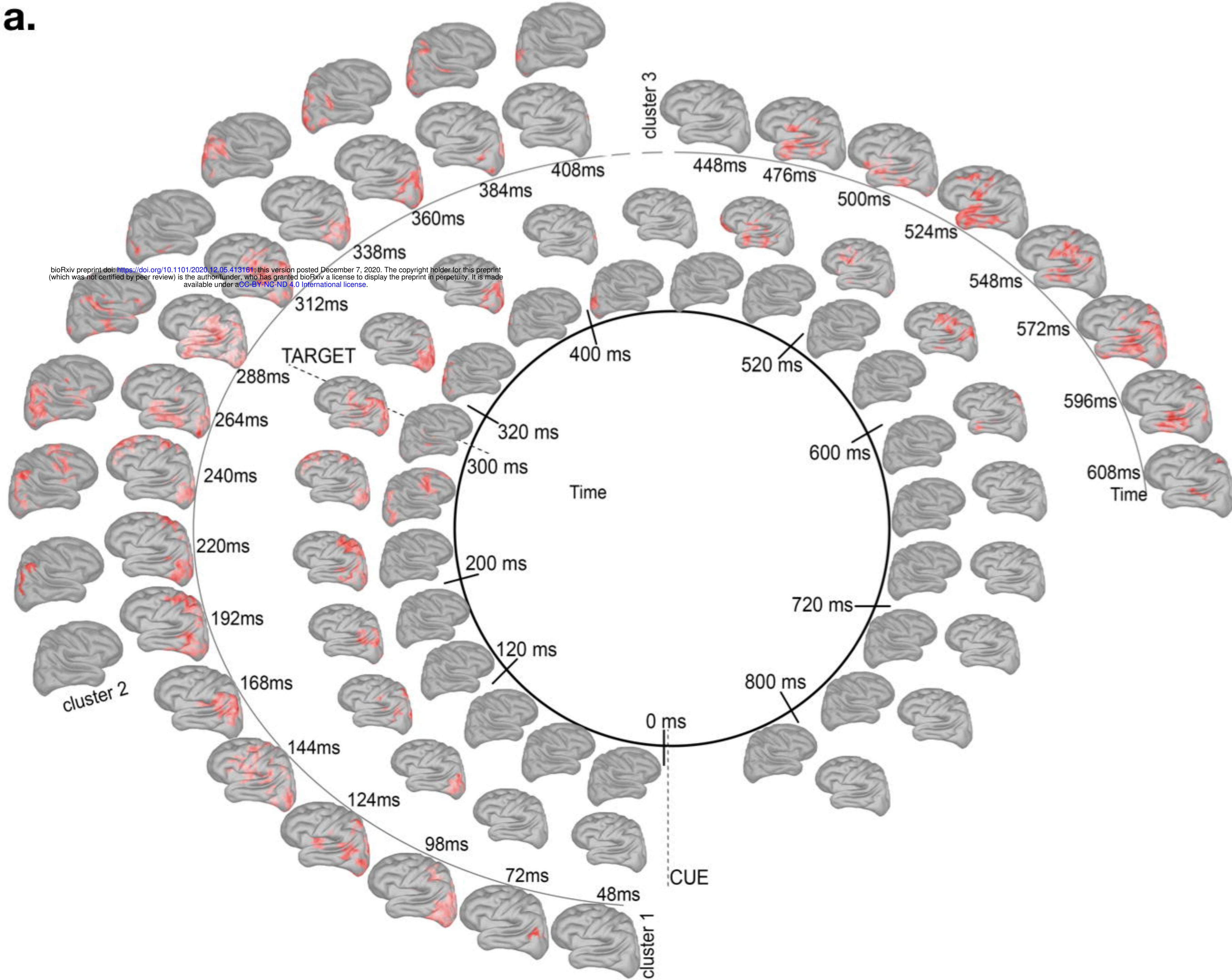
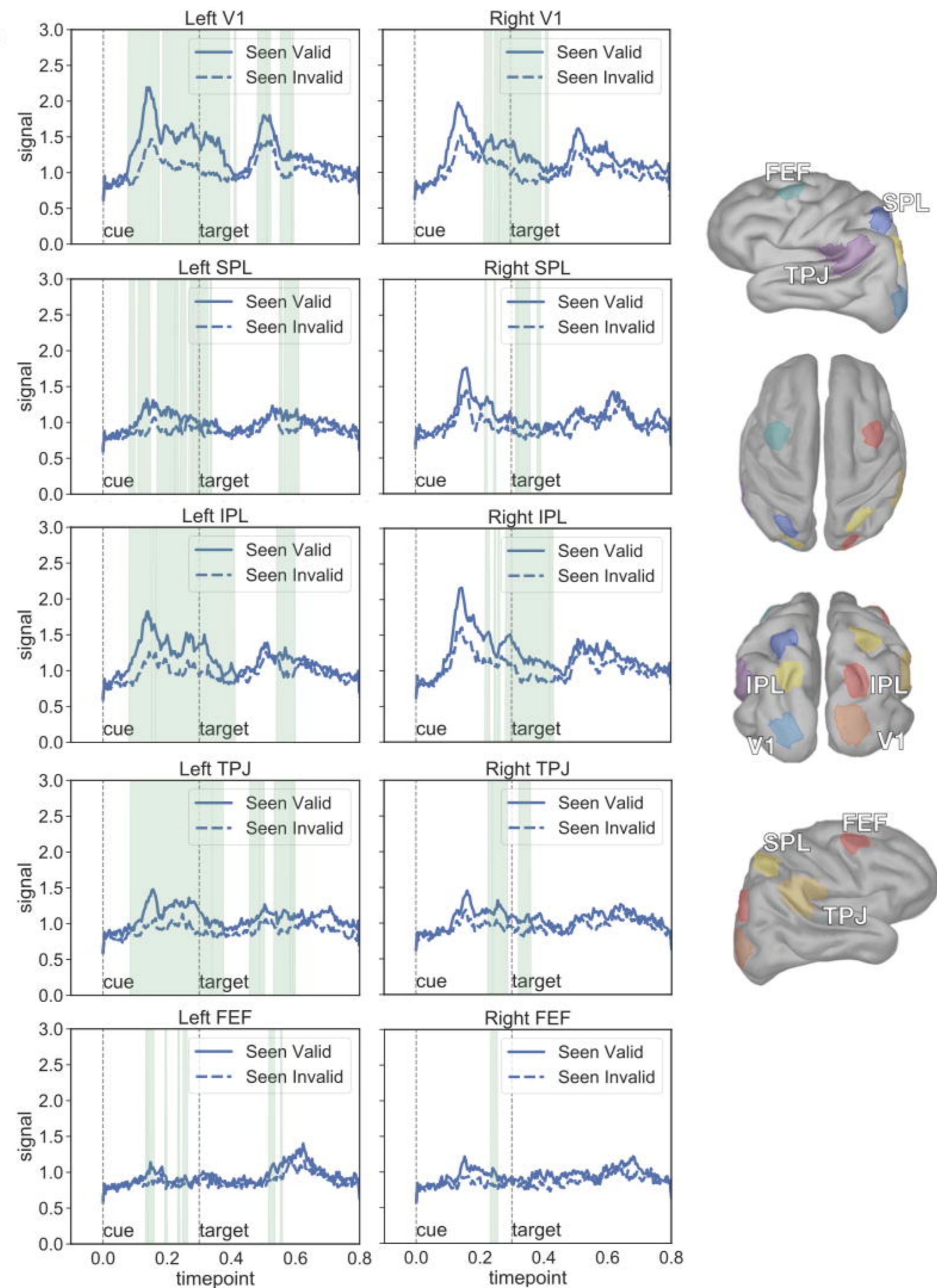
c. *NonPredCue* AEC: Seen Invalid vs Unseen Invalid ( $p_{fdr} < .005$ )



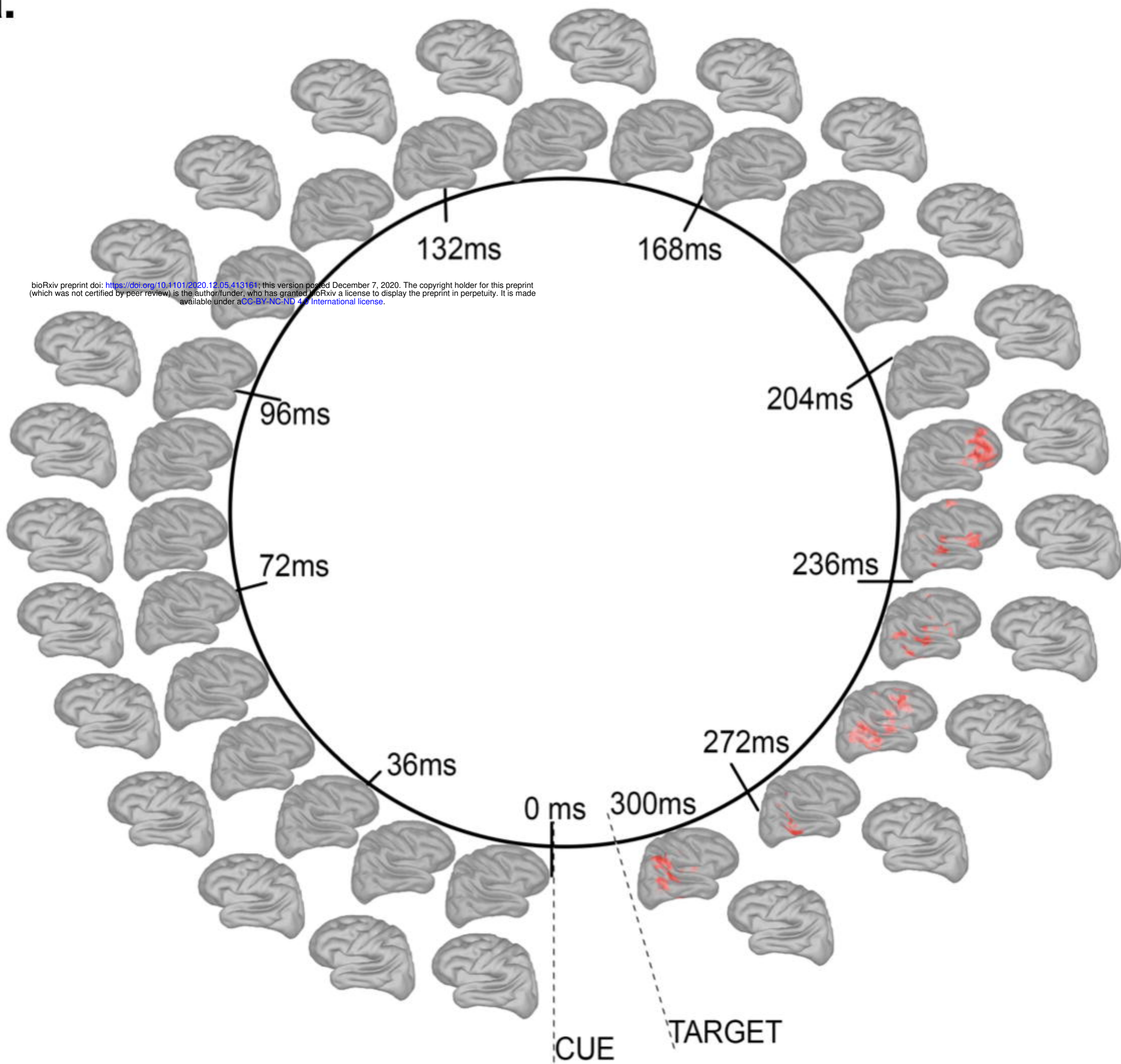
d. *PredCue* AEC: Seen Valid vs Seen Invalid ( $p_{fdr} < .005$ )





**a.****b.**



**a.****b.**