

PERIPHERAL FACE-PREVIEW

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**Previewing a face in the periphery reduces the fN170:**

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**Combined EEG and eye-tracking suggests two stages of trans-saccadic predictive processes**

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### 12 **Abstract**

13 The world appears stable despite saccadic eye-movements. One possible explanation for this  
14 phenomenon is that the visual system predicts upcoming input across saccadic eye-  
15 movements, based on peripheral preview of the saccadic target. We tested this idea using  
16 concurrent electroencephalography (EEG) and eye-tracking. Participants made cued  
17 saccades to peripheral upright or inverted face stimuli that could change (invalid preview) or  
18 keep their orientation (valid preview) across the saccade. Experiment 1 demonstrated better  
19 discrimination performance and a reduced fixation-locked N170 (fN170) with valid than with  
20 invalid preview demonstrating integration of pre- and post-saccadic information. Moreover,  
21 the early fixation-locked EEG showed a preview face inversion effect suggesting that we  
22 perceive pre-saccadic input up to about 170 ms post fixation-onset, at least for face  
23 orientation. Experiment 2 replicated Experiment 1 and manipulated the proportion of valid  
24 and invalid trials (mostly valid versus mostly invalid, 66.6% to 33.3%) to test whether the  
25 preview effect reflected active expectations. A whole-scalp Bayes factor analysis provided  
26 evidence for no influence of proportion on the fN170 preview effect. Instead, before the  
27 saccade the preview face orientation effect declined earlier in the mostly invalid than in the  
28 mostly valid block suggesting some form of pre-saccadic expectations. We conclude that  
29 visual stability is achieved by two trans-saccadic integration processes: pre-saccadic  
30 prediction, reflected in the pre-saccadic proportion modulation, and early post-saccadic  
31 change-detection reflected in the fN170 preview effect.

### 32 **Keywords**

33 Trans-saccadic perception; preview effect; prediction; EEG; eye tracking

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### 34 1. Introduction

35 Visual perception appears surprisingly stable despite being interrupted by saccadic eye  
36 movements about three times per second. One source of visual stability may be the  
37 integration of pre- and post-saccadic visual information (Helmholtz, 1867; Melcher, 2011;  
38 Wurtz, 2008). Recent gaze-contingent experimental designs have revealed that orientation  
39 (Ganmor et al., 2015; Wolf and Schütz, 2015; Zimmermann et al., 2017), object size  
40 (Valsecchi and Gegenfurtner, 2016), visual motion (Fabius et al., 2016), and whole-object  
41 information (Castelhano and Pereira, 2017; Schut et al., 2016) are integrated across saccades  
42 in a statistically optimal fashion taking into account the relative reliability of pre-saccadic  
43 and post-saccadic input (Ganmor et al., 2015; Herwig, 2015; Wolf and Schütz, 2015).

44 Nonetheless, the time-course of trans-saccadic perception and, in particular, the content of  
45 perception immediately after fixation-onset remain controversial (for review, Melcher and  
46 Morrone, 2015)

47 Here, we investigated the time-course of trans-saccadic perception with combined EEG and  
48 eye-tracking (Huber-Huber et al., 2016; Kovalenko and Busch, 2016). Using a similar  
49 methodology, reading research has discovered a *preview positivity* in the fixation-locked EEG  
50 starting at around 200 ms in which the evoked response is more positive for valid than for  
51 invalid preview (Dimigen et al., 2012; Kornrumpf et al., 2016; Li et al., 2015), suggesting that  
52 pre- and post-saccadic information are compared and integrated by around 200 ms.

53 We investigated whether the preview positivity known from reading research is also elicited  
54 by non-word stimuli, namely by faces. One advantage of using face stimuli is that the time  
55 course of face processing is well known (e.g. Bentin et al., 1996). In Experiment 1,  
56 participants made saccades to peripheral face stimuli. During the saccade, the face  
57 orientation (upright, inverted) could change (invalid preview) or remain the same (valid

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58 preview). If the reading preview positivity reflected a general trans-saccadic integration  
59 mechanism, a similar change in the fixation-locked component should be elicited by preview  
60 of the target face. However, we hypothesized that faces might show a different preview  
61 effect than words, possibly in the N170 component. Repeated presentation of faces has  
62 been shown to reduce the N170 component (Caharel et al., 2009; Ewbank et al., 2008).  
63 Moreover, inverting faces generates a larger and sometimes later N170 (Bentin et al., 1996;  
64 Eimer, 2000; Eimer et al., 2010; Roxane J Itier and Taylor, 2004; Roxane J. Itier and Taylor,  
65 2004; Rossion et al., 2000; Towler et al., 2012; Watanabe et al., 2003).  
66 Sensory mismatches, like an invalid preview, usually lead to more pronounced neural  
67 responses (Dimigen et al., 2012; Näätänen and Kreegipuu, 2011), which is central to current  
68 notions of perception (De Lange et al., 2018) and has been interpreted in terms of prediction  
69 errors in predictive coding frameworks (Friston, 2010, 2005; Friston and Kiebel, 2009;  
70 Garrido et al., 2008; Stefanics et al., 2014). With respect to trans-saccadic perception, the  
71 interpretation of the preview effect as a predictive process is particularly intriguing, because  
72 a crucial idea for explaining visual stability is that upcoming foveal visual input is predicted  
73 based on pre-saccadic peripheral information and a copy of the motor command sent to  
74 perceptual brain areas (Cavanaugh et al., 2016; Friston et al., 2012; Melcher and Colby,  
75 2008; Wurtz, 2008).  
76 In Experiment 2, we asked whether the preview effect across a saccade reflects a predictive  
77 process across multiple trials. We manipulated the proportion of valid and invalid trials to  
78 generate blocks with mostly valid (66.6% valid) and mostly invalid (33.3% valid) trials.  
79 Proportion manipulations have successfully demonstrated the predictive nature of sensory  
80 processing (Grotheer et al., 2014; Kovács et al., 2012; Mayrhauser et al., 2014; Summerfield  
81 et al., 2011, 2008), with the rationale that a more frequent event is more expected than a

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82 less frequent event and, therefore, elicits a reduced neural response. Thus, if the preview  
83 effect reflected a predictive process, it should become smaller in the mostly invalid and  
84 larger in the mostly valid block.

## 85 2. Materials & Methods

### 86 2.1. Participants

87 Twenty volunteers participated in each experiment in return for a monetary reimbursement.  
88 All participants gave written informed consent and reported normal or corrected to normal  
89 vision that was additionally confirmed by an eye-sight test. In Experiment 1, two participants  
90 had to be excluded because of poor performance in the tilt discrimination task. Of the  
91 remaining 18 participants, 16 were right-handed, 7 were male, and mean age was 24 years  
92 (range: 19-30 years). In Experiment 2, one participant had to be excluded because of bad  
93 EEG data resulting from a technical problem during data collection . Of the 19 remaining  
94 participants, 16 were right-handed, 6 were male, and mean age was 25 years (range 20-40  
95 years). The procedures of both experiments were approved by the local ethics committee.  
96

### 97 2.2. Stimuli

98 Stimuli were presented on a VIEWPixx/EEG monitor (VPixx Technologies Inc., Canada) at  
99 120 Hz screen refresh rate and 1920 x 1080 display resolution. In Experiment 1, 42 face  
100 images were taken from the Nottingham face database  
101 (<http://pics.stir.ac.uk/zips/nottingham.zip>) and from the Faces 1999 (Front) dataset  
102 (<http://www.vision.caltech.edu/archive.html>); 21 of which were female and 21 male. In  
103 Experiment 2, we selected a set of 16 face images only from the Nottingham face database,  
104 of which eight were male and eight female. The face images in this reduced set were more

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105 uniform concerning the distribution of facial features across images. For the face images of  
106 both experiments, a circular mask with a diameter of  $2.88^\circ$  was centered at the tip of the  
107 nose and the image was sized to contain all relevant facial features. The images were placed  
108 at  $8^\circ$  eccentricity from screen center. For each original face image, we generated a phase-  
109 scrambled counterpart that was presented as a transient (for the duration of 2 frames)  
110 during the saccade to achieve the same level of visual change in the display for both valid  
111 and invalid preview conditions. The stimuli were processed with the SHINE toolbox  
112 (Willenbockel et al., 2010) in Matlab, in order to equate low-level image features that could  
113 otherwise present a confound in the EEG signal. We used the function histMatch with the  
114 mask option to match the luminance histogram of all face cut-outs and their scrambled  
115 counterparts to the average histogram of all face cut-outs within each of the two  
116 experiments.

117

### 118 2.3. Procedure

119 Each trial started with a placeholder display consisting of a fixation cross ( $0.5^\circ$  by  $0.5^\circ$ ) at the  
120 screen center and white rings (width 1 pixel) framing the position of the upcoming faces  
121 (Figure 1A). In Experiment 1, one white ring appeared on either side of the fixation cross  
122 (Figure...), in Experiment 2, only one ring appeared to the left of fixation. Stable fixation  
123 within an area of  $2^\circ$  around screen center for 1 second triggered the preview display. In  
124 Experiment 1, the preview display contained two faces one at either side from fixation; in  
125 Experiment 2, there was only one face to the left of fixation. The face images replaced the  
126 placeholder rings. Keeping stable fixation at the center of the preview display for 500 ms  
127 triggered the color cue. In Experiment 1, the fixation cross turned either blue or green  
128 indicating the saccade direction (color-to-direction assignment counterbalanced across

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129 participants). In Experiment 2, the fixation cross turned grey, prompting for a saccade to the  
130 single face on the left. Participants had been instructed to respond as quickly and accurately  
131 as possible to the cue by making one single eye-movement to the corresponding face  
132 stimulus. Saccade onsets were detected online, and upon detection a scrambled version of  
133 the preview face was presented for two frames (16.7 ms); in Experiment 1, the faces on both  
134 sides were scrambled. The transient occurred no more than 3.5 frames (~30 ms) after  
135 saccade onset, with the delay reflecting the computational requirements of saccade  
136 detection and the screen refresh rate (Figure 1B). Given a total saccade duration of around  
137 40-60 ms, the target face was presented before fixation onset in most trials (Figure 1C). The  
138 purpose of this transient was to roughly equalize the amount of change in the display across  
139 all conditions.

140 During the saccade the faces could change their overall orientation from upright to inverted  
141 (or vice versa) or they could remain the same. In Experiment 1, all possible combinations of  
142 target and non-target face orientations and changes were realized once with each individual  
143 target face, yielding a total set of 672 trials (168 per cell in the crossing of Preview [valid,  
144 invalid] and Target Face [upright, inverted] conditions; Figure 2A). In Experiment 2, which  
145 employed a smaller set of face images, all possible combinations of target orientations and  
146 changes were repeated 16 times for each face. In addition, to investigate whether the  
147 preview effect found in Experiment 1 reflected active predictions accumulating across trials,  
148 Experiment 2 consisted of two blocks, one containing mostly valid trials (66.6% valid, 33.3%  
149 invalid) and the other one containing mostly invalid trials (33.3% valid, 66.6% invalid) (Figure  
150 2B). We expected the preview effect - the difference in the dependent variable between  
151 invalid minus valid trials - to be larger in the mostly valid block and smaller in the mostly  
152 invalid block (Figure 3). The order of blocks was counterbalanced across participants.

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153 Experiment 2 was thus composed of 1024 (with either 171 or 85 per cell in the crossing of  
154 Preview [valid, invalid], Target face [upright, inverted], and Proportion [mostly valid, mostly  
155 invalid] conditions). For instance, in the mostly valid block, there were 171 valid trials with  
156 target upright, 171 valid trials with target inverted, 85 invalid trials with target upright, and  
157 85 invalid trials with target inverted. Importantly, the proportion manipulation was not  
158 mentioned to the participants at any point.

159 In addition to its main orientation (upright or inverted), each target face was slightly tilted  
160 ( $1.8^\circ$ ) either to the left or right, counterbalanced across trials. The non-target face in  
161 Experiment 1 had the same amount of tilt as the target face (on the other side of fixation),  
162 but its direction (left or right) was random. The target face tilt direction had to be reported  
163 by the participants via a computer keyboard with the left and right index finger after they  
164 had made an eye-movement to the target face. The purpose of the tilt discrimination task  
165 was to ensure that participants paid attention to the target face and gave a response that  
166 was orthogonal to all experimental manipulations. In fact, the preview images were not  
167 tilted, making them task-irrelevant for the perceptual tilt discrimination response. Correct  
168 saccades (end point at least within  $2.16^\circ$  of target face center) were detected online, and  
169 participants received feedback in case of incorrect response or if the recorded gaze position  
170 was too far from the expected saccade start or end locations. The eye-tracker was  
171 recalibrated when it failed to correctly track gaze position, meaning that the experiment did  
172 not advance automatically although the participant was adhering to the instructed gaze  
173 procedure.

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### 175 2.4. EEG and eye-tracking data recording

176 The electroencephalogram (EEG) was recorded from 62 electrodes placed at a subset of the  
177 locations of the 10-10 system. The right mastoid served as online reference.  
178 Eye-movement data was recorded by an Eyelink 1000 video-based eye-tracker (SR Research,  
179 Ontario, Canada) in the desktop mount setup. Default settings for saccade detection were  
180 used (velocity threshold 35°/sec, acceleration threshold 9500°/sec<sup>2</sup>). The online saccade  
181 detection that triggered the scrambled transient (see Procedure) was, however, based on a  
182 custom-made algorithm, since the default saccade start events were not transferred quickly  
183 enough from the eye-tracking host computer to the experiment workspace in Matlab. We  
184 set the heuristic\_filter option of the eye-tracker to level 2 in order to receive cleaner gaze  
185 position data, despite the minimal additional delay introduced by the higher filter level. A  
186 gaze position difference of 0.18° between two subsequent samples, converted to screen  
187 pixels depending on individually measured viewing distance of each participant, triggered  
188 presentation of the scrambled transient at the next possible screen refresh. This procedure  
189 resulted in quick and satisfactory saccade detection in most of the trials (cf. Figure 1B).  
190 Both eye-tracking and EEG data were recorded at 1000 Hz sampling rate. Trigger signals  
191 were sent to both data acquisition systems by means of a parallel port splitter cable. The  
192 trigger signals were used offline to synchronize both data streams for subsequent analysis.  
193

### 194 2.5. EEG and eye-tracking data analysis

195 EEG and eye-tracking data was processed in Matlab with the EEGLAB (Delorme and Makeig,  
196 2004) and CoSMoMvPA (Oosterhof et al., 2016) toolboxes. The eye-tracking data was  
197 synchronized with the EEG by means of the eyeeg plugin (Dimigen et al., 2011). Upon  
198 synchronization, the signal was down-sampled to 250 Hz, low-pass filtered (Hamming

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199 windowed sinc FIR filter, 40 Hz, transition band width 10 Hz, cutoff frequency [-6 dB] 45 Hz),  
200 and re-referenced to average reference (Hinojosa et al., 2015). The EEG data was then  
201 visually inspected for major artifacts. Portions of data with severe artifacts were removed  
202 and bad channels were spherical-spline interpolated.

203 In order to correct eye movement artifacts in the EEG, we applied independent component  
204 analysis (ICA; Makeig, Bell, Jung, & Sejnowski, 1996). Eye-movement related components  
205 were determined based on the variance ratio of component activation during periods of eye-  
206 movements (blinks and saccades) versus periods of fixations (Plöchl et al., 2012). ICA was  
207 conducted in a separate processing pipeline containing an additional high-pass filter  
208 (Hamming windowed sinc FIR, 1 Hz, cutoff frequency [-6 dB] 0.5 Hz) that was applied after  
209 down-sampling and before low-pass filtering. The ICA algorithm was infomax (Bell and  
210 Sejnowski, 1995) with the pca option to ensure proper rank of the data matrix. The ICA  
211 results (sphere and weights) were transferred to the corresponding datasets in the original  
212 processing pipeline without the severe high-pass filter. Components were then rejected if  
213 the mean variance of their activation across eye-movement periods was 10% greater than  
214 the mean variance across fixation periods.

215 In both experiments, we extracted epochs of interest for periods of target fixation. Target  
216 fixation epochs were extracted from -200 to 600 ms with respect to target face fixation  
217 onset. Baseline correction was conducted with respect to the 200 ms period before onset of  
218 the preview display. This approach was adopted for two reasons: first, to compare the post-  
219 saccadic activity to a period in which there was no visual input, and, second, to prevent  
220 possible residual eye-movement-related activity from confounding the baseline correction.

221 In Experiment 2, we also extracted epochs of interest for the time of preview display, from -

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222 200 to 800 ms with respect to preview display onset, with baseline correction for the 200 ms  
223 prior to preview display onset.

224 Only trials with correct responses and trials in which participants had followed the gaze  
225 instructions in the experimental procedure were included in the analysis. These were trials in  
226 which participants kept stable fixation within 2° of screen center, made no saccades before  
227 cue onset, and the saccade end point had to be within 2.16° of target face center. If the  
228 target had not been presented before fixation onset, due to a delay in saccade detection,  
229 the time difference between fixation onset and target onset had to be less than 20 ms (see  
230 Figure 1C and Procedure for details), which is largely within the time course of saccadic  
231 suppression (Benedetto and Morrone, 2017; Bremmer et al., 2009; Diamond et al., 2000).

232 This restriction was disregarded in Experiment 2 for the preview-locked analysis only,  
233 because this analysis focused on the time period before the saccade and disregarding this  
234 criterion increased the number of available trials. Finally, trials with very fast and very slow  
235 responses in the tilt discrimination task were excluded by a median absolute deviation filter  
236 with a conservative criterion of 3 (Leys et al., 2013). In Experiment 1, these strict criteria led  
237 to acceptance of a median number of 104 trials ranging from 58 to 139 across participants  
238 and cells of the design preview by target orientation. In the fixation-locked analysis of  
239 Experiment 2, median number of accepted trials was 78, ranging from 32 to 165, across cells  
240 of the same design extended by the factor proportion. For the preview-locked analysis of  
241 Experiment 2, the median number was 79, and the range was the same. The extended range  
242 in Experiment 2 compared to Experiment 1 was due to the proportion manipulation which  
243 lead to an unbalanced number of trials across cells of the design.

244 To determine whether and how the pre-saccadic preview affected processing of the post-  
245 saccadic target face, we investigated the time course of Preview orientation (upright,

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246 inverted) and Target orientation (upright, inverted) effects in the EEG with a whole-scalp  
247 Bayes factor analysis. ERP components are known to differ across tasks, and since we used a  
248 novel gaze contingent task, such an analysis reduces the risk of false positive findings (Luck  
249 and Gaspelin, 2017). Note, that the same conditions resulting from the factors Preview  
250 orientation (upright, inverted) and Target orientation (upright, inverted) can be modelled  
251 equally well by either of the factors Target or Preview orientation (upright, inverted)  
252 together with a Preview factor (valid, invalid) which indicates whether the target and the  
253 preview face were of the same (valid) or different (invalid) orientation.

254 Experiment 1 included the factor Cue direction (left, right; synonymous with saccade  
255 direction) and, for lateral electrodes, also the factor Laterality (contra, ipsi; with respect to  
256 cue direction). To create the Laterality factor, EEG data from trials with saccades to the left  
257 were swapped across hemispheres in order to assign left hemisphere electrodes to the  
258 contralateral, and right hemisphere electrodes to the ipsilateral condition. For instance, the  
259 signal at electrode PO7 was assigned the label *ipsilateral* for leftward saccade trials and the  
260 label *contralateral* for rightward saccades trials. The signal at electrode PO8 was treated in  
261 the opposite way. In contrast to Experiment 1, Experiment 2 omitted the factors Cue  
262 direction and Laterality, because there was only one target face to the left to which saccades  
263 were directed, but instead it included the factor Proportion (mostly valid, mostly invalid). For  
264 Experiment 2, we additionally analyzed the data time-locked to the preview display in order  
265 to determine any pre-saccadic expectation effects introduced by the proportion  
266 manipulation.

267 The preview-display locked analysis of the EEG data revealed an interesting unexpected  
268 result, with the face inversion effect in the N170 triggered by the preview display occurring  
269 later than the face inversion effect triggered by the target display. We tested the reliability

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270 of this delay by analyzing onset latencies of the N170 face inversion effect. Since this was a  
271 post-hoc analysis, this result might be less reliable.

272 In addition to the whole-scalp Bayes factor, we also computed common repeated measures  
273 Anovas on average ERPs at selected electrode sites and for time-windows of main interest to  
274 further consolidate the results.

275

### 276 2.6. Whole-scalp analysis

277 At each electrode and time point, we computed a Bayes factor (BF) based on the average  
278 EEG voltage across trials per participant and condition. We used the BayesFactor package  
279 (version 0.9.12-2) in R (R Core Team, 2013) with fixed-effect priors set to the default Cauchy  
280 distribution at location 0 and scale 0.5. This prior can be verbally expressed as expectation of  
281 a medium-sized effect with smaller effects being more likely than larger effects (Rouder et  
282 al., 2009). In contrast to null-hypothesis significance testing, the Bayes factor provides a  
283 measure of graded evidence for the presence versus absence of an effect (Dienes, 2016;  
284 Rouder et al., 2016; Wagenmakers, 2007). In line with common practice, we consider a BF  
285 greater than 3 as positive evidence, a BF lower than 1/3 as negative evidence, and a BF  
286 between 1/3 and 3 as non-decisive (Raftery, 1995).

287 To obtain a BF for a main or an interaction effect in a multifactor design, such as in the  
288 present study, it is advisable to calculate the so-called BF *across matched models*. This is  
289 because the BF is a likelihood ratio that results from comparing two models, which is usually  
290 the likelihood of the data given the alternative hypothesis/model divided by the likelihood of  
291 the data given the null hypothesis/model. A multifactor design offers many pairs of models  
292 with one model containing the effect of interest and the other not. Thus, there are many  
293 possible likelihood ratios which could be considered as providing the BF for a certain effect.

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294 The most straightforward way to solve this problem is to compute the sum of the likelihoods  
295 of all of the models with the effect of interest and divide it by the sum of the likelihoods of  
296 all of the corresponding models without the effect of interest. Models containing higher-  
297 order interactions with the effect of interest are disregarded. This procedure is, for instance,  
298 implemented in the software JASP (JASP Team, 2018).

## 299 3. Results

### 300 3.1. Experiment 1: Valid peripheral preview improves post-saccadic tilt 301 discrimination performance

302 We analyzed manual response times in the tilt discrimination task only for those trials that  
303 entered the EEG analysis, which also excludes tilt discrimination errors. Error trials were,  
304 however, included in the error rate analysis, which still excluded trials with incorrect  
305 saccades (see Methods). For both computations the design contained three factors: Target  
306 Orientation (upright, inverted), Preview (valid, invalid), and Cue Direction (left, right;  
307 equivalent with saccade direction).

308 As expected, a valid preview led to on average shorter response times than an invalid  
309 preview (valid 1,200 ms, invalid 1,229 ms),  $F(1,17) = 16.26$ ,  $p = .001$ ,  $BF = 13.20$  (Figure 4A)  
310 which is in line with the behavioral preview benefit effect in reading research (Rayner, 1975;  
311 for a review see Schotter et al., 2012). Error rates were the same in both preview conditions  
312 (valid 17 %, invalid 18 %),  $F(1,17) = 0.80$ ,  $p = .382$ ,  $BF = 0.24$  (Figure 4B). Performance was  
313 also affected by target face orientation. Upright target faces led to a faster response than  
314 inverted target faces (1,186 ms versus 1,243 ms),  $F(1,17) = 24.31$ ,  $p < .001$ ,  $BF > 100$ . Upright  
315 faces were also less error prone (15 %) than inverted ones (20 %),  $F(1,17) = 21.97$ ,  $p < .001$ ,  
316  $BF > 100$ . This effect was, however, not of primary interest in the current study.

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317 The ANOVA also suggested that the Preview effect might have been influenced by Cue  
318 Direction, with a marginally significant interaction in response times,  $F(1,17) = 4.29, p = .054$ ,  
319 and significant interaction in error rates,  $F(1,17) = 10.56, p = .005$ . In response times, this  
320 effect indicated a larger preview effect for right side targets; for error rates it indicated the  
321 opposite pattern. However, the BF for response times was  $BF = 0.65$  and for error rates it  
322 was  $BF = 0.79$ , suggesting that strong conclusions should not be drawn from these results.

323

### 324 3.2. Experiment 1: Valid peripheral preview reduces the fixation-locked N170 325 (fN170) amplitude

326 The results of the fixation-locked whole-scalp Bayes factor analysis are illustrated in Figures  
327 4 and 5. Figure 5 shows the BF for the theoretically most relevant effects of Preview  
328 Orientation (panel A, aka Preview x Target Orientation interaction), Target Orientation  
329 (panel B), and the Preview effect (panel C, aka Preview Orientation x Target Orientation  
330 interaction). The ERPs corresponding to these effects are illustrated in panel D. Note that the  
331 Preview Orientation (upright, inverted) main effect is expressed as a Preview x Target  
332 Orientation interaction.<sup>1</sup>

333 Interestingly, as can be seen from Figure 5, the initial phase of the fixation-locked EEG  
334 response already showed some evidence for an influence of the orientation of the preview

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<sup>1</sup> We checked the equivalence of the Preview Orientation main effect and the Preview x Target Orientation interaction explicitly with two Anovas computed on the average amplitude within 300-400 ms post fixation onset at electrode pair PO7/8. One Anova contained the effect of Preview Orientation whereas the other Anova coded the same data with the effect of Preview instead. The first Anova showed a main effect of Preview Orientation with the values  $F(1,17) = 4.39, p = .051$ . The second Anova showed a Preview x Target Orientation interaction with exactly the same values  $F(1,17) = 4.39, p = .051$ . Besides that, the main effect of Target Orientation was also exactly the same for both Anovas,  $F(1,17) = 8.92, p = .008$ . Clearly, the Preview Orientation main effect translates into a Preview x Target Orientation interaction, and vice versa.

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335 face (panel A), which became decisively positive ( $BF > 3$ , color-coded in blue within white  
336 contour lines) from around 110 to 170 ms post fixation onset. During this relatively early  
337 period after fixation onset the preview face was no longer presented on the screen but  
338 instead had been replaced by the target face, which could have had a different orientation  
339 than the preview face. Nevertheless, an inverted preview face led to a more negative EEG  
340 response than an upright preview face (see panel D), which perhaps indicates that a late face  
341 processing sensitive component, such as the N250 or N400, carried over from the pre-  
342 saccadic period. This effect is quite interesting because it could reflect a mechanism relevant  
343 for the experience of visual stability. Immediately after the fixation, the EEG signal initially  
344 reflects what we perceived before the saccade and expect to see after the saccade, until  
345 new post-saccadic information is incorporated (Mirpour and Bisley, 2016). For face  
346 orientation this updating process apparently happens at around 170 ms. Indeed, the switch  
347 at 170 ms is consistent with the timing of the face-selective N170 component.  
348 Almost exactly at 170 ms the main influence on the EEG signal switched from the preview  
349 face to the target face (cf. Figures 5A and 5B), which elicited a more negative response for  
350 inverted than for upright target faces (Figure 5D). This modulation perfectly matches the  
351 classic N170 face inversion effect (Bentin et al., 1996; Eimer, 2000; Eimer et al., 2010;  
352 Roxane J Itier and Taylor, 2004; Roxane J. Itier and Taylor, 2004; Rossion et al., 2000; Towler  
353 et al., 2012; Watanabe et al., 2003). We consider this target orientation effect around 170-  
354 220 ms post fixation as a modulation of the fixation-locked N170 component, the fN170.  
355 Most importantly, for a period of about 80 ms before and after the crucial time point of  
356 170 ms, the preview orientation and target orientation factors interacted (Figure 5C),  
357 showing a more pronounced neural response when the preview face and target face  
358 orientations matched (valid preview) compared to when they did not match (invalid



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359 preview) (Figure 5D). As can be seen from Figure 5D, the fN170 component in particular was  
360 more pronounced in invalid (dashed lines) than in valid preview (solid lines) conditions,  
361 which is consistent with the idea of a trans-saccadic prediction error. The role of prediction  
362 was further explored in Experiment 2.

363 As can be seen from Figure 5D, Preview effect and Target Orientation interacted again from  
364 around 320 ms post fixation for a duration of about 80 ms in particular at central parietal  
365 electrodes. The target orientation effect here consisted in a more negative deflection for  
366 inverted compared to upright target faces and this face inversion effect was larger for invalid  
367 than for valid preview conditions. This interaction probably reflected increased processing of  
368 the target face orientation in invalid than in valid preview conditions, which appears  
369 intuitively plausible. With an invalid preview, the target face presented new information  
370 which requiring more in-depth processing of the critical feature face orientation.

371 As can be seen from Figure 6, Preview and Target Orientation factors did, with one  
372 exception (three-way interaction with Cue Direction, Figure 6H), not interact with other  
373 factors. This interaction with Cue Direction showed sufficient positive evidence before and  
374 around the time of the saccade and suggested that the Preview x Target Orientation  
375 interaction, aka Preview Orientation main effect consisted in a more negative EEG for  
376 inverted compared to upright preview faces, which was more pronounced for cue/saccade  
377 right trials than for cue/saccade left trials (direction of effects not illustrated). Given the  
378 posterior lateral distribution of this effect (electrodes O1/2, PO9/10), and the time periods  
379 before and around the time of the saccade, this effect might have reflected saccade-related  
380 perceptual processes.

381 Additional effects of less theoretical significance were identified in our analyses, including a  
382 main effect of Cue Direction (Figure 6A), and the substantial effects of Laterality (Figure 6B)

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383 as well as the Laterality x Cue Direction interaction (Figure 6G). The Cue Direction effect  
384 indicated evidence for differences between right side and left side saccade trials at posterior  
385 lateral electrodes from ca. 100 to 160 ms and at central electrodes from during the saccade  
386 to 170 ms post fixation (Figure 6A). The Laterality effect showed strong evidence for  
387 widespread effects across the whole post-saccadic time period (Figure 6B). Finally, Laterality  
388 and Cue Direction showed a pronounced interaction across several electrode sites and  
389 across the whole analysis time window (Figure 6G). Such laterality effects might be related  
390 to face processing differences between hemispheres (Frässle et al., 2016; Schweinberger et  
391 al., 2004) or some of fact which is not particularly central to the current study. These factors  
392 were modeled in the analysis in order to control for potential interactions with the preview  
393 and target orientation effects, which were of more central theoretical interest.

394

### 395 3.3. Experiment 1: Anova on average ERPs in the fN170 time window in line 396 with the whole-scalp analysis

397 To provide a statistical assessment of the main results from a frequentist perspective, we  
398 computed repeated measures Anovas on average ERPs at electrode pair PO7/8, which is  
399 known to show the most pronounced N170 effects (Hinojosa et al., 2015), in the time  
400 window from 165 to 250 ms. This time window is later than the usual time window in ERPs  
401 studies on the N170 effect (Bentin et al., 1996), but seems to be more appropriate given the  
402 extended N170 in the invalid preview conditions in our experiment (cf. Figure 5). To assess  
403 the later central-parietal Preview x Target Orientation interaction, we additionally computed  
404 a repeated measures Anova at electrode CPz for the later time window of 320 to 400 ms.  
405 The Anova results were in line with the evidence from the whole-scalp BF analysis. The  
406 Anova showed clear main effects of Preview,  $F(1,17) = 36.55$ ,  $p < .001$ , and Target

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407 Orientation,  $F(1,17) = 8.50$ ,  $p = .010$ , which corroborated the more pronounced N170 in  
408 invalid compared to valid preview conditions and the more pronounced N170 for inverted  
409 compared to upright target faces. The Target Orientation x Cue Direction interaction was  
410 almost significant,  $F(1,17) = 4.01$ ,  $p = .062$ , but the corresponding  $BF = 0.30$  suggested that  
411 the evidence for this effect is negative. We will, therefore, not consider this effect any  
412 further. There was also a clear effect of Laterality,  $F(1,17) = 20.16$ ,  $p < .001$ , indicating a  
413 more negative ERP contralateral to the side of the target face.

414 One effect markedly differed between the Anova on average ERPs and the whole-scalp BF  
415 analysis. The Anova showed a highly significant Preview x Laterality interaction,  $F(1,17) =$   
416  $21.53$ ,  $p < .001$ , with, however, a very low  $BF = 0.33$  calculated on the same values (see also  
417 Figure 6E) indicating that this interaction did not have an effect. This discrepancy between  
418 frequentist and Bayesian results suggests that the effect is not very reliable, although it  
419 would have been theoretically meaningful. The direction of the interaction suggested a  
420 larger preview effect, i.e. difference between valid and invalid trials, at electrodes  
421 contralateral to target/saccade side compared to ipsilateral electrodes. If anything, one  
422 would have expected this direction of the effect, because the contralateral hemisphere is  
423 the hemisphere to which the preview stimulus is projected.

424 The Anova at electrode CPz on average amplitudes for the 320 to 400 ms time window  
425 confirmed the Preview x Target Orientation interaction,  $F(1,17) = 10.68$ ,  $p = .005$ , and  
426 corroborated the more pronounced target face inversion effect (upright minus inverted)  
427 with an invalid ( $-1.19 \mu\text{V}$ ) compared to with a valid ( $-0.07 \mu\text{V}$ ) preview. This Anova also  
428 showed a main effect of Target Orientation,  $F(1,18) = 5.90$ ,  $p = .027$ . No other effects were  
429 statistically significant.

430

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431        3.4. Experiment 2 replicates the effects from Experiment 1 in tilt  
432                discrimination performance and in the fixation-locked EEG  
433        In contrast to Experiment 1, Experiment 2 contained a more restrictive selection of face  
434        stimuli, which were only presented to the left of fixation and the proportion of valid and  
435        invalid trials was manipulated to achieve a mostly valid (66.6% valid, 33.3% invalid) and a  
436        mostly invalid (33.3% valid, 66.6% invalid) block. Overall, Experiment 2 replicated the  
437        preview effects in both behavioral (Figure 7) and fixation-locked EEG data (Figure 8).  
438        Response times in the tilt discrimination task were faster in valid than in invalid preview  
439        conditions,  $F(1,18) = 31.58$ ,  $p < .001$ ,  $BF = 4.89$  (Figure 7A). There was no preview effect in  
440        error rates  $F(1,18) < 1$ ,  $BF = 0.19$  (Figure 7B). The fixation-locked EEG exhibited again a  
441        pronounced preview effect in the fN170 component (Figure 8E), which was corroborated by  
442        a repeated measures Anova on average ERPs at right hemisphere electrode PO8 in the time  
443        window 165 to 250 ms,  $F(1,22) = 41.46$ ,  $p < .001$ . Note that, since preview face stimuli were  
444        only presented in the left visual field in this experiment, we focused the ERP analysis on the  
445        right hemisphere, that is at posterior-lateral electrode PO8. The evidence for the preview  
446        effect was, however, similar at the corresponding electrodes on the left hemisphere as can  
447        be seen from Figure 8E.  
448        Like the preview effect, also the clear target orientation effect from Experiment 1 was  
449        replicated in Experiment 2. Responses in the tilt discrimination task were faster,  $F(1,18) =$   
450         $14.23$ ,  $p = .001$ ,  $BF = 10.00$ , and clearly more accurate,  $F(1,18) = 36.94$ ,  $p < .001$ ,  $BF > 100$ , for  
451        upright than for inverted target faces. Also the fixation-locked EEG showed again a clear  
452        target face inversion effect from about 150 ms onwards that further extended across the  
453        whole post-fixation period. Importantly, the target orientation effect was present in the  
454        fN170 component consisting in a more negative deflection for inverted compared to upright

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455 target faces (BF evidence in Figure 9A, ERPs in Figure 9E). This effect was confirmed in an  
456 Anova at PO8, time window 165 to 250 ms, with  $F(1,18) = 14.54$ ,  $p = .001$ .

457 Additionally, error rates indicated an interaction of Preview and Target Orientation factors,  
458  $F(1,18) = 7.00$ ,  $p = .016$ , which can be interpreted as a Preview Orientation main effect. This  
459 effect indicated slightly higher error rate with inverted (21.8%) compared to with upright  
460 (20.5%) preview faces. The BF for this effect was, however, indecisive and, if anything,  
461 suggested the absence an effect,  $BF = 0.47$ . We, therefore, do not consider this small effect  
462 (1.3% points difference) as very reliable.

463 As in Experiment 1, the early fixation-locked EEG also showed a clear Preview x Target  
464 Orientation interaction, equivalent to a Preview Orientation main effect, starting around  
465 50 ms and extending to 170 ms post fixation onset (Figure 9C). As can be seen from Figure  
466 9E, this effect indicated a more negative P1 with inverted compared to with upright preview  
467 faces, although the preview face was replaced by the target face at that point of the trial and  
468 the target face could have had a different overall orientation.

469 Again as in Experiment 1, evidence for the Preview x Target Orientation interaction became  
470 positive a second time around 350 ms at a set of central-parietal electrodes (Figure 9C).  
471 Again evaluated at electrodes CPz in the time window 320 to 400 ms, the target orientation  
472 effect consisting in a stronger negativity for inverted compared to upright targets, main  
473 effect  $F(1,18) = 5.59$ ,  $p = .030$ , was more pronounced with an invalid ( $-1.20 \mu\text{V}$ ) compared to  
474 with a valid preview ( $0.13 \mu\text{V}$ ),  $F(1,18) = 11.49$ ,  $p = .003$ , which likely again reflected  
475 increased processing of the target face orientation if the target presented new information  
476 different from the preview face. Thus, overall the results of Experiment 2 confirmed the  
477 main effects found in Experiment 1.

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479       3.5. Experiment 2: The proportion manipulation affected tilt discrimination  
480           performance and the fixation-locked EEG, but it did not modulate the  
481           fN170 preview effect

482   Experiment 2 tested whether the preview effect found in Experiment 1 is the result of a  
483   more extensive prediction mechanism across trials, in the sense that it is influenced by  
484   expectations based on the frequency of events over an extended period of time rather than  
485   a single saccade. If the preview effect results from such a prediction mechanisms, then it  
486   should be larger in a block with mostly valid trials (66.6% valid, 33.3% invalid) than in a block  
487   with mostly invalid trials (33.3% valid, 66.6% invalid) (Figure 3). We, therefore, expected to  
488   find a Preview x Proportion interaction in the behavioral data of the tilt discrimination task  
489   and in the fN170 component of the fixation-locked EEG.

490   Interestingly, some hint for a Preview x Proportion interaction was provided by response  
491   times,  $F(1,18) = 5.64$ ,  $p = .029$ , suggesting a slightly larger preview effect (57 ms) in the  
492   mostly valid block compared to the mostly invalid block (34 ms), which was the expected  
493   direction of the effect. However, the corresponding  $BF = 0.29$  suggested no effect of this  
494   interaction, which renders the evidence rather uncertain. Another inconsistency in the  
495   response time data manifested in the main effect of Proportion which was not significant,  
496    $F(1,18) = 2.14$ ,  $p = .161$ , but exhibited a relatively high  $BF = 38.23$ .

497   In the error rates, the Preview x Proportion interaction was not significant,  $F(1,18) < 1$ ,  
498   absence of effect confirmed by  $BF = 0.33$ , and also the Proportion main effect was not  
499   significant,  $F(1,18) = 0.05$ ,  $p = .828$ , absence of effect confirmed by  $BF = 0.18$ .

500   In contrast to these equivocal behavioral results, the EEG data provided compelling evidence  
501   for the same fN170 preview effect in both mostly valid and mostly invalid blocks. BF values  
502   less than 1/3 at posterior lateral electrodes, where the fN170 preview effect is located,

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503 indicated the clear absence of a Preview x Proportion interaction (Figure 8F). This interaction  
504 was also not significant in a repeated measures Anova on average ERPs at PO8 from 165 to  
505 250 ms,  $F(1,18) = 0.32$ ,  $p = .581$ , at PO7,  $F(1,18) = 0.57$ ,  $p = .462$ . As can be seen from the  
506 ERPs in Figure 8G, the difference in the amplitude between valid (solid line) and invalid trials  
507 (dashed line) was the same in mostly valid and in mostly invalid blocks. This crucial result  
508 suggests that the trans-saccadic preview effect in the fN170 component is not the result of  
509 context-sensitive predictions, which contrasts ideas about the predictive nature of the N170  
510 (Johnston et al., 2017).

511 One might argue that the proportion manipulation was simply not strong enough to trigger a  
512 change in the fN170 preview effect. The proportion manipulation had, however, a  
513 pronounced influence on the fixation-locked EEG, in particular contralateral to the target  
514 face (right hemisphere) at posterior electrodes (Figure 9B). The direction of this effect at  
515 electrode PO8 is illustrated in Figure 8G. A more negative fN170 component occurred in the  
516 mostly valid than in the mostly invalid block, further corroborated by an Anova on average  
517 ERPs at PO8, time window 165 to 250 ms,  $F(1,18) = 12.77$ ,  $p = .002$ . This clear influence of  
518 the proportion manipulation evidences that the 66.6% versus 33.3% manipulation was  
519 indeed strong enough to affect the fixation-locked EEG, showing that the proportion  
520 manipulation did influence face preview processing, but still it did not modulate the fN170  
521 preview effect.

522 Apart from these Proportion effects of main interest, the factor Proportion interacted with  
523 Target Orientation later in the fixation-locked EEG and, surprisingly, in ipsilateral electrodes  
524 (Figure 9D, 9G). The effect was significant in an Anova on average ERPs at PO7, time window  
525 550 to 800 ms,  $F(1,18) = 6.34$ ,  $p = .021$ , suggesting that the late target face orientation  
526 effect was larger in the mostly valid than in the mostly invalid block. This effect probably

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527 indicates some variation in higher-level processing of the target face depending on the long-  
528 run frequency of valid and invalid trials. The reasons for its direction and for its ipsilateral  
529 location are, however, unclear. In any case, this finding does not influence our conclusions  
530 about the preview effect and its modulation by proportion.

531

### 532 3.6. Experiment 2: Evidence for pre-saccadic expectations in the preview- 533 locked EEG response

534 If the proportion manipulation consisting in a block of mostly valid and a block of mostly  
535 invalid trials introduced expectations about the validity of a single trial, the preview face  
536 might have already been processed differently in mostly valid compared to mostly invalid  
537 blocks. Thus, expectation or prediction effects might already be present before the eye-  
538 movement during the preview period. We, therefore, analyzed the pre-saccadic period of  
539 the EEG signal, time-locked to the preview face display onset, with the factors Preview  
540 Orientation (upright, inverted), Proportion (mostly valid, mostly invalid), and also Target  
541 Orientation (valid, invalid). It is important to note that target orientation was unknown  
542 during the preview period and that the preview face was actually task-irrelevant since the  
543 task only involved the tilt of the post-saccadic target stimulus.

544 First, we found a classical N170 face inversion effect in response to preview face orientation  
545 as expected from an EEG study using face stimuli. Strong evidence from a whole-scalp BF  
546 (Figure 8A) demonstrated a more pronounced N170 for inverted compared to upright  
547 preview faces (Figure 8C). This effect was corroborated by an Anova on average ERPs at PO8,  
548 from 200 to 260 ms,  $F(1,18) = 29.63$ ,  $p < .001$ . Compared to previous EEG studies on face  
549 perception showing an onset of the N170 largely around 150 to 200 ms (Bentin et al., 1996;  
550 Eimer, 2000; Eimer et al., 2010; Roxane J Itier and Taylor, 2004; Roxane J. Itier and Taylor,



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551 2004; Rossion et al., 2000; Towler et al., 2012; Watanabe et al., 2003), our N170 appeared  
552 rather late at 200 ms (Figure 8A). This discrepancy might be explained by a difference in  
553 stimulus material. Previous studies on the N170 usually presented faces at the fovea in  
554 portrait format (for an exception see Pajani et al., 2017). The faces in our study were cut-  
555 outs excluding hair and the shape of the head, presented in the periphery, which might have  
556 slowed down face recognition processes and therefore might have led to a later N170 face  
557 inversion effect.

558 Instead of impacting on early stages of post-saccadic processing, the proportion  
559 manipulation influenced later stages of a face inversion effect. In about the second half of  
560 the preview period, an inverted preview face led to a more negative deflection than an  
561 upright preview face (Figure 8A, 8C), corroborated by an Anova on average ERPs at PO8,  
562 from 300 to 450 ms,  $F(1,18) = 21.70$ ,  $p < .001$ . This effect possibly reflected a modulation of  
563 the N250 or N400 face processing components. Interestingly, as can be seen from Figure 8C,  
564 this late preview face orientation effect declined earlier in the mostly invalid than in the  
565 mostly valid block. In particular, between cue onset (at 500 ms) and saccade onset (see the  
566 histogram of saccade latencies in Figure 8D) the preview face orientation effect was gone in  
567 the mostly invalid block but still present in the mostly valid block. This earlier reduction of  
568 the preview face orientation effect in the mostly invalid compared to the mostly valid blocks  
569 around the time of cue onset is further illustrated in the scalp maps in Figure 10. BF evidence  
570 for the corresponding Preview Orientation x Proportion interaction is presented in Figure 8B.  
571 An Anova on average ERPs at PO8, 450 to 600 ms post preview onset, corroborated this  
572 interaction,  $F(1,18) = 16.99$ ,  $p = .001$ . Critically, this effect could not simply be explained by a  
573 difference in saccade latencies between mostly valid and mostly invalid blocks, because  
574 saccade latencies did not differ between Preview Orientation and Proportion conditions:

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575 Proportion main effect,  $F(1,18) = 0.63$ ,  $p = .439$ ,  $BF = 1.14$ , Preview Orientation main effect,  
576  $F(1,18) = 0.14$ ,  $p = .714$ ,  $BF = 0.17$ , Preview Orientation x Proportion,  $F(1,18) = 0.00$ ,  $p =$   
577  $.997$ ,  $BF = 0.24$ . As expected, also the factor Target Orientation did not affect saccade  
578 latencies, all  $ps > .089$ , all  $BFs < 0.29$ . The more sustained preview orientation effect in the  
579 mostly valid compared to the mostly invalid block might have, thus, reflected expectations  
580 about the upcoming target orientation based on the pre-saccadic input.

581 Apart from these effects of main interest, the whole-scalp analysis of the pre-saccadic period  
582 revealed also a main effect of Proportion (Figure 11A), and some unsystematic effects  
583 involving Target Orientation (Figure 11B-E). The main effect of Proportion simply suggested a  
584 more positive ERP primarily at PO10 and at central-parietal electrodes in the mostly invalid  
585 compared to the mostly valid condition between cue onset and saccade onset, corroborated  
586 by an Anova on average ERPs, 500 to 650 ms after preview onset, at PO10,  $F(1,18) = 17.54$ ,  $p$   
587  $= .001$ . This effect emphasizes that the influenced of Proportion on the EEG response in  
588 general. Compared to the other effects observed in this dataset, the effects involving Target  
589 Orientation were very short-lived and their spatiotemporal pattern varied considerably  
590 (Figure 11B-E).

591

592 3.7. Experiment 2: The onset of the N170 face inversion effect in the preview  
593 period was later than the onset of the fixation-locked fN170 face  
594 inversion effect

595 As can be seen from Figure 8, the N170 elicited by the onset of the preview display appeared  
596 a bit later than the fixation-locked N170 (see in particular Figure 8C and 8G). To determine  
597 the statistical evidence for this effect, we computed onset latencies of the face inversion  
598 effect expressed as difference waveform between trials with upright and inverted faces at

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599 electrode PO8. We computed upright-minus-inverted preview orientation ERPs separately  
600 for mostly valid and mostly invalid blocks for the preview-display-locked data. For the  
601 fixation-locked data, we computed upright-minus-inverted target orientation ERPs  
602 separately for mostly valid and mostly invalid blocks and also separately for trials with valid  
603 and invalid preview. The design for the latency onset analysis was, thus, a 2 (Proportion:  
604 mostly valid, mostly invalid) by 3 (Preview: valid/fixation-locked, invalid/fixation-locked,  
605 none/preview-locked) design. Onset latencies of the face inversion effect were defined via a  
606 50% peak amplitude criterion based on jack-knifed subsamples. In other words, the onset  
607 latency was the time stamp of the sample at which the leave-one-participant-out averaged  
608 difference waves between upright-minus-inverted face ERPs reached the value closest to  
609 50% of its maximum activation within 100 to 250 ms after preview-display-onset/fixation-  
610 onset (Miller et al., 1998; Ulrich and Miller, 2001). These latency onset values were  
611 subjected to a repeated measures Anova with the factors Preview (valid, invalid, none) and  
612 Proportion (mostly valid, mostly invalid). The resulting F and p-values were corrected for the  
613 reduced error introduced by jack-knifing (Ulrich and Miller, 2001). It is at present unclear  
614 how a Bayes factor would have to be corrected for the reduced error due to jack-knifing. To  
615 avoid this issue, we applied the correction factor that counteracts the reduction in error,  $(n-1)^2$   
616 (Ulrich and Miller, 2001, see in particular Appendix), to the error sum of squares term  
617 obtained from the Anova, which further allowed Bayes factor approximations (Huber-Huber,  
618 2016; Masson, 2011; Nathoo and Masson, 2016; Wagenmakers, 2007).

619 This latency onset analysis of the preview-locked and the fixation-locked face inversion  
620 difference waves showed a main effect of Preview (valid/fixation-locked, invalid/fixation-  
621 locked, none/preview-locked),  $F(2,36) = 27.18$ ,  $p < .001$ ,  $BF_{\text{approx}} > 100$ . Post-hoc tests based  
622 on Scheffe's interval as critical difference (Ulrich and Miller, 2001) revealed a significant

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623 difference (at alpha-level .05) between the valid/fixation-locked and the invalid/fixation-  
624 locked face inversion effect, between the valid/fixation-locked face inversion effect and the  
625 face inversion effect without preview, but not between the invalid/fixation-locked face  
626 inversion effect and the face inversion effect without preview (Figure 12). Both the factor  
627 Proportion,  $F(1,18) = 0.70$ ,  $p = .413$ ,  $BF_{\text{approx}} = 0.330$ , and the Preview x Proportion  
628 interaction,  $F(2,36) = 0.15$ ,  $p = .863$ ,  $BF_{\text{approx}} = 0.031$ , were not significant.

629

## 630 4. Discussion

631 We investigated the time course of trans-saccadic perception in a combined EEG and eye-  
632 tracking study. In Experiment 1, we established a preview effect in behavioral data and in  
633 the lateralized posterior fN170. Participants were more efficient in discriminating target-face  
634 tilt with a valid preview than with an invalid preview. In line with this result, the fN170  
635 component was clearly more pronounced with an invalid than with a valid preview, which is  
636 the same effect direction as the preview positivity known from reading research (Dimigen et  
637 al., 2012, in particular Figure 3B). Our preview effect with faces emerged, however, much  
638 earlier than the preview positivity for reading (ca. 120 ms versus ca. 200 ms post fixation).  
639 We also found a later central-parietal effect similar to the later and more central preview  
640 component in reading research (Dimigen et al., 2012, Figure 3B). Again our late effect  
641 started earlier and instead of consisting in a Preview main effect it consisted in a Preview x  
642 Target Orientation interaction suggesting more in-depth processing of the target face  
643 orientation with invalid compared to with valid preview. These results suggest that trans-  
644 saccadic integration effects can be found at different temporal scales for different types of  
645 stimuli, possibly related to the different timing for processing these stimuli (Herrmann et al.,  
646 2005; e.g. Sereno and Rayner, 2003).

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647 In addition to the trans-saccadic preview effect in the fN170, we found a clear face inversion  
648 effect (Bentin et al., 1996; Eimer, 2000; Eimer et al., 2010; Roxane J Itier and Taylor, 2004;  
649 Roxane J. Itier and Taylor, 2004; Rossion et al., 2000; Towler et al., 2012; Watanabe et al.,  
650 2003). This effect was also clearly present in response times and error rates in the expected  
651 direction of better performance with upright than with inverted target faces. Importantly,  
652 the target orientation and preview effects were additive suggesting that they reflect two  
653 independent processing stages, one for face detection and one for trans-saccadic  
654 integration. Only at a later stage, target orientation and preview interacted, which could  
655 mean that the outcomes of the two separate early processes are combined at this later  
656 stage: if there was a change during the saccade, then target face orientation received more  
657 in-depth processing.

658 In addition to increasing the amplitude of the fN170 in general, an invalid preview also  
659 delayed the face inversion effect to a similar onset as the face inversion effect triggered by  
660 the preview face itself. This result suggests that EEG studies in controlled experimental  
661 settings without eye movements underestimate the latency of visual EEG components in  
662 normal viewing, because real-world perception is usually preceded by a pre-saccadic  
663 preview, resembling the valid condition. In contrast, most experimental settings that prevent  
664 eye movements are like the preview onset locked condition, which triggered a later N170  
665 face inversion effect compared to the fixated-evoked effect.

666 In Experiment 2, we asked whether the beneficial effect of the preview for post-saccadic  
667 processing, in particular on the fN170 component, was the result of a contextually-sensitive  
668 prediction process. In other words, does the trans-saccadic effect across a single eye  
669 movement take into account the frequency of valid and invalid trials? The direction of the  
670 fN170 preview effect, with a larger fN170 for invalid than for valid conditions, is consistent

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671 with a prediction error signal (Friston, 2010, 2005; Friston et al., 2012; Summerfield and  
672 Egner, 2009). If the fN170 preview effect reflected a context-sensitive predictive process, we  
673 reasoned that it should adapt to the frequency of events such that it would become larger in  
674 a block with more valid trials and smaller in a block with more invalid trials (Summerfield et  
675 al., 2008). The results of Experiment 2, however, contradicted this idea: The same preview  
676 effect was found in both blocks and confirmed by strong statistical evidence from a Bayes  
677 factor analysis. Our results, therefore, indicate that the fN170 preview effect occurs  
678 regardless of context or recent experience, making it different from many classical  
679 prediction effects. Still, we observed a more negative fN170 in the mostly-valid compared to  
680 mostly-invalid block, which suggests that the proportion manipulation with 33.3% versus  
681 66.6% was strong enough to be picked-up by the participants and influence face processing  
682 to some extent, though not impacting the preview effect.

683 In the response time data, the effect of the proportion manipulation was less clear. The  
684 Anova provided some hint for a larger preview effect with mostly valid than with mostly  
685 invalid trials. The BF, however, provided negative evidence casting some doubt on the Anova  
686 result. In error rates, there was clearly no such modulation. This discrepancy between the  
687 behavioral and the EEG data suggests that behavior in the task was not only determined by  
688 the early stages of post-saccadic processing reflected in the fN170. It is useful to note, in this  
689 context, that the preview in our design was task-irrelevant, since the response was based on  
690 information (tilt of the target face) which was only present in the target and not in the  
691 preview.

692 Our results contrast previous notions of the N170 as being related to visual predictions. In an  
693 elegant study, Johnston and colleagues (2017) showed that violating visual predictions  
694 derived from a sequences of image changes viewed without eye movements elicited an

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695 N170. They even proposed to use this component to study sensory predictions across  
696 saccadic eye-movements. Moreover, the source of visual prediction errors signals has been  
697 localized in the fusiform face area (de Gardelle et al., 2013a, 2013b) which has also been  
698 identified as one of the neural generators of the N170 component (e.g. Corrigan et al.,  
699 2009). Our results, however, necessitate a reconsideration of the function of the  
700 N170/fN170 in predictive perception, in the classical sense of predictions that take account  
701 of context and recent experience.

702 One possibility is that predictions across saccadic eye movements (Edwards et al., 2017;  
703 Ehinger et al., 2015) might not obey the same principles as concurrent sensory predictions in  
704 the visual system without saccades (Alink et al., 2010; Johnston et al., 2017). This conjecture  
705 implies that the N170 and the fN170 respond differently to the same type of prediction  
706 manipulation, which has not yet been tested.

707 An alternative is that, although all types of prediction and expectation effects are based on  
708 the regularities and statistics of the environment, there are numerous ways of how these  
709 effects can be introduced (De Lange et al., 2018) and this might have implications for the  
710 precise neural mechanism that is targeted by the prediction manipulation. Johnston and  
711 colleagues (2017) studied visual prediction error signals by contrasting predictable and  
712 unpredictable image transitions within systematic sequences of images. The frequency of  
713 predictable and unpredictable trials was, however, balanced. In the present study, we  
714 manipulated the frequency of valid and invalid trials. This methodological difference could  
715 have been critical for the discrepant findings.

716 Finally, although proportion manipulations of 25% versus 75% have been successful in the  
717 past (Summerfield et al., 2008) and our proportion manipulation with 33.3% versus 66.6%  
718 was similar, it might still not have been strong enough to trigger an adaptation of trans-

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719 saccadic predictions (Kovács and Vogels, 2014; Mayrhauser et al., 2014). It is well-known  
720 that effects of expectation scale with validity of the prediction just like endogenous  
721 attention scales with cue validity (Giordano et al., 2009; Kok et al., 2012). Hence, more  
722 extensive training with trans-saccadic changes than the one realized in the present design  
723 (e.g. Herwig et al., 2015; Valsecchi and Gegenfurtner, 2016) might modulate the fN170  
724 preview effect.

725 Overall, our results are consistent with the idea of two stages of visual predictions. The  
726 trans-saccadic preview effect found relatively early (100 – 170 ms) was independent of the  
727 proportion manipulation. It might be relatively automatic and resistant to change over a  
728 brief time period of a few trials. In terms of the second stage, the preview face inversion  
729 effect before the saccade was more sustained in blocks with mostly valid compared to blocks  
730 with mostly invalid trials. This result suggests that, based on the proportion manipulation,  
731 there was an expectation for the same face orientation again as target in the mostly valid  
732 block, less so in the mostly invalid block. Because saccades are executed in sequence in  
733 natural vision, a pre-saccadic effect could be considered as a late post-saccadic effect. With  
734 this assumption, our findings are consistent with the idea that later stages of perceptual  
735 processing are more susceptible to global stimulus regularities than early stages like the one  
736 of the fN170 (see also Pajani et al., 2017; Summerfield et al., 2011).

737 In any case, the preview effect in the fN170 can still be interpreted as a prediction error in  
738 terms of predictive coding (Grotheer and Kovács, 2016). In a computational sense, predictive  
739 coding only means that, instead of transmitting the complete bottom-up signal from lower  
740 to higher processing levels, only the prediction error is propagated in a feed-forward fashion  
741 (Friston, 2010; Spratling, 2017). Predictive coding does not imply anything about critical  
742 frequencies of events required for adjusting top-down predictions. Thus, even though the



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743 proportion manipulation did not influence the fN170 preview effect, the preview effect itself  
744 might still have resulted from predictive coding circuits (Bastos et al., 2012), with these  
745 circuits not influenced by our proportion manipulation.

746 In conclusion, the current results show a strong effect of a task-irrelevant preview face on  
747 post-saccadic face processing. We make about three saccades every second, and it takes  
748 about 100 ms until visual information arrives at object recognition areas (Foxye and Simpson,  
749 2002). If there was no perception during that time we would be blind for about four hours  
750 each day (Melcher and Colby, 2008). Our results confirm that perception does not start  
751 anew with a new fixation. What we see in the periphery before we make an eye-movement  
752 affects post-saccadic processing. Moreover, our data even showed a *preview face*  
753 orientation effect in the early stage of *post-saccadic* processing (cf. Mirpour and Bisley,  
754 2016). This particular result suggests that, instead of being blind after fixation onset, we  
755 perceive what was there before the eye movement which, in natural viewing, is also what  
756 will be there at the beginning of the new fixation. However, only after roughly 100-120 ms  
757 post-saccadic visual processing reflects what is actually in front of our eyes.

758

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1008

1009

## 1010 Figure legends

### 1011 Figure 1

1012 Panel A. Experimental procedure. Stable fixation for 1000 ms triggered the Preview display.  
1013 Further fixation for 500 ms triggered the color cue indicating saccade direction and, thus, the  
1014 target face (e.g. green left/blue right, counterbalanced across participants). Both the target  
1015 (cued) face and non-target face (opposite side) could be either upright or inverted, and  
1016 could both either change orientation of remain the same across the saccade. After detection  
1017 of the saccade, scrambled versions of the faces were presented as transients. The speed of  
1018 saccade detection is illustrated in panel B. The transient was presented most of the time in  
1019 less than 25-30 ms after actual saccade onset. The transient was replaced by the target  
1020 display after two frames. The target display contained both target and distractor faces with  
1021 additional slight tilt (left/right). The target face tilt had to be reported by button press upon  
1022 fixation onset. The timing of target onset and fixation onset is illustrated in panel C. Fixation  
1023 onset was most of the time after target onset. Timeline, stimulus size, and target face tilt are  
1024 not drawn to scale.

1025

### 1026 Figure 2

1027 Panel A shows the four possible preview and target face orientation conditions. Both  
1028 preview orientation and target orientation could be upright or inverted leading to in total

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1029 four conditions, two of which contained a valid preview (preview orientation and target  
1030 orientation matched) and two an invalid one (preview orientation and target orientation did  
1031 not match). Panel B shows the proportion of valid and invalid trials in Experiment 1 and 2. In  
1032 Experiment 1, valid and invalid trials occurred at a frequency of 50% throughout the  
1033 experiment. Experiment 2 consisted of two blocks, one with mostly valid (66.6% valid, 33.3%  
1034 invalid) and one with mostly invalid trials (33.3% valid, 66.6% invalid). Block order was  
1035 counterbalanced across participants.

1036

### 1037 Figure 3

1038 Illustration of the logic of the proportion manipulation to determine the predictive nature of  
1039 the preview effect (difference on the y-axis between valid, solid, and invalid, dashed,  
1040 conditions). If the preview effect is predictive, a block with more valid trials is expected to  
1041 increase the preview effect, and a block with more invalid trials is expected to decrease the  
1042 preview effect.

1043

### 1044 Figure 4

1045 Mean response times (panel A) and error rates (panel B) in the tilt discrimination task in  
1046 Experiment 1, split by the factors Cue Direction, Target Orientation, and Preview.  
1047 Participants were faster in valid (solid) than in invalid preview conditions. Target orientation  
1048 also affected the response: Participants responded faster (panel A) and made fewer errors  
1049 (panel B) in trials with upright (Up) compare to with inverted (In) target faces.

1050

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### 1051 Figure 5

1052 Whole-scalp Bayes factor (BF) analysis of EEG data time-locked to fixation-onset on the  
1053 target face (panels A-C). Panel D illustrates the corresponding ERPs at electrode pair PO7/8.  
1054 Each horizontal row of panel A-C represents the time-course of the BF for one contra-  
1055 ipsilateral electrode pair, sorted from frontal (top) to posterior (bottom) sites and within this  
1056 order further from lateral (top) to medial (bottom) sites. Values greater than 3 (blue) denote  
1057 positive evidence, values less than 1/3 (red) negative evidence. Values in-between are  
1058 indecisive (white). The thresholds 3 and 1/3 are indicated by two-dimensional white contour  
1059 lines. The vertical dashed line at 170 ms only serves as visual guide and does not indicate any  
1060 event in the experiment.

1061 Panel A shows the Preview x Target Orientation interaction, aka Preview Orientation main  
1062 effect. From ca. 100 ms post fixation onset to 170 ms the orientation of the preview face  
1063 dominated the posterior lateral EEG signal (see also panel D). Evidence for this effect  
1064 became positive again between ca. 300 to 400 ms primarily at central-parietal sites. Panel B  
1065 illustrates the main effect of Target Orientation. Evidence for this effect became positive  
1066 from ca. 170 ms post fixation-onset at lateral posterior and some central sites and, after  
1067 some decrease in evidence from ca. 250 to 300 ms extended throughout the post-saccadic  
1068 time-window. The corresponding face inversion effect in the fN170 is illustrated in panel D.  
1069 Panel C shows evidence for the crucial Preview effect, aka Preview Orientation x Target  
1070 Orientation interaction. In time windows of ca. 50 ms before and after 170 ms the EEG  
1071 response was more pronounced in valid (preview orientation and target orientation  
1072 matched) compared to invalid (no match) conditions. The ERPs in panel D show this effect in  
1073 the fN170 component at electrode pair PO7/8.

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1074 Note that baseline correction was conducted with respect to the time window -200 to 0 ms  
1075 before preview display onset which is outside the plotted time period (cf. Figure 1).

1076

### 1077 Figure 6

1078 Whole-scalp Bayes factor (BF) for all the remaining main and interaction effects of  
1079 Experiment 1 not illustrated in Figure 5. Importantly, the Preview and Target Orientation  
1080 effects did not interact with other factors in particular not in the spatio-temporal window of  
1081 the f170 preview effect at lateral posterior electrodes ca. 50 ms before and after the 170 ms  
1082 time stamp.

1083

### 1084 Figure 7

1085 Behavioral results of Experiment 2. Response times (panel A) were faster in valid than in  
1086 invalid trials, and faster for upright (Up) than for inverted (In) targets. The evidence for the  
1087 Preview (valid, invalid) by Proportion (mostly valid, mostly invalid) interaction was unclear  
1088 (see text). Error rate (panel B) was lower for upright than for inverted targets.

1089

### 1090 Figure 8

1091 Whole-scalp Bayes factor (BF) for Experiment 2, time-locked to preview display onset (panels  
1092 A-C), histograms of saccade latencies (panel D), and time-locked to fixation-onset on the  
1093 target face (panels E-G). The preview period (panel A) showed positive evidence for a  
1094 Preview Orientation effect in the N170 and in a later component from ca. 300 ms in with  
1095 more negative deflections for inverted faces (panel C). With cue onset and before onset of  
1096 most of the saccades (pane D) this face inversion effect at posterior lateral electrodes  
1097 disappeared earlier in the mostly invalid than in the mostly valid block (panel C) as

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1098 evidenced by a Preview Orientation x Proportion interaction (panel B).  
1099 The preview effect in the fN170 established in Experiment 1 was replicated in Experiment 2  
1100 (panel E). Crucially, the fN170 preview effect was the same in mostly valid and mostly invalid  
1101 blocks (panel G) as evidenced by a BF clearly lower than 1/3 for the Preview x Proportion  
1102 interaction (panel F). Panel G contains ERPs averaged across both target orientations  
1103 (upright, inverted). For effects of target orientation see Figure 9.  
1104 Note that baseline correction was conducted for the -200 to 0 ms time window before  
1105 preview display onset (panel C).

1106

### 1107 Figure 9

1108 Fixation-locked whole-scalp Bayes factor (BF) for the remaining main and interaction effects  
1109 of Experiment 2 not illustrated in Figure 8. The effects of Experiment 1 were replicated.  
1110 Target Orientation elicited again a pronounced face inversion effect in the fN170 and a later  
1111 component commencing at ca. 300 ms post-fixation onset (panel A, panel E). Preview  
1112 Orientation showed again a face inversion effect in the initial phase of post-saccadic  
1113 processing before 170 ms after fixation onset (panel C, panel E). In addition, the evidence for  
1114 a more negative fN170 in mostly valid compared to mostly invalid blocks was clearly positive  
1115 (Proportion main effect, panel B, corresponding ERPs in Figure 8G). The Target Orientation  
1116 effect was more sustained in the mostly valid compared to the mostly invalid blocks in a very  
1117 late time window and surprisingly at ipsilateral sites (panel D). Evidence for the three-way  
1118 interaction was largely indecisive (panel F).

1119



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### 1120 Figure 10

1121 Scalp map of the preview-display-onset locked face inversion effect at lateral posterior sites  
1122 (upright minus inverted). In the mostly valid block (upper row) the late face inversion effect  
1123 remained, whereas it declined before cue onset and disappeared with cue onset in the  
1124 mostly invalid block (lower row). Evidence for the corresponding Preview Orientation x  
1125 Proportion interaction in Figure 8B.

1126

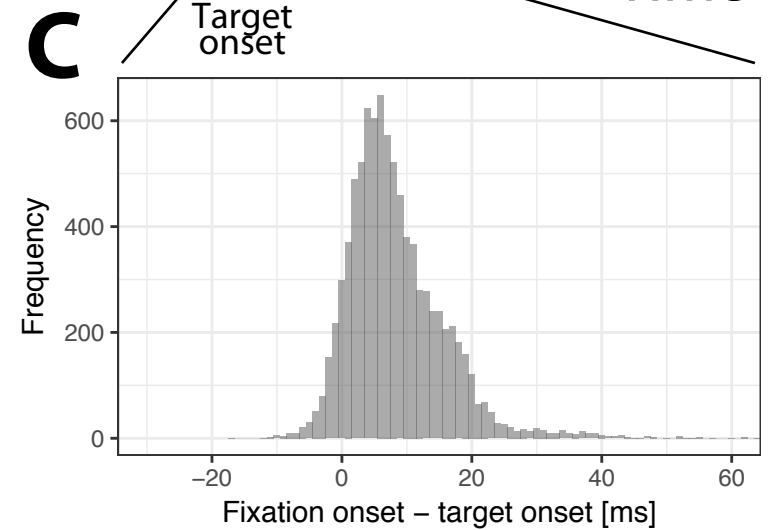
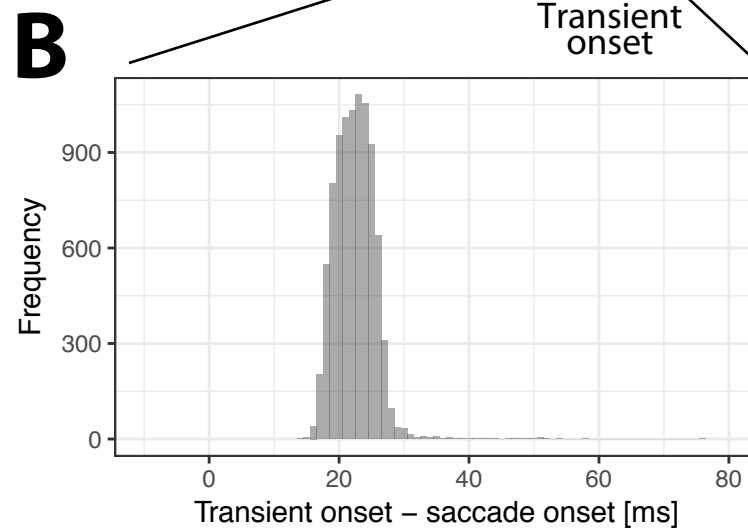
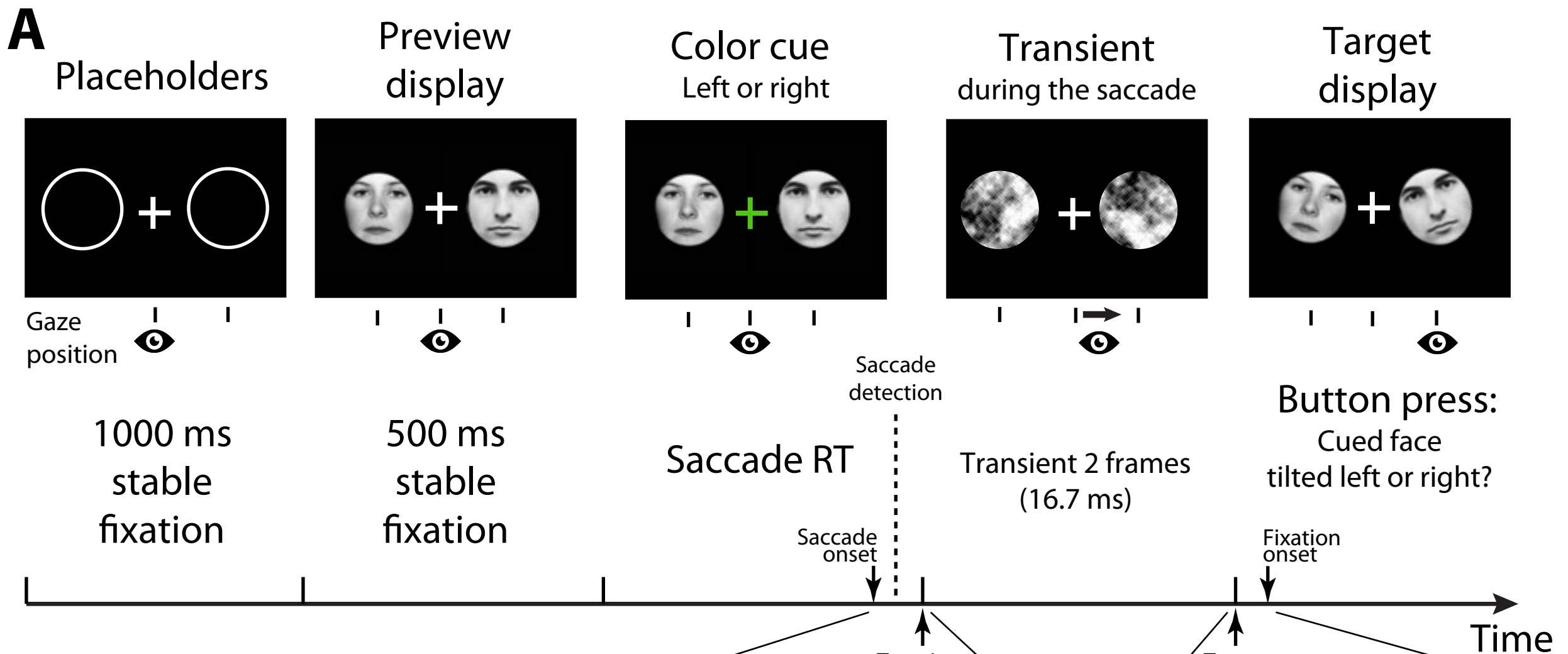
### 1127 Figure 11

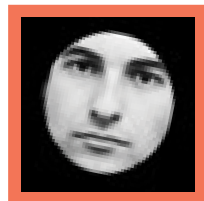
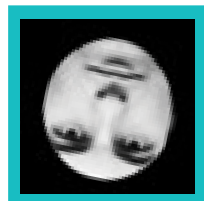
1128 Preview-onset-locked whole-scalp Bayes factor (BF) for the remaining main and interaction  
1129 effects of Experiment 2 not illustrated in Figure 8. Some positive evidence for a main effect  
1130 of proportion was present primarily at PO10 and some central-parietal electrodes (panel A).  
1131 The other effects involving Target Orientation (panel B-E) showed spatio-temporally  
1132 extremely limited and unsystematic patterns of occasional positive evidence.

1133

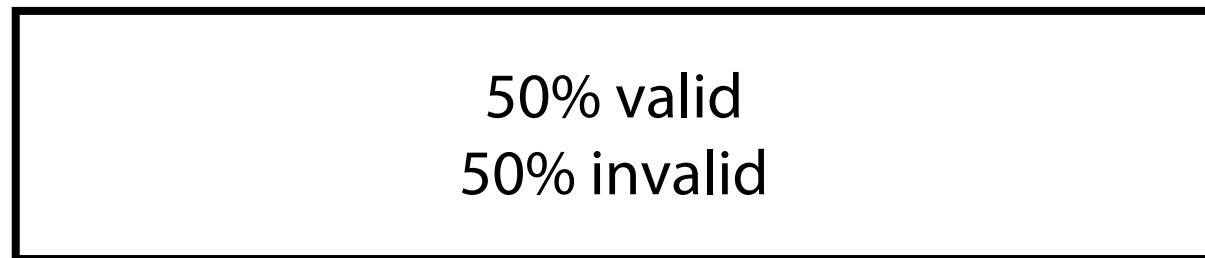
### 1134 Figure 12

1135 Time course of the face inversion effect calculated as difference between ERPs to upright  
1136 faces minus ERPs to inverted faces separately for fixation-locked data (upper panel) and  
1137 preview-display onset locked data averaged across both target face orientation (lower  
1138 panel). The onset of the face inversion effect was earliest in the post-fixation period with a  
1139 valid preview peaking at 170 ms (solid lines, upper panel). In contrast, an invalid preview  
1140 delayed the face inversion effect (dashed lines upper panel). The latest face inversion effect  
1141 occurred in response to the preview display, that is, before any eye movement was made  
1142 (lower panel). The Proportion factor did not affect face inversion effect latency.

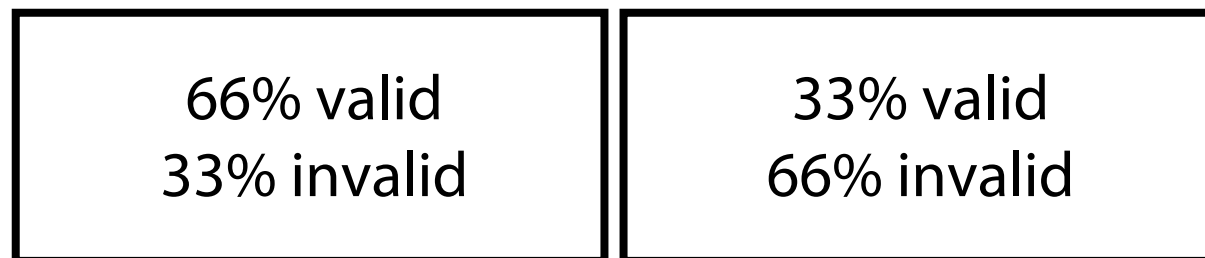


**A**Preview  
faceTarget  
facevalid  
uprightvalid  
invertedinvalid  
uprightinvalid  
inverted**B**

Experiment 1

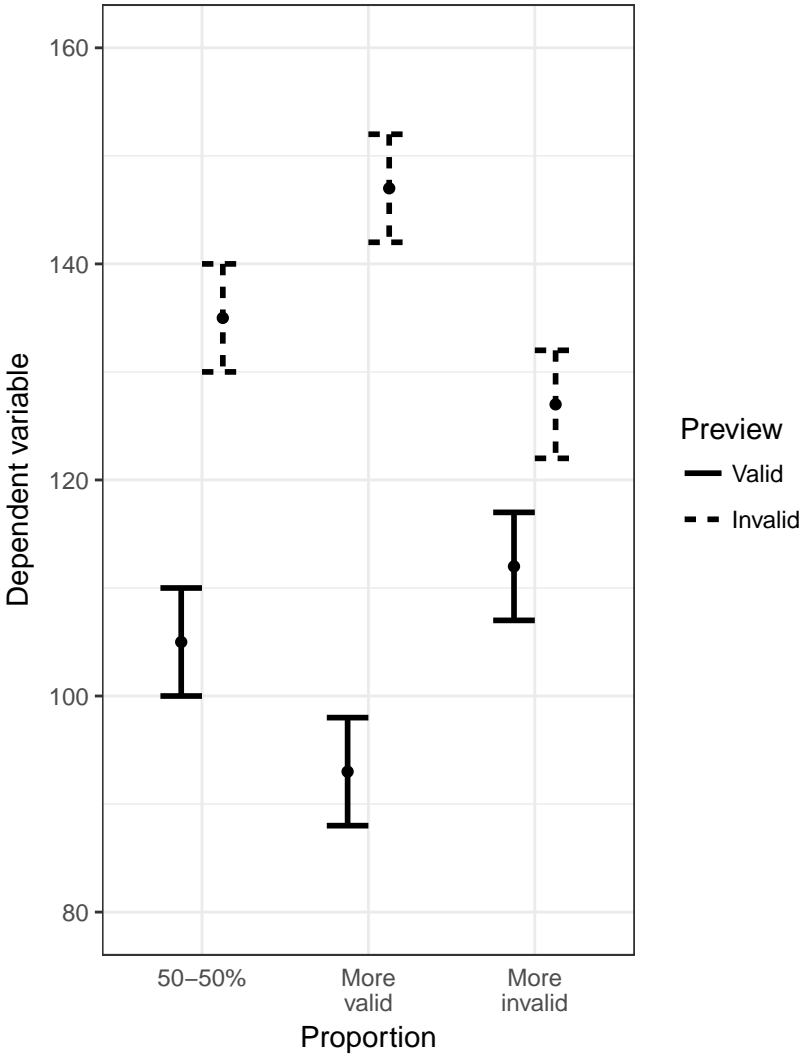


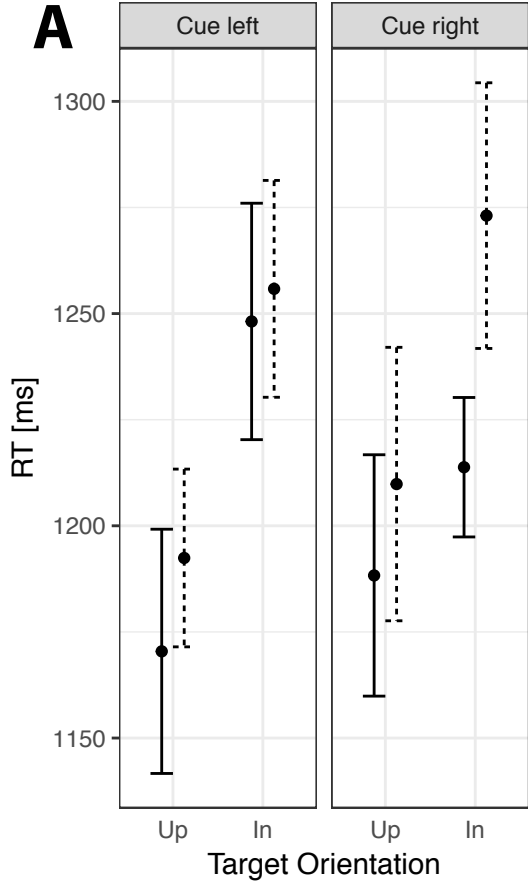
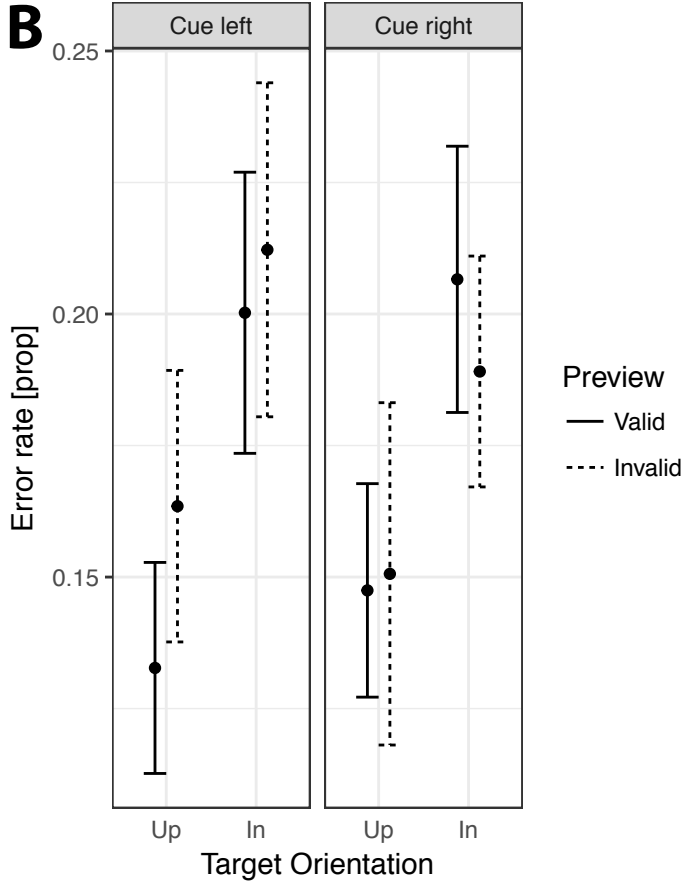
Experiment 2

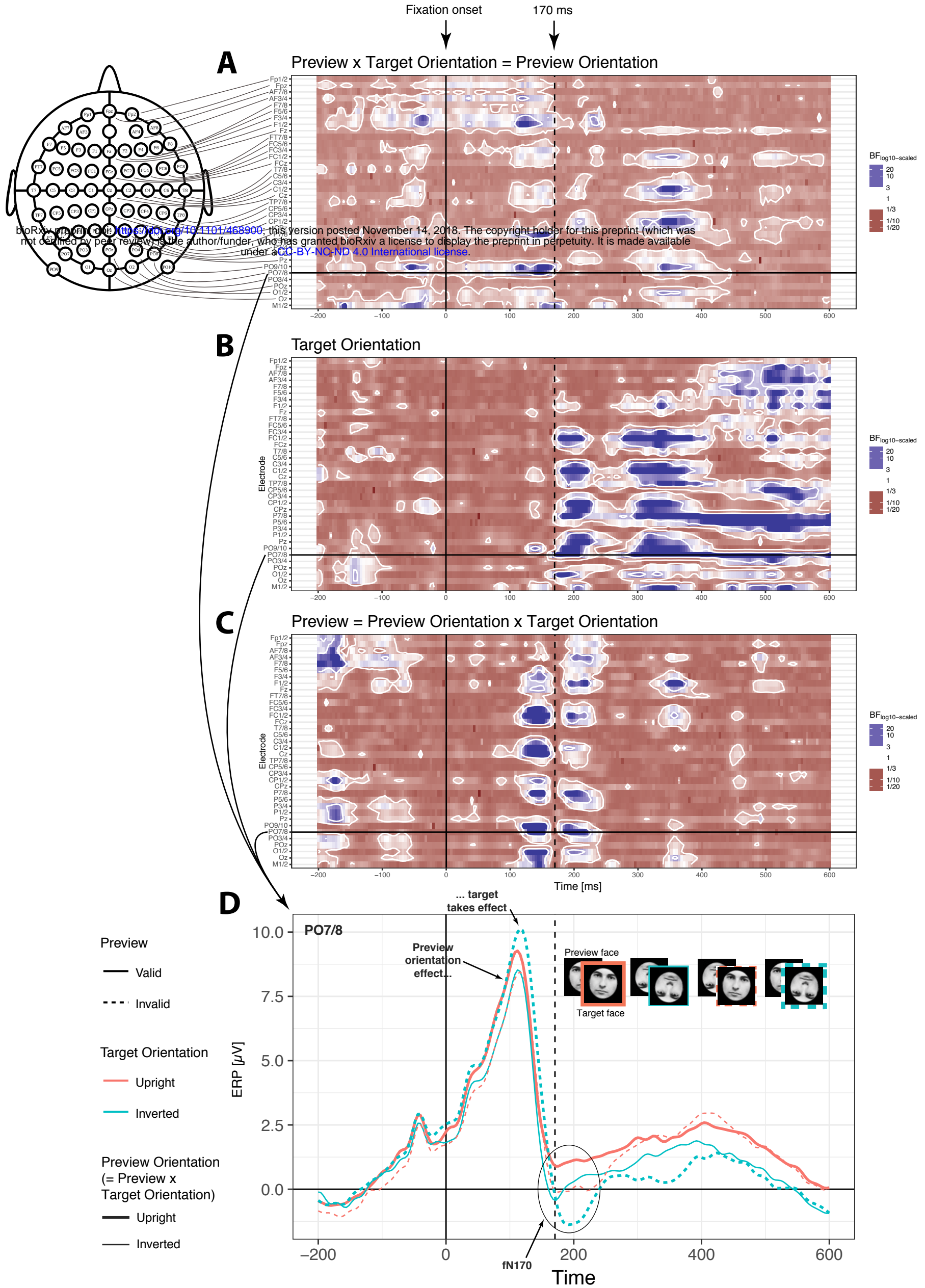


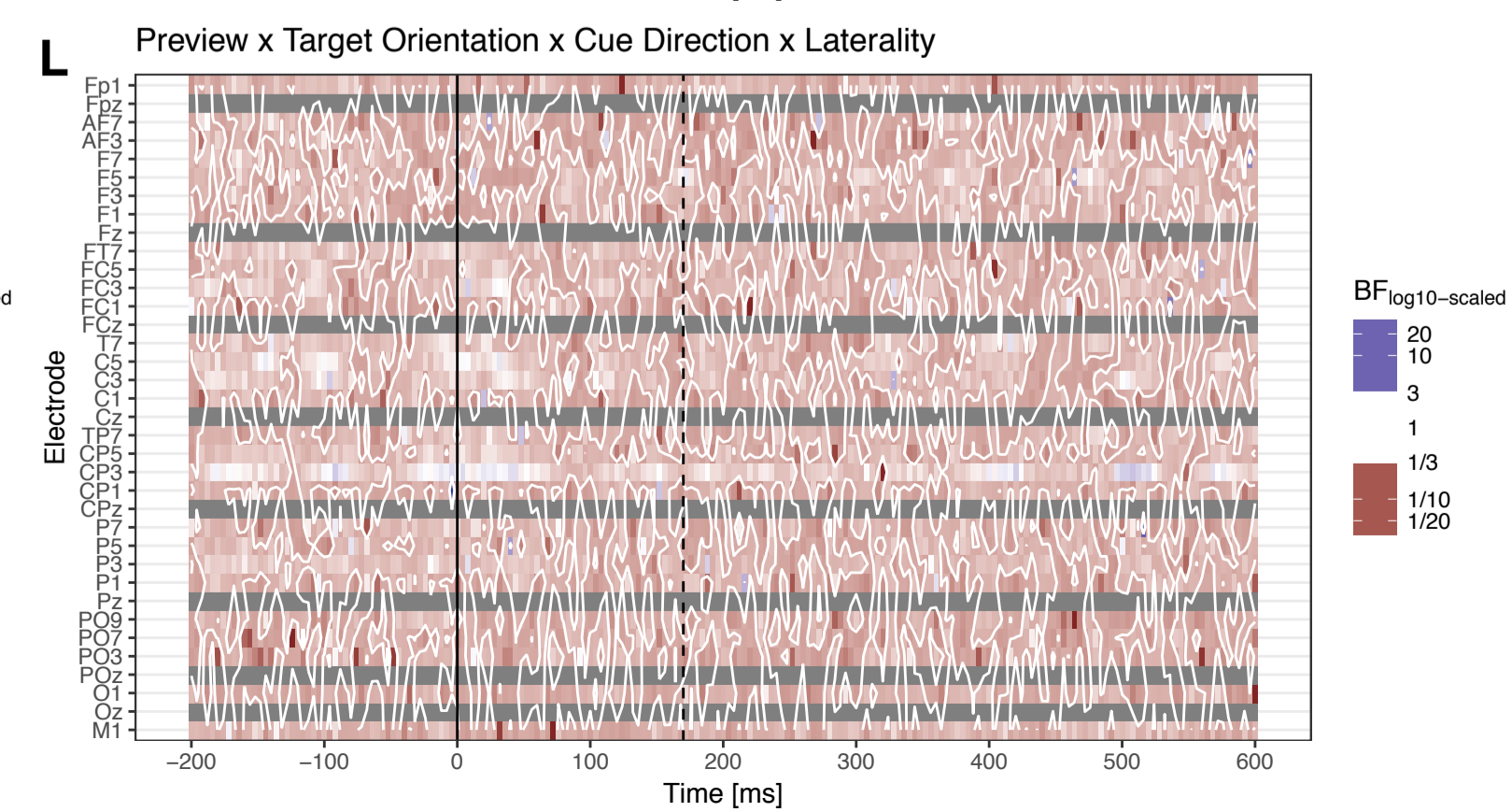
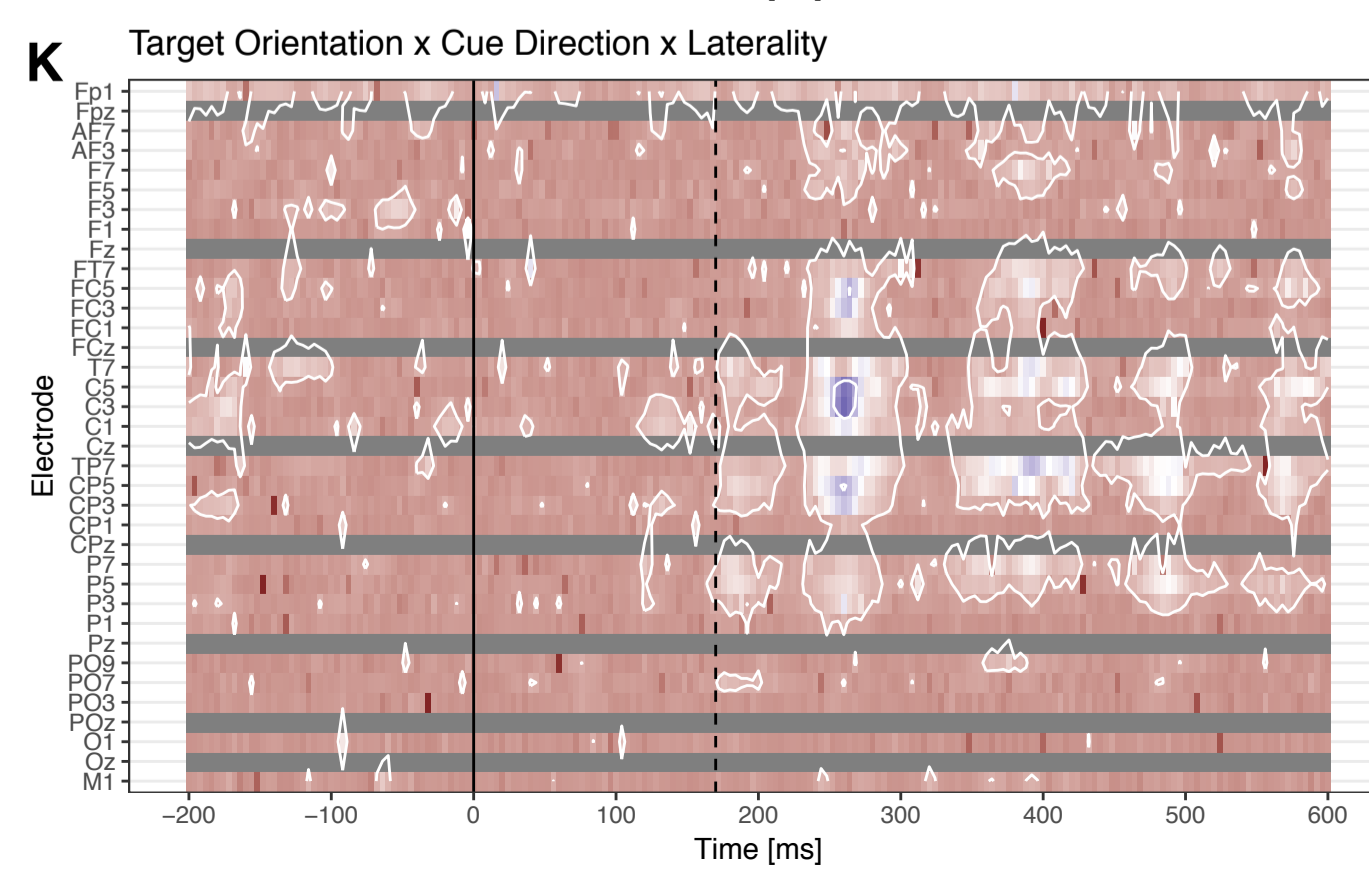
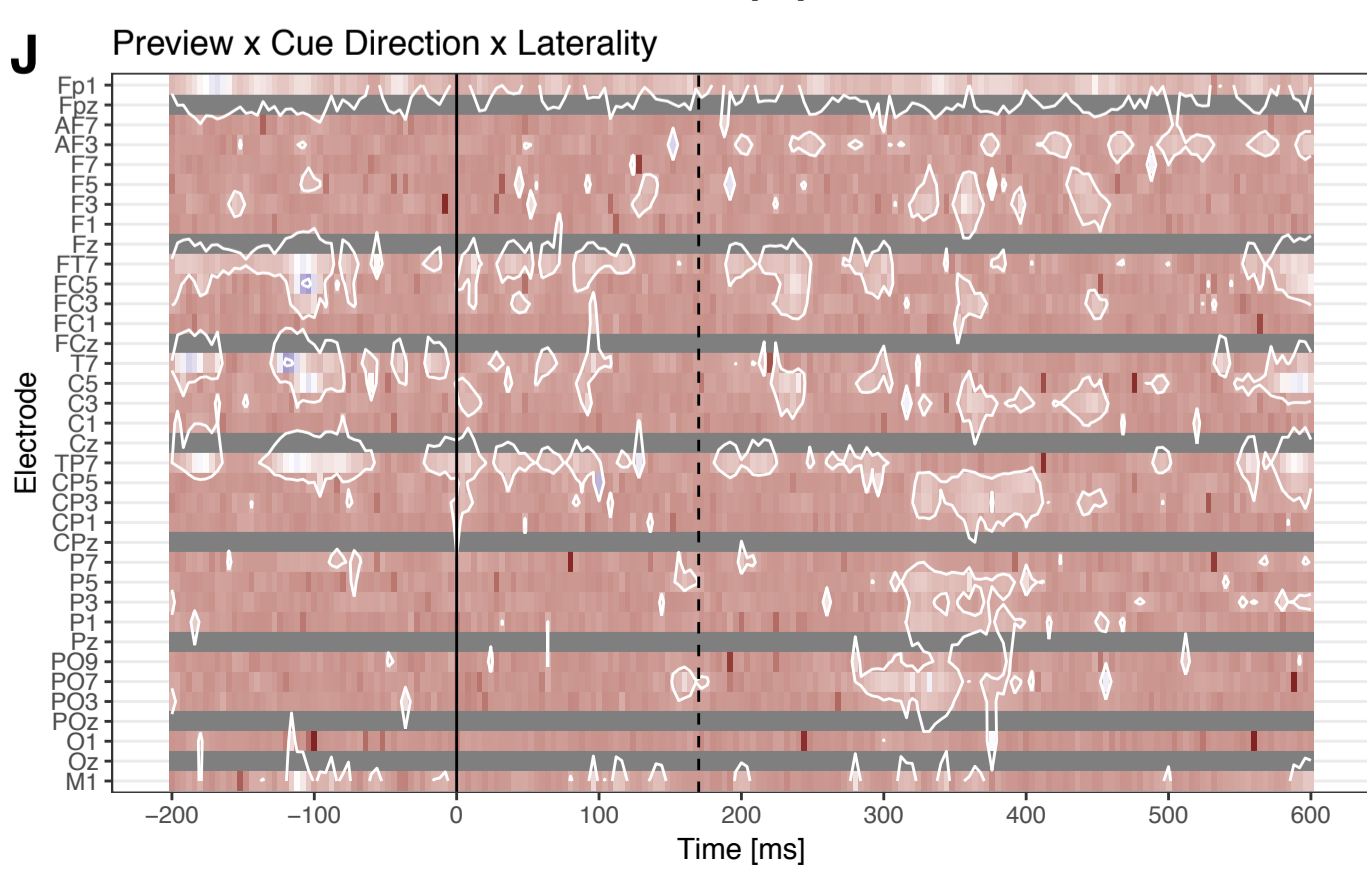
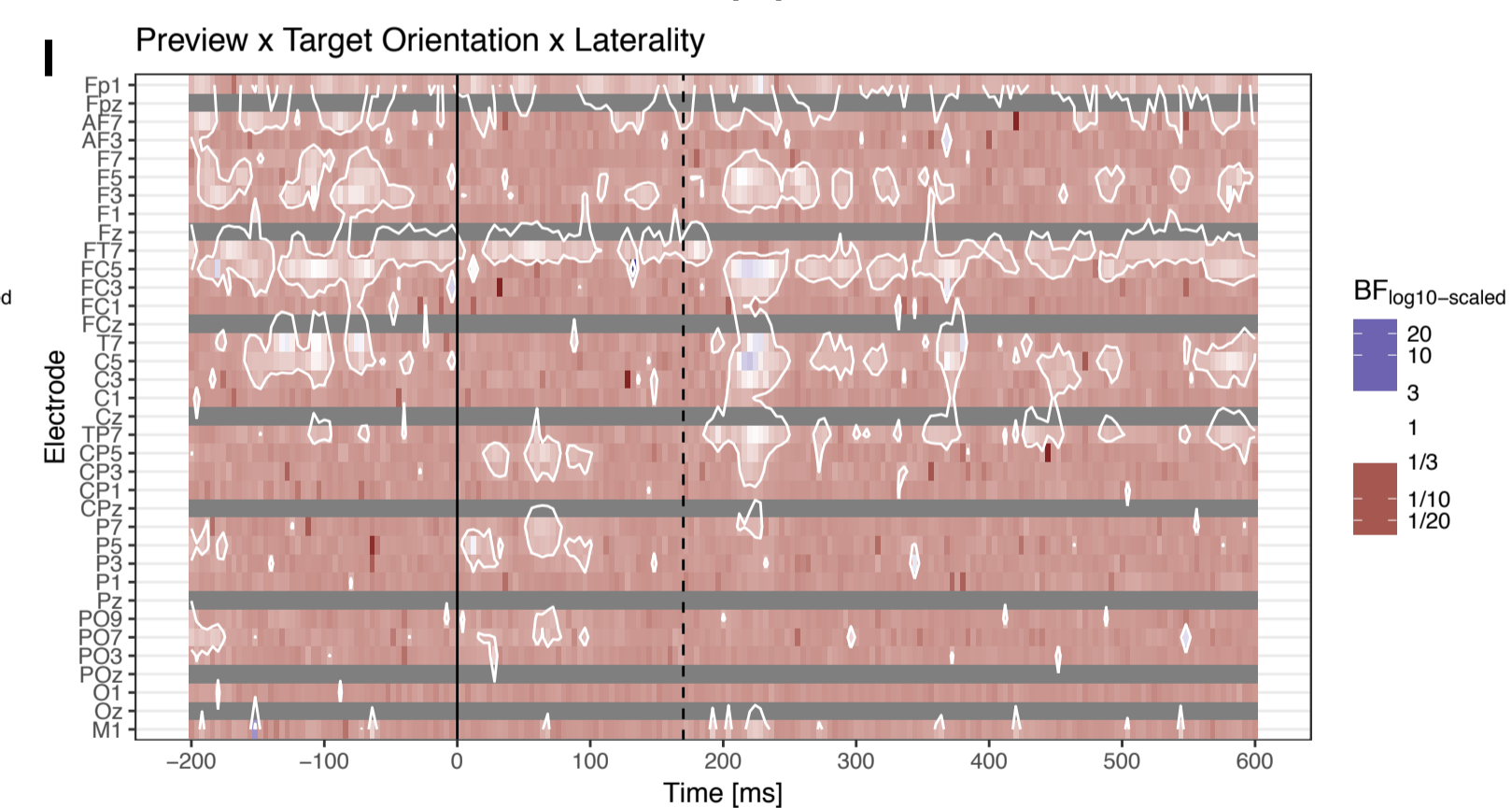
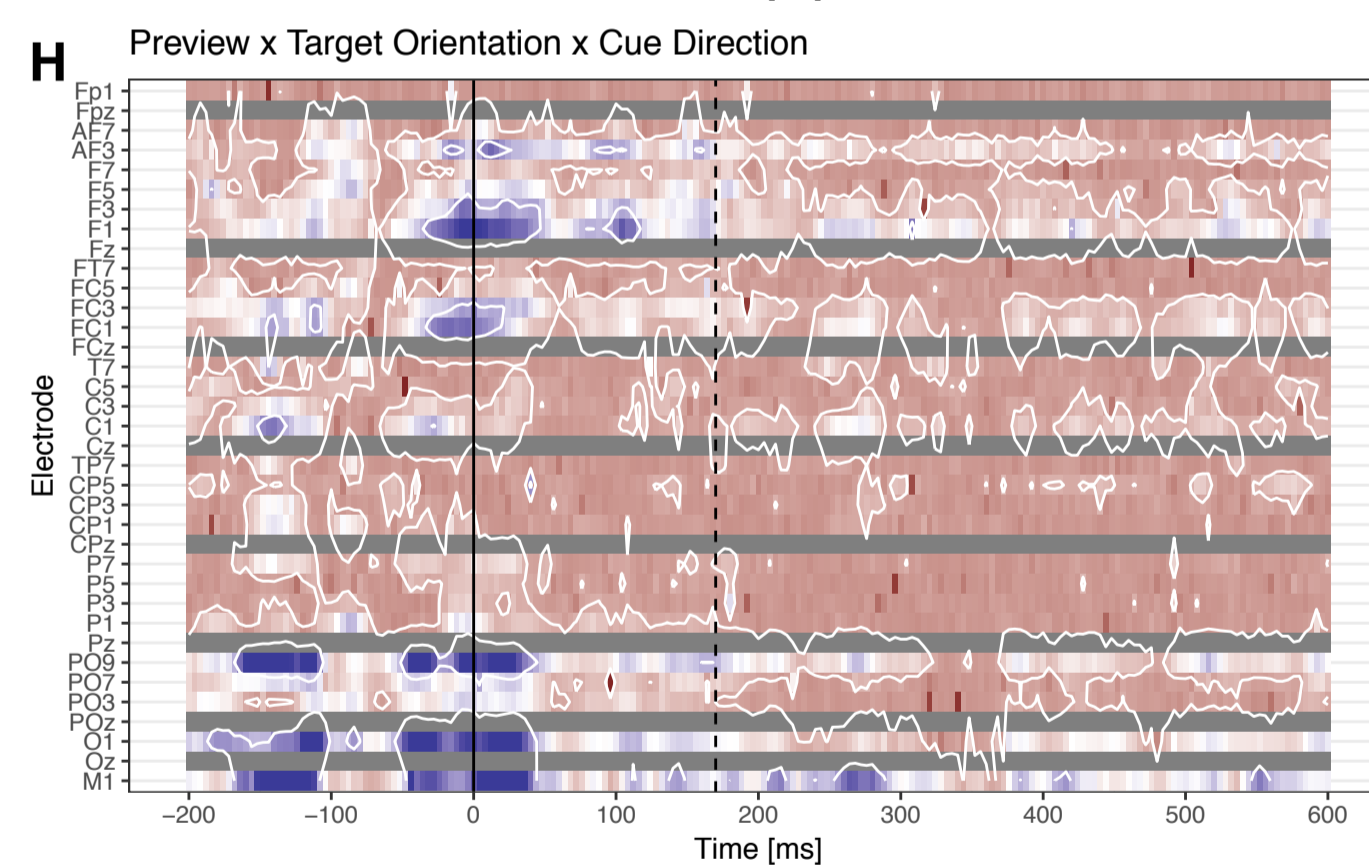
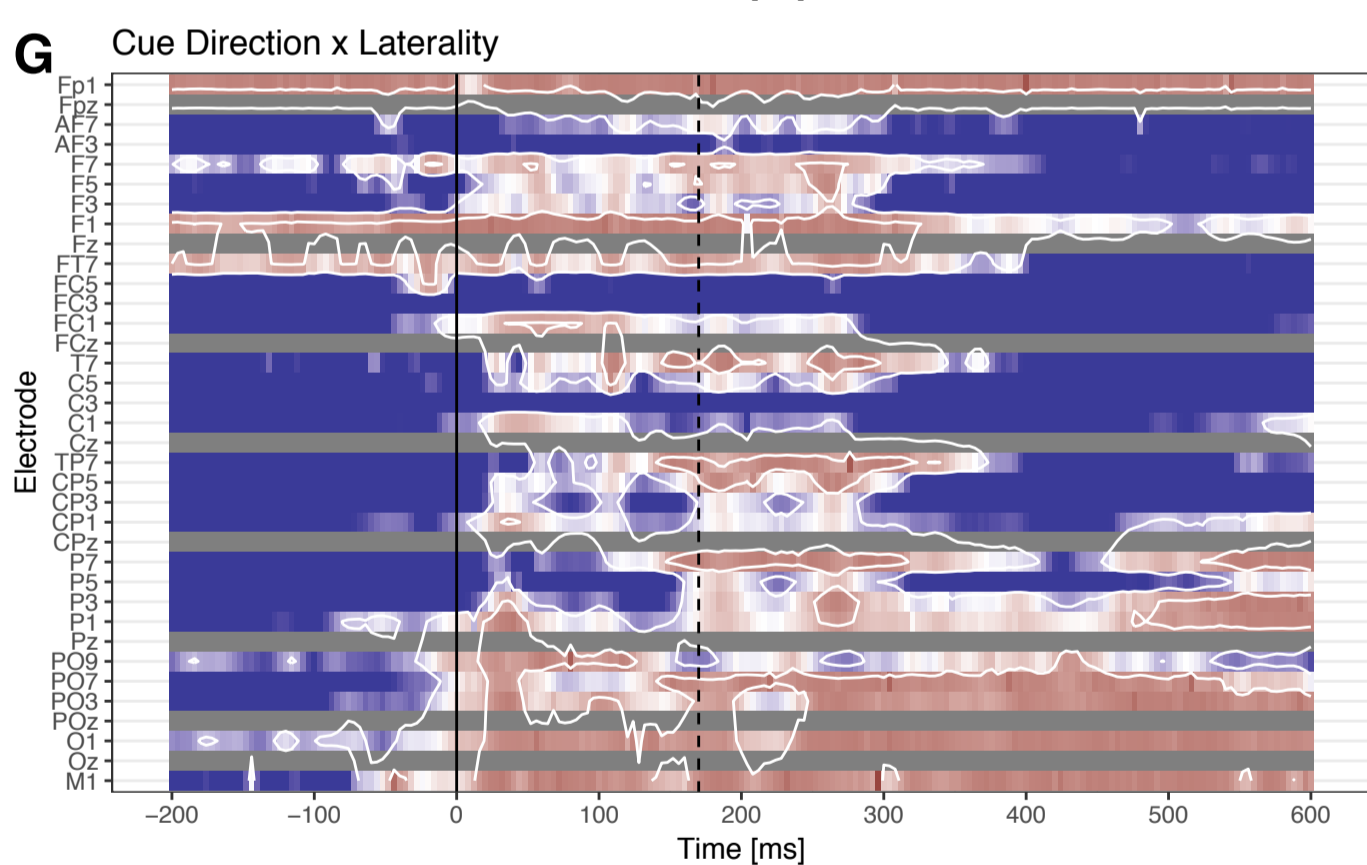
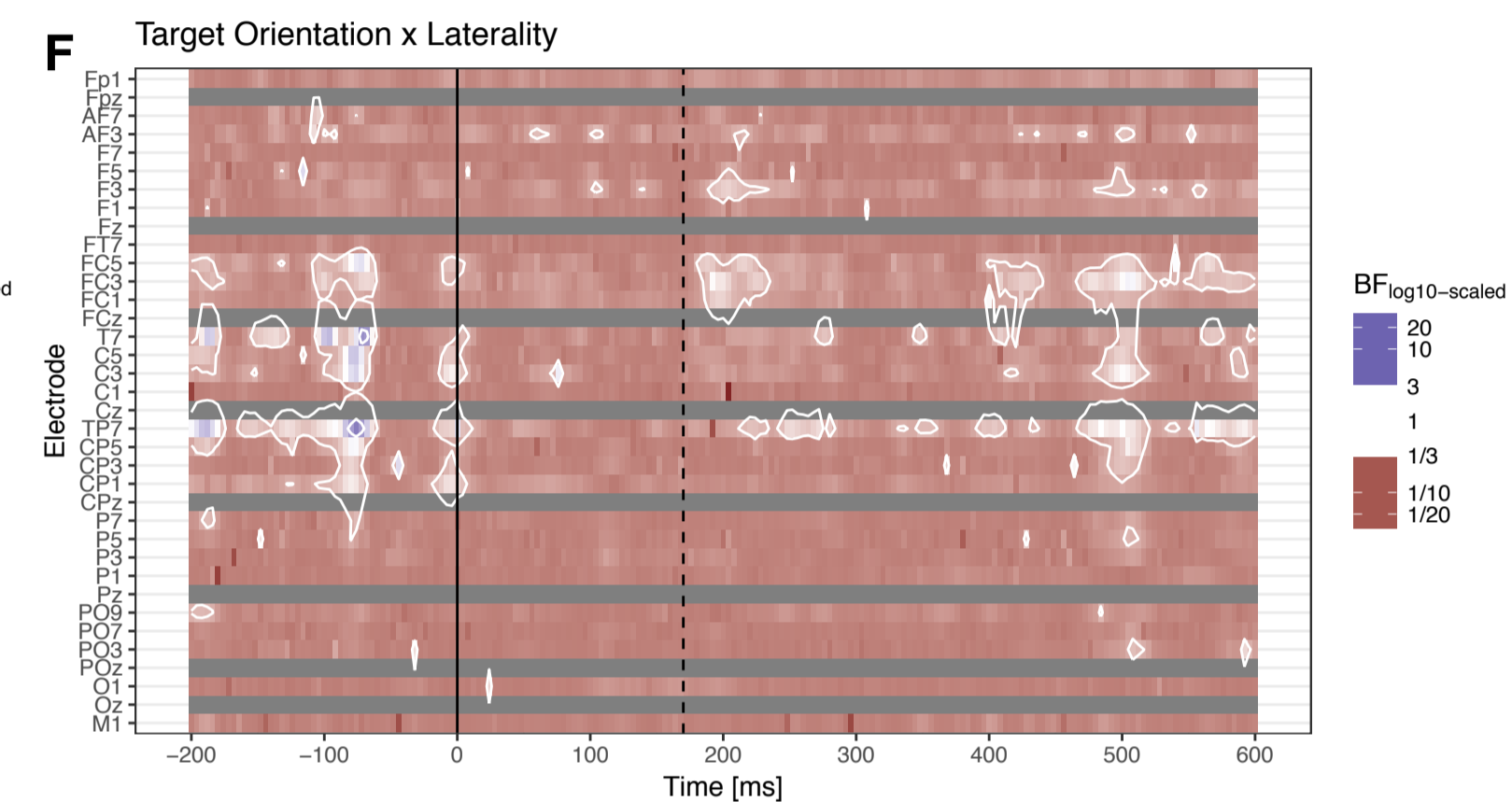
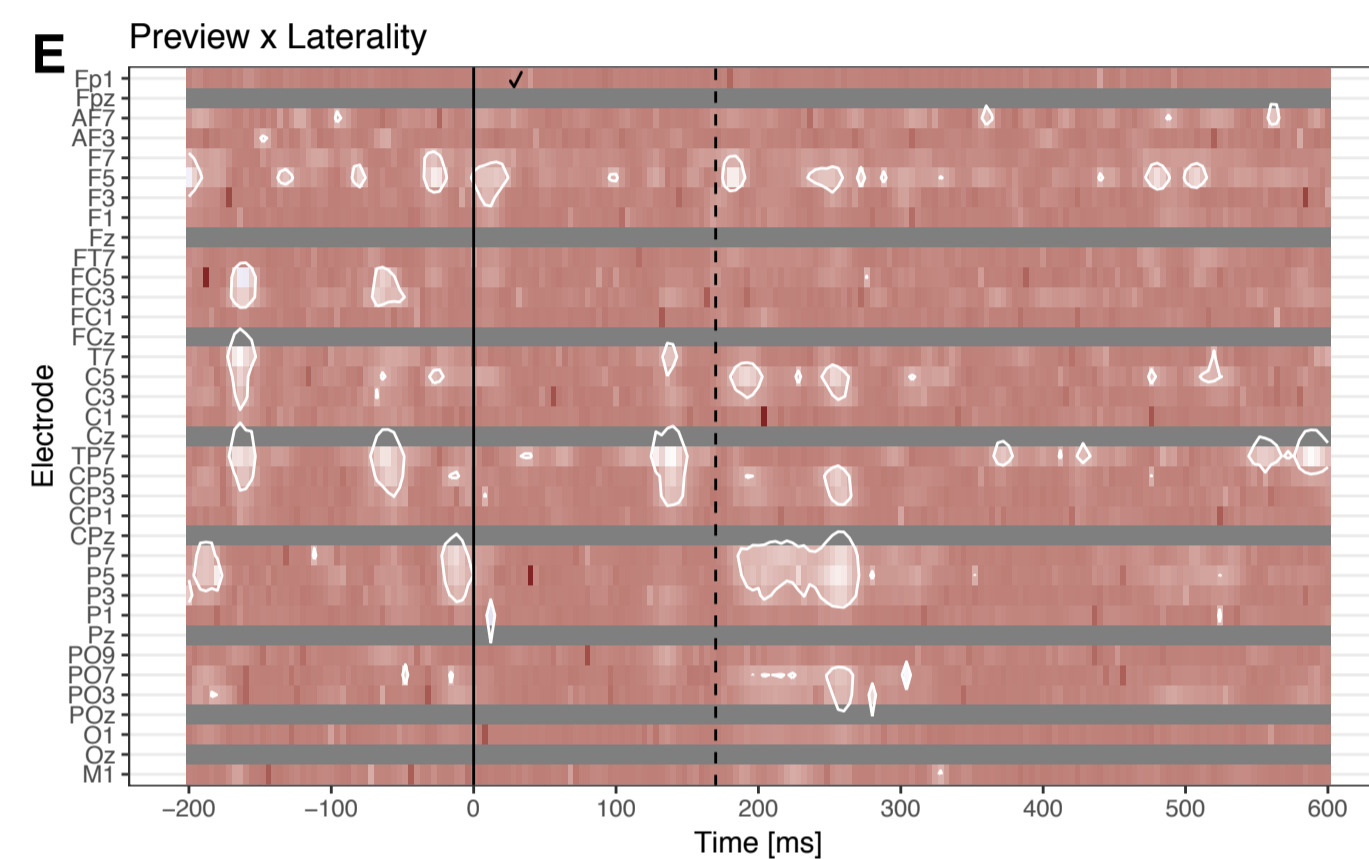
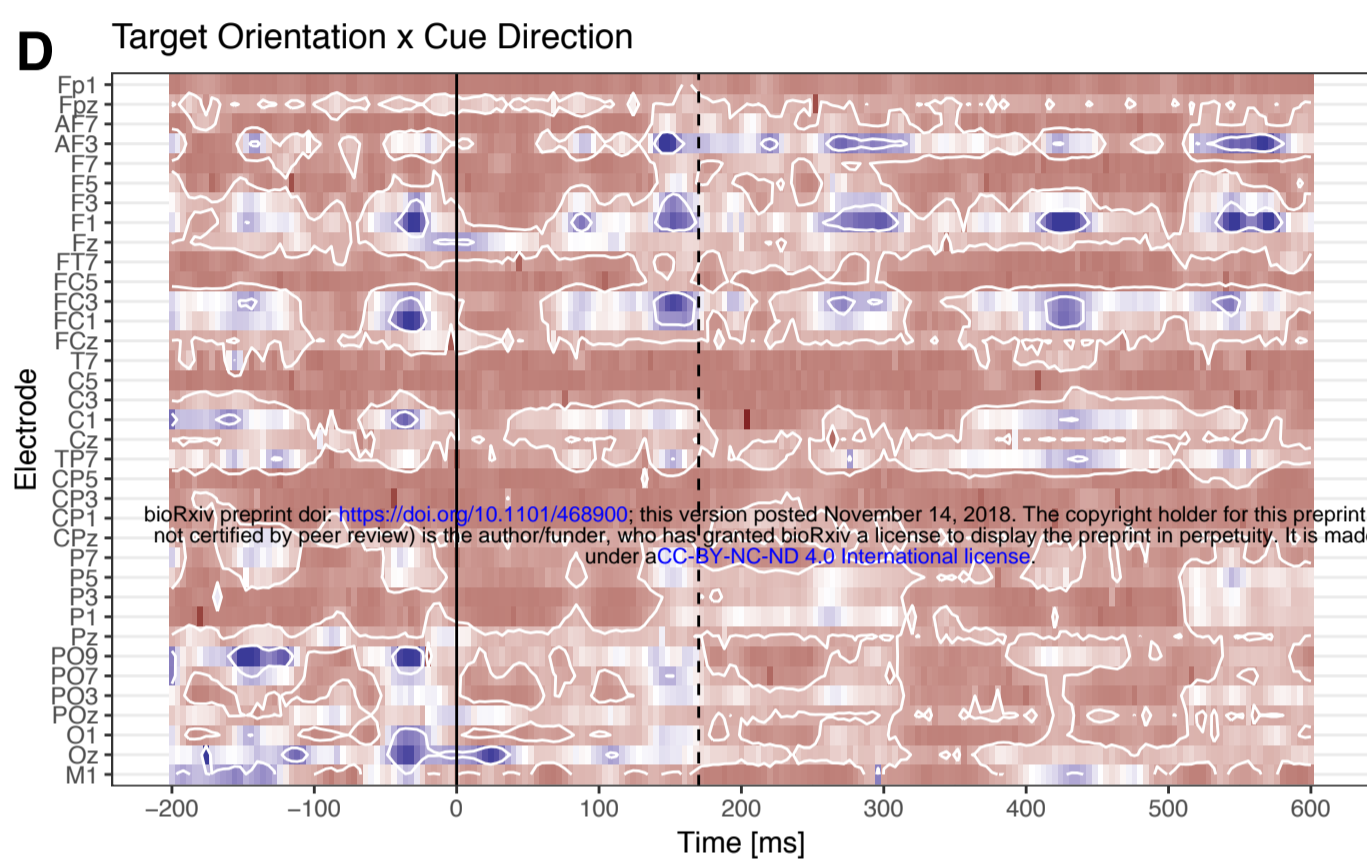
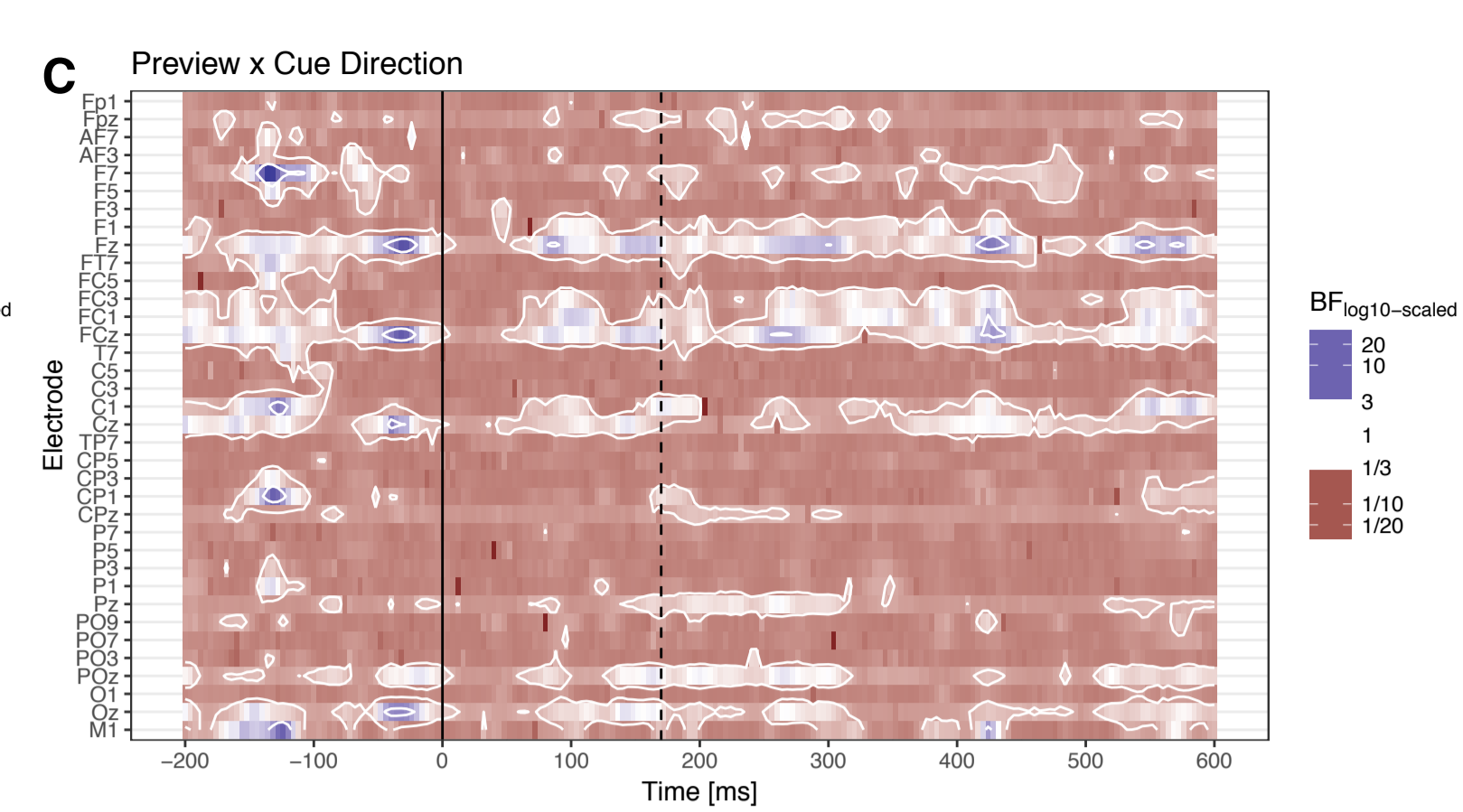
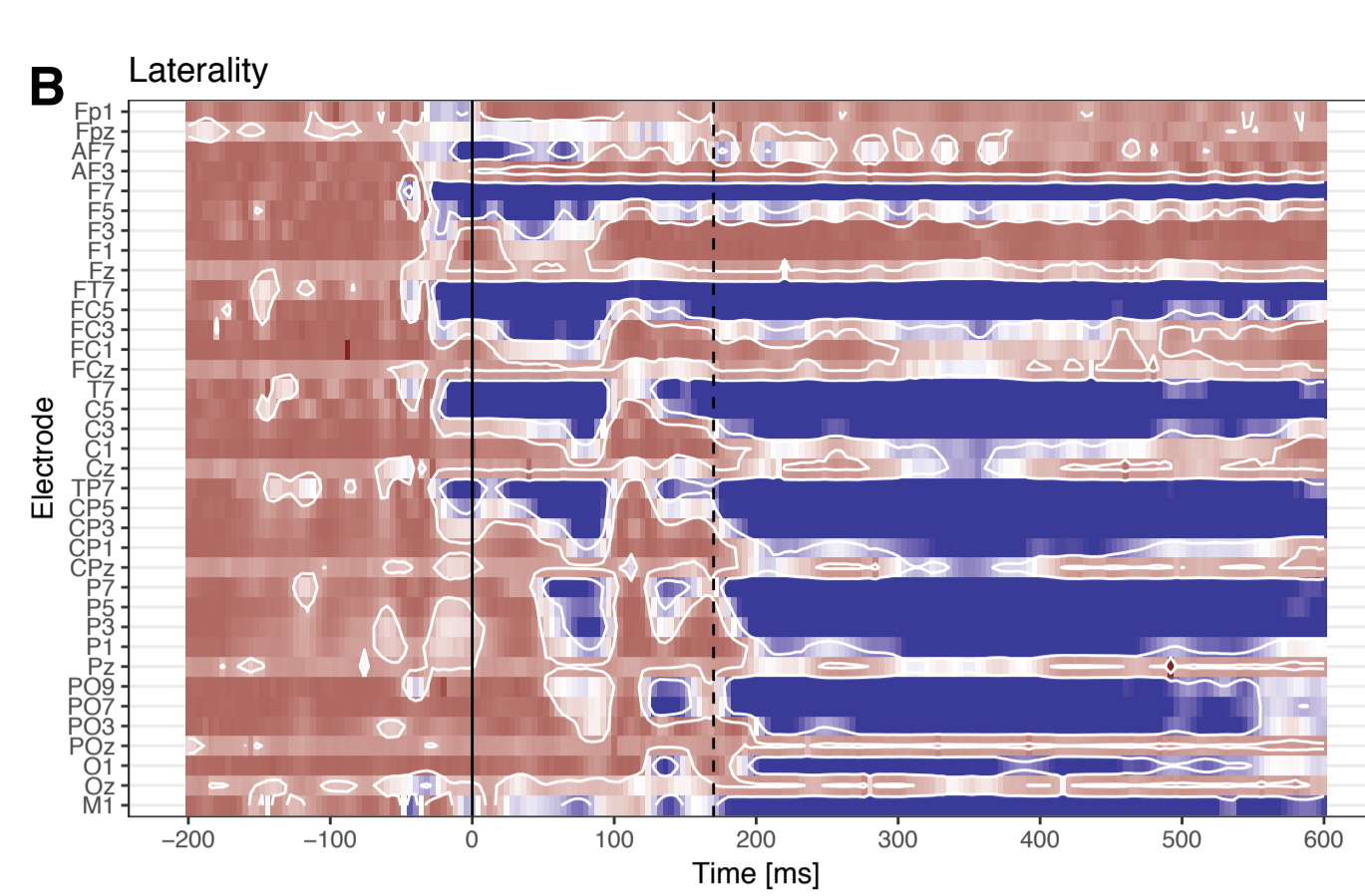
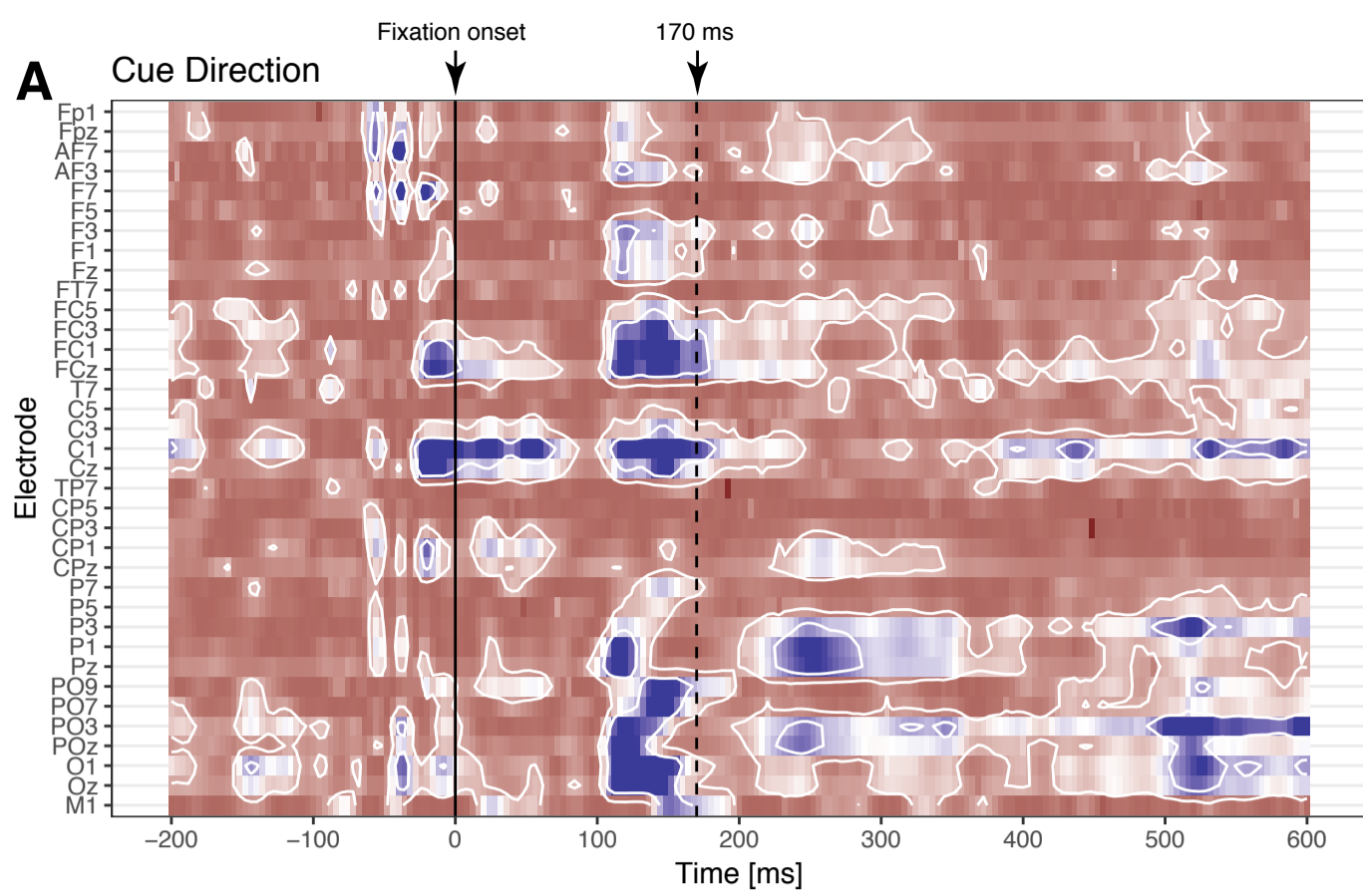
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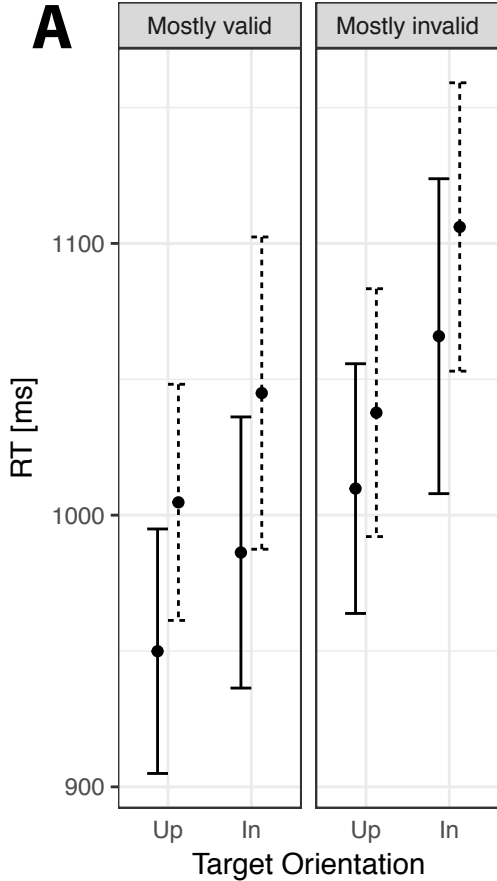
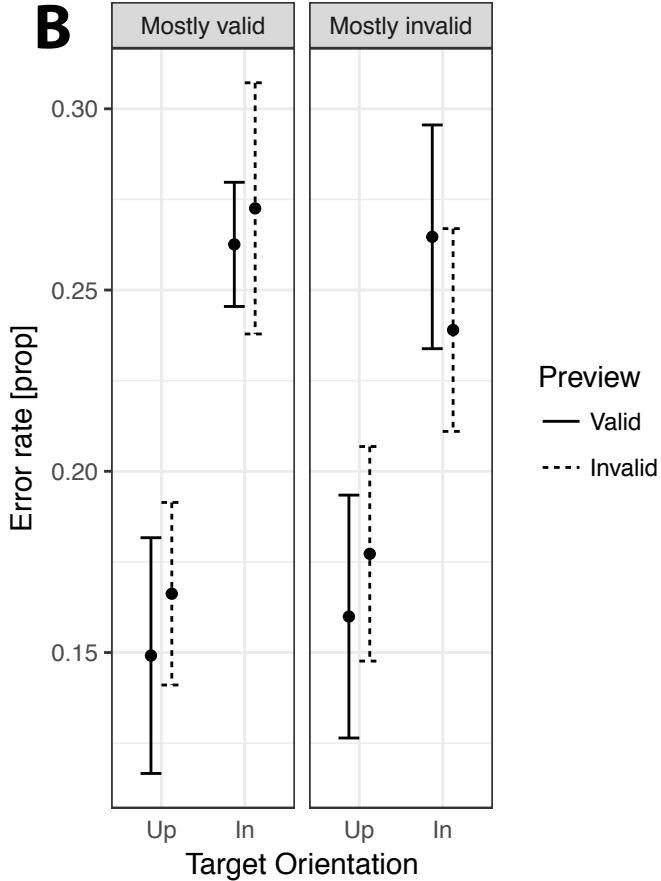
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**A****B**





**A****B**

Preview

— Valid

- - - Invalid



