

## Repetition suppression and prediction error

1 **Running head:** Repetition suppression and prediction error

### 3 **Prediction Error and Repetition Suppression Have Distinct Effects**

#### 4 **on Neural Representations of Visual Information**

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## Repetition suppression and prediction error

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### Abstract

25 Predictive coding theories argue that recent experience establishes expectations in  
26 the brain that generate *prediction errors* when violated. Prediction errors provide a  
27 possible explanation for *repetition suppression*, where evoked neural activity is  
28 attenuated across repeated presentations of the same stimulus. The predictive  
29 coding account argues repetition suppression arises because repeated stimuli are  
30 expected, whereas non-repeated stimuli are unexpected and thus elicit larger neural  
31 responses. Here we employed electroencephalography in humans to test the  
32 predictive coding account of repetition suppression by presenting sequences of  
33 visual gratings with orientations that were expected either to repeat or change in  
34 separate blocks of trials. We applied multivariate forward modelling to determine  
35 how orientation selectivity was affected by repetition and prediction. Unexpected  
36 stimuli were associated with significantly enhanced orientation selectivity, whereas  
37 selectivity was unaffected for repeated stimuli. Our results suggest that repetition  
38 suppression and expectation have separable effects on neural representations of  
39 visual feature information.

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### Introduction

42 At any moment in time, the brain receives more sensory information than can  
43 be responded to, creating the need for selection and efficient processing of  
44 incoming signals. One mechanism by which the brain might reduce its information  
45 processing load is to encode successive presentations of the same stimulus in a  
46 more efficient form, a process known as *neural adaptation* (Fairhall, Lewen, Bialek,  
47 & de Ruyter van Steveninck, 2001; Kvale & Schreiner, 2004; Smirnakis, Berry,  
48 Warland, Bialek, & Meister, 1997). Such adaptation has been observed across  
49 different sensory modalities and species, and has been suggested as a potential  
50 mechanism for enhancing the coding efficiency of individual neurons and neuronal  
51 populations (Adibi, McDonald, Clifford, & Arabzadeh, 2013; Benucci, Saleem, &  
52 Carandini, 2013; Maravall, Petersen, Fairhall, Arabzadeh, & Diamond, 2007). A  
53 particular form of neuronal adaptation, known as *repetition suppression*, is  
54 characterised by attenuated neural responses to repeated presentations of the  
55 same stimulus (Diederer, Spencer, Vestergaard, Fletcher, & Schultz, 2016; Gross,  
56 Schiller, Wells, & Gerstein, 1967; Keller et al., 2017; Movshon & Lennie, 1979;  
57 Rasmussen, Schwartz, & Chase, 2017). Here we asked whether predictive coding  
58 theory, which assumes that sensory processing is influenced by prior exposure, can  
59 account for changes in neural representations observed with repetition suppression.

60 The phenomenon of repetition suppression has been widely exploited to  
61 investigate neural representations of sensory information. Repeated exposures allow  
62 for more efficient representation of subsequent stimuli, as manifested in improved  
63 behavioural performance despite a significant reduction in neural activity (Henson &

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64 Rugg, 2003; Schacter & Buckner, 1998). Repetition suppression paradigms have  
65 been used extensively in human neuroimaging because they are commonly  
66 considered to be analogous to the single-cell adaptation effects observed in animal  
67 models (see Barron, Garvert, & Behrens, 2016 for review). The exact relationship  
68 between the effects seen in human neuroimaging studies and animal  
69 neurophysiology has, however, yet to be fully established.

70 The view that repetition suppression observed in human neuroimaging  
71 studies reflects neuronal adaptation has recently been challenged by hierarchical  
72 predictive coding theories (Auksztulewicz & Friston, 2016; Summerfield, Tritschuh,  
73 Monti, Mesulam, & Egner, 2008). These theories argue that the brain interprets  
74 incoming sensory events based on what would be expected from the recent history  
75 of exposure to such stimuli (Friston, 2005; Rao & Ballard, 1999). According to these  
76 theories, predictions are generated within each cortical area, and are bi-directionally  
77 propagated from higher to lower areas, including to primary sensory regions,  
78 allowing for more efficient representation of expected stimuli. When there is a  
79 precise expectation, incoming information can be efficiently represented by  
80 recruiting a small pool of relevant neurons (Friston, 2005). When there is a mismatch  
81 between an expectation and the stimulus presented, i.e., when there is a *prediction  
82 error*, the stimulus is less efficiently represented and thus elicits a larger neural  
83 response.

84 The majority of evidence for predictive coding comes from human  
85 neuroimaging experiments in which the presentation of an unexpected stimulus  
86 generates a larger response than the presentation of an expected stimulus. In

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87 studies employing electroencephalography (EEG) and magnetoencephalography  
88 (MEG), this effect is known as the *mismatch negativity* (Garrido, Kilner, Stephan, &  
89 Friston, 2009; Näätänen, Paavilainen, Rinne, & Alho, 2007; Wacongne et al., 2011),  
90 where an unexpected stimulus evokes significantly greater negativity than an  
91 expected stimulus. To date, however, no study has tested a key premise of  
92 predictive coding, namely, that expected stimuli are more efficiently encoded in the  
93 brain relative to unexpected stimuli, in terms of their elementary feature  
94 representations. Nor has any previous investigation examined whether the  
95 mismatch negativity response is associated with a change in neural tuning to  
96 stimulus features such as orientation.

97 To test the hypothesis that prediction error can account for repetition  
98 suppression effects, Summerfield and colleagues (2008) introduced an experimental  
99 paradigm in which the identity of a face stimulus was either repeated in 80% of  
100 trials (making the repetition *expected*) or was changed in 80% of trials (making the  
101 repetition *unexpected*). There was greater attenuation of the BOLD response in the  
102 fusiform face area when a face repetition was expected, relative to when it was  
103 unexpected, suggesting that repetition suppression is reduced by unexpected  
104 stimuli. This attenuation of repetition suppression by failures of expectation has also  
105 been replicated using fMRI (Larsson & Smith, 2012) and M/EEG, using high-level  
106 stimuli such as faces (Summerfield, Wyart, Mareike Johnen, & de Gardelle, 2011),  
107 and simple stimuli such as tones (Todorovic & de Lange, 2012; Todorovic, van Ede,  
108 Maris, & de Lange, 2011).

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109 A potential reconciliation of the relationship between expectation and  
110 repetition suppression comes from work showing that while expectations decrease  
111 the overall amount of neural activity, they can also yield sharper representations of  
112 sensory stimuli (Kok, Jehee, & de Lange, 2012). This work goes beyond  
113 conventional neuroimaging approaches, which typically only measure overall levels  
114 of neural activity (Buckner et al., 1998; Kourtzi & Kanwisher, 2001; Tootell, Reppas,  
115 Dale, & Look, 1995). Such amplitude changes could in principle be produced by one  
116 or more different types of change in the underlying neural representations. For  
117 instance, both sharpening, where the response to only unpredicted features is  
118 suppressed, and gain reduction, where a multiplicative suppression occurs for all  
119 features, could be associated with decreased population activity, even though the  
120 amount of information carried by the representations will be markedly different.  
121 Recently introduced multivariate pattern analytic approaches to human neuroimaging  
122 – specifically forward encoding modelling – allow for the quantification of stimulus-  
123 selective information contained within patterns of neural activity in human observers  
124 (Brouwer & Heeger, 2009; Garcia, Srinivasan, & Serences, 2013; King, Pescetelli, &  
125 Dehaene, 2016; Kok, Mostert, & de Lange, 2017; Myers et al., 2015; Salti et al.,  
126 2015; Wolff, Jochim, Akyürek, & Stokes, 2017a). This approach goes beyond typical  
127 multivariate pattern analyses (which normally produce only accuracy scores) by  
128 quantifying neural representations evoked by sensory stimuli to reveal both the  
129 accuracy and the *tuning fidelity* for the specific feature-dimension of interest.  
130 Here we used multivariate forward encoding methods to test whether  
131 repetition suppression and expectation have different effects on the way the brain

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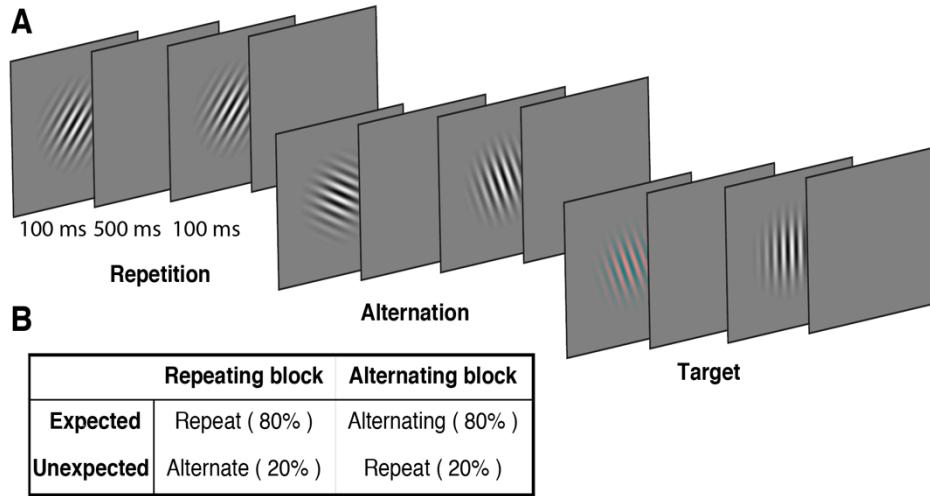
132 represents visual information, in this case the orientation of grating stimuli. To  
133 anticipate the results, we found that soon after stimulus onset, repetition  
134 suppression had no effect on visual orientation selectivity, but violated expectations  
135 were associated with a significantly increased orientation-selective response  
136 through gain modulation, with no corresponding change in response fidelity. This  
137 representation was transiently re-activated at around 200 ms post-stimulus onset,  
138 suggesting that feedback influences initial sensory encoding of an unexpected  
139 stimulus, which in turn allows for updating of the sensory prior.

140 **Results**

141 We used a modified version of the paradigm introduced by Summerfield and  
142 colleagues (2008), replacing the face stimuli used in that study with oriented  
143 Gabor. These low-level stimuli allowed us to quantify the degree of orientation  
144 selectivity in EEG activity to determine how the representation of orientation is  
145 affected by prediction error and repetition suppression. Each of fifteen observers  
146 participated in two EEG sessions. On each trial, two Gabor were presented  
147 sequentially (100 ms presentation, 600 ms stimulus onset asynchrony), and these  
148 stimulus pairs either repeated or alternated in their orientation (Figure 1A, Movie 1).  
149 The predictability of the repeated and alternating pairs was varied in a block-wise  
150 manner to manipulate expectation. In a *repeating* block, the orientations of the two  
151 Gabor in a pair repeated in 80% of trials, and alternated in the remaining 20%.  
152 These contingencies were reversed in the *alternating* block (Figure 1B). The  
153 orientations of successive stimuli across a block were randomized to limit any  
154 accumulated effects of adaptation and prediction. As repetition suppression and

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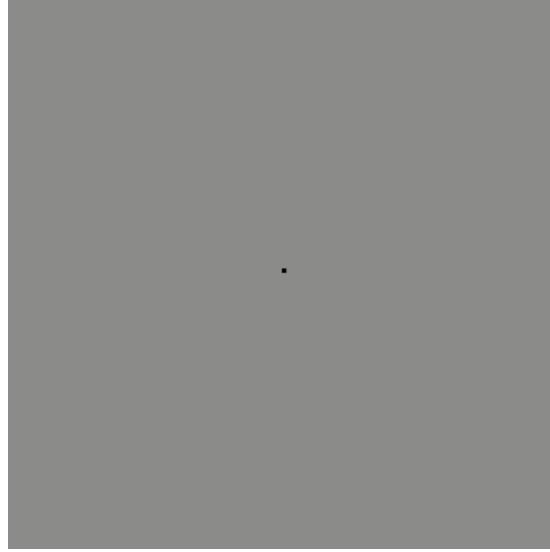
155 expectation from orthogonal dimensions of the task, the design allowed us to  
156 isolate their respective contributions to neural responses. Participants completed an  
157 unrelated task of discriminating (red vs blue) rare coloured Gabors (which occurred  
158 on 10% of trials).



159

160 **Figure 1.** Example stimulus displays and task design. **(A)** Schematic of the stimuli  
161 and timing used in the experiment. Participants viewed a rapid stream of pairs of  
162 Gabors and monitored for an infrequent coloured target (10% of trials). The stimulus  
163 orientations varied pseudorandomly across trials between 0° and 160° (in 20°  
164 steps), allowing estimation of orientation-selective information contained within  
165 patterns of EEG activity. **(B)** The orientation of the pairs of Gabors could either  
166 repeat or alternate. In one type of block, 80% of trials were orientation repeats and  
167 the remaining 20% alternated (Repeating blocks); in the other type of block these  
168 contingencies were reversed (Alternating blocks).  
169

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171 **Movie 1.** Example of a stimulus sequence of Gabors in a typical repetition block.

172

173 **Repetition suppression and prediction error affect the overall level of neural**  
174 **activity**

175 The Gabors elicited a large response over occipital-parietal areas (Figure 2A).

176 Consistent with previous work (Cui, Wang, Park, Demb, & Butts, 2016; Keller et al.,

177 2017; Rentzeperis, Nikolaev, Kiper, & Van Leeuwen, 2012; Summerfield et al., 2011;

178 Todorovic et al., 2011; Todorovic & de Lange, 2012; Tootell et al., 1998), there was

179 a significant repetition suppression effect (Repeat < Alternating), such that the

180 response to repeated stimuli was significantly reduced compared with the response

181 to alternating stimuli (Figure 2A). The repetition suppression effect was evident over

182 a large cluster of occipital-parietal electrodes at two time intervals: an early effect

183 from 79 to 230 ms, and a later effect at 250 to 540 ms after the onset of the second

184 stimulus (cluster  $p < .025$ ; Figure 2B and caption). A large cluster of frontal

185 electrodes mirrored the repetition suppression effect with a similar time course: the

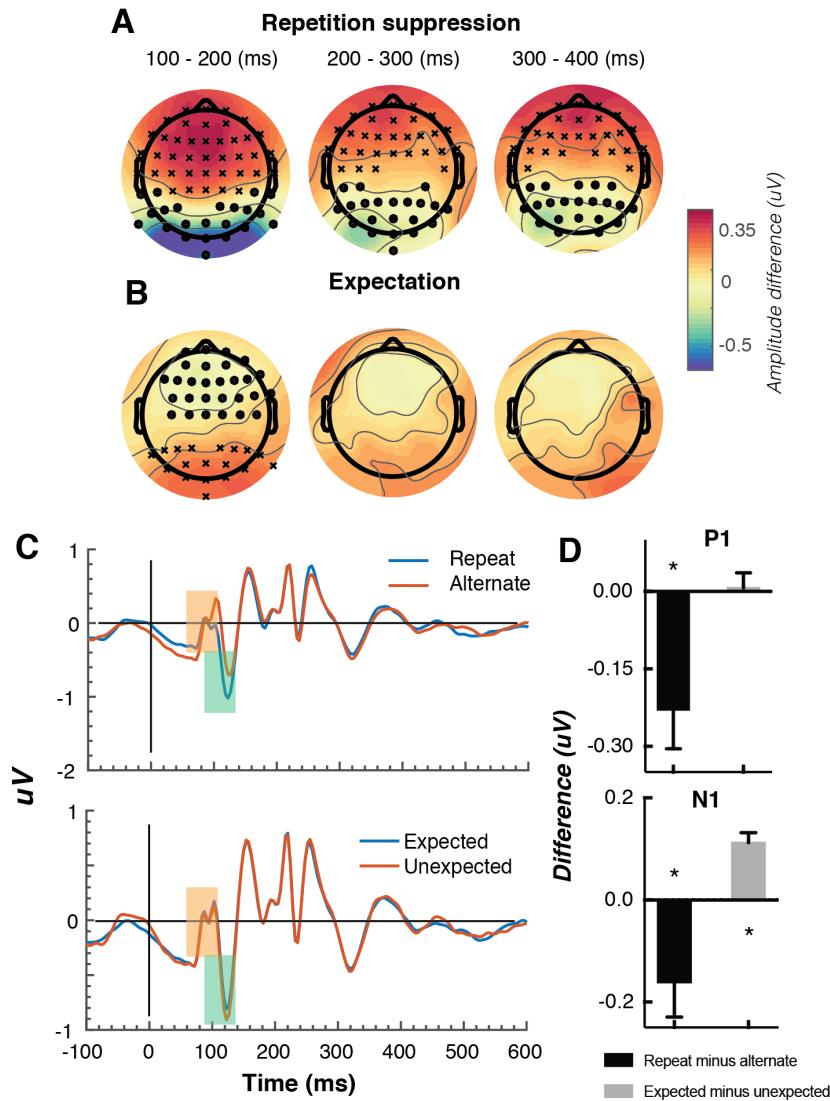
186 ERP over these frontal sites had the same pattern, but was reversed in sign,

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187 suggesting it originated from the same dipole as the occipital response.

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190 **Figure 2.** Univariate EEG results for the effect of repetition suppression and  
191 expectation on the second stimulus in a pair. Panels A and B show the main effects  
192 of repetition suppression and expectation, respectively, over three post-stimulus  
193 epochs (100-200ms, 200-300 ms, 300-400 ms) and across all electrodes. The main  
194 effect of repetition suppression is displayed as Repeating minus Alternating trials.  
195 The main effect of expectation is displayed as Expected minus Unexpected trials.  
196 Circles indicate clusters of electrodes with significantly reduced activity, and  
197 crosses indicate clusters of electrodes with significantly increased activity (alpha  $p$   
198  $< .05$ , cluster  $p < .025$ , N permutations = 1500). **(C)** Bandpass filtered (2-40 Hz)  
199 event-related potentials (ERPs) for the two conditions, averaged over occipital-  
200 parietal electrodes (O1, O2, Oz, POz, PO7, PO3, PO8, PO4, P3, Pz, P2). A peak  
201 analysis was conducted to aid comparison with previous studies. Orange shading  
202 indicates the P1 component; green shading indicates the N1 component. **(D)** Peak  
203 analysis results for P1 and N1 components. Note that the plotted values represent  
204 *differences* between conditions, as indicated, rather than condition-specific evoked  
205 responses. Asterisks indicate  $p < .05$ . Error bars indicate  $\pm 1$  standard error.

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206 Also consistent with previous results (Garrido et al., 2009; Summerfield et al.,  
207 2011; Todorovic et al., 2011; Todorovic & de Lange, 2012), there was a significant  
208 expectation effect (Expected < Unexpected). Specifically, there was a significantly  
209 greater negativity for unexpected versus expected stimuli, and this effect was most  
210 prominent over a cluster of occipital-parietal electrodes around 75-150 ms after  
211 stimulus presentation (Figure 2C). As with the repetition suppression result  
212 described above, there was an expectation effect of opposite polarity over  
213 occipital-parietal electrodes. This effect was significant at an early time point post-  
214 stimulus (79-130 ms), but not at later time points (320-390 ms; Figure 2D). Finally,  
215 there was no interaction between repetition suppression and expectation (i.e., no  
216 significant positive or negative clusters, all  $p > .05$ ). Taken together, these results  
217 reveal both repetition suppression and expectation effects in the neural data, which  
218 were indexed separately as shown in Figure 2.

219 We conducted a further traditional peak analysis, to aid comparison with  
220 previously published studies on the mismatch negativity (Garrido, Sahani, & Dolan,  
221 2013; Näätänen et al., 2007; Saarinen, Paavilainen, Schöger, Tervaniemi, &  
222 Näätänen, 1992). We bandpass filtered the ERPs (2-40 Hz) to recover the  
223 stereotypic waveform (Figure 2C) and examined two classic early components – the  
224 N1 and P1 – averaged across a broad grouping of occipital-parietal electrodes (O1,  
225 O2, Oz, POz, PO7, PO3, PO8, PO4, P3, Pz, P2). As in previous studies (Caharel,  
226 d'Arripe, Ramon, Jacques, & Rossion, 2009; Dehaene et al., 2001), we defined the  
227 P1 as the largest positivity between 80 and 110 ms after stimulus presentation, and  
228 the N1 as the largest negativity between 90 and 130 ms after stimulus presentation.

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229 A relatively wide temporal window was used to capture inter-individual response  
230 variation. As expected, for the P1 component the repeated stimulus evoked a  
231 significantly smaller positivity ( $t(14) = 3.03, p = .009$ ) than the alternating stimulus  
232 (Figure 2D), reflecting a repetition suppression effect. There was no such effect of  
233 expectation on the P1 ( $t(14) = 0.26, p = .80$ ). By contrast, as predicted from previous  
234 work (Garrido et al., 2013; Näätänen et al., 2007; Saarinen et al., 1992), analysis of  
235 the N1 component showed that the unexpected stimulus evoked a significantly  
236 greater negativity than the expected stimulus, ( $t(14) = 5.75, p < .0001$ ). The  
237 repetition suppression effect was also present in the N1 ( $t(14) = 2.39, p = .03$ ), but  
238 critically in the opposite direction as the expectation effect.

239 **Expectations increase orientation-selective information contained within  
240 patterns of EEG activity**

241 We next examined the key question of whether repetition suppression and  
242 expectation differentially affect neural representations of orientation information. To  
243 do this, we used a forward encoding approach to reconstruct orientation-selective  
244 information contained within the multivariate pattern of EEG activity distributed  
245 across the scalp (Figure 3; see Methods for details). Briefly, this technique  
246 transforms sensor-level responses into tuned ‘feature’ channels (Brouwer & Heeger,  
247 2009; Garcia et al., 2013; Kay, Naselaris, Prenger, & Gallant, 2008; Myers et al.,  
248 2015), in this case, orientation-selective features. For each trial, the presented  
249 orientation was convolved with a canonical, orientation-selective tuning function  
250 and regressed against the pattern of EEG activity across all sensors at each time  
251 point. This created a spatial filter of the multivariate EEG activity that differentiated

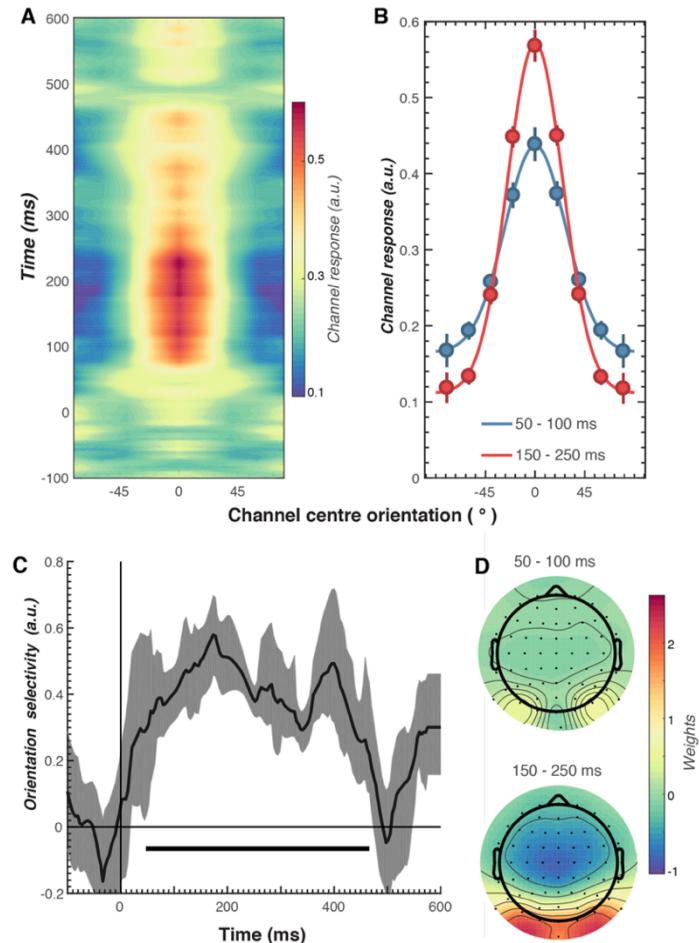
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252 orientations (Figure 3D). These weights were then inverted to reconstruct the model,  
253 and multiplied against an independent set of test trials to produce responses in the  
254 modelled orientation channels. These sets of responses were then used to evaluate  
255 the degree of orientation selectivity in those trials. The procedure was repeated for  
256 all time points in the trial, and a cross-validated approach was used until all trials  
257 had been used for both training and testing.

258 As shown in Figure 3, the forward encoding revealed a strong, orientation-  
259 selective response derived from the multivariate pattern of EEG activity. This  
260 orientation-tuned response was evident from ~50 to ~470 ms after stimulus onset,  
261 and peaked between ~120-250 ms (Figure 3C). Examination of the regression  
262 weights revealed that this response was largely driven by activity centred over  
263 occipital-parietal areas (Figure 3D).

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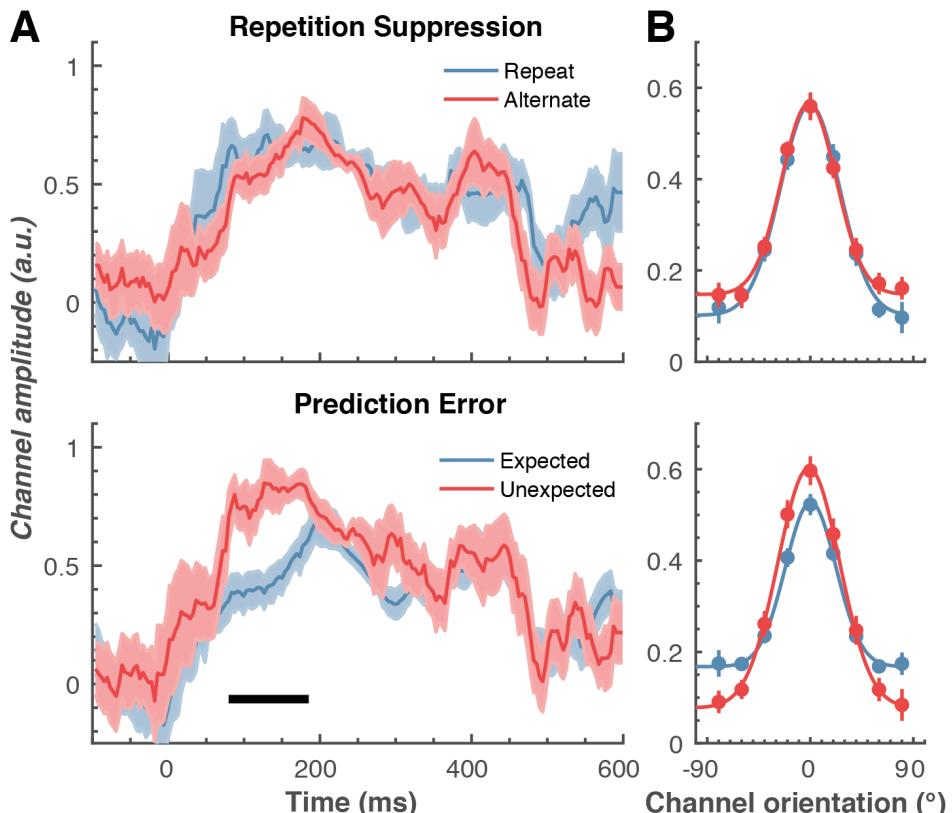
266 **Figure 3.** Results of the forward encoding modelling for orientation-selectivity. **(A)**  
267 Time-resolved orientation tuning curve across all participants and conditions in  
268 response to the second Gabor in the pair. The forward encoding approach resulted  
269 in a tuning curve for each of the nine presented orientations. These tuning curves  
270 were then centred at each presented orientation (here labelled as 0°) to combine  
271 across all orientations. The orientation-selective response is contained within the  
272 overall pattern of EEG; activity begins soon after stimulus onset and peaks at  
273 around 250 ms before declining. **(B)** Population tuning curve of the stimulus  
274 reconstruction across participants, averaged between 50-100 ms and 150-250 ms  
275 after stimulus presentation. Each line is a fitted Gaussian response with a variable  
276 offset used to quantify orientation selectivity. Error bars indicate  $\pm 1$  standard error  
277 of the mean across participants. **(C)** Amplitude of the channel response over time,  
278 averaged across all conditions (black line). The thick black line indicates significant  
279 encoding of stimulus orientation based on a cluster-permutation test across  
280 participants (cluster  $p < .05$ ,  $N$  permutations = 20,000). Encoding accuracy was  
281 reliable from 52 to 470 ms post-stimulus onset. The error shading (in grey) indicates  
282 bootstrapped 95% confidence intervals of the mean. **(D)** Topographic plots of the  
283 weights (averaged across the 9 orientation channels across all participants) derived  
284 from forward encoding at the corresponding time points shown in panel B. (a.u. =  
285 arbitrary units).

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286 To examine our central question of whether repetition suppression and  
287 expectation have differential effects on neural representations of orientation, we  
288 split and averaged the results of the forward encoding by trial type, and fitted these  
289 with Gaussians (see Methods) to quantify orientation selectivity (Figure 4).  
290 Repetition suppression did not affect the amount of orientation selectivity contained  
291 within the EEG data, with similar selectivity for repeated and alternating trials. This  
292 was the case even though the repeated trials had a markedly smaller EEG response  
293 over occipital and parietal electrodes (see Figure 2A), where the forward encoding  
294 model was maximally sensitive. This result is consistent with the ‘efficient  
295 representation’ hypothesis of repetition suppression (Gotts, Chow, & Martin, 2012),  
296 which argues that the overall neural response is smaller with repetition suppression  
297 due to more efficient coding of stimulus information.

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300 **Figure 4.** The effect of repetition suppression and expectation on orientation  
301 selectivity measured using forward encoding modelling. (A) Amount of orientation-  
302 selective information (given by the amplitude of the fitted gaussian) from the EEG  
303 signal in response to the second Gabor in a pair, shown separately for repetition  
304 suppression (upper panel) and expectation (lower panel). The thick black line  
305 indicates significant differences between the conditions (two-tailed cluster-  
306 permutation, alpha  $p < .05$ , cluster alpha  $p < .05$ , N permutations = 20,000). (B)  
307 Population tuning curves averaged over the significant time period (79 – 185 ms)  
308 depicted in panel A. The curves, shown as fitted Gaussians, illustrate how overall  
309 stimulus representations are affected by repetition and expectation. While there was  
310 no difference in orientation tuning for repeated versus alternate stimuli (upper  
311 panel), the amplitude of the orientation response increased significantly, and the  
312 baseline decreased, for unexpected relative to expected stimuli. Error bars indicate  
313  $\pm 1$  standard error.

314

315 Examining the effect of expectation revealed a markedly different pattern of  
316 results. As shown in Figure 4A, at 79 - 185 ms after the onset of the second  
317 stimulus in the pair, orientation-selectivity increased significantly ( $p < .0001$ ) when  
318 the stimulus was unexpected relative to when it was expected, and this effect arose  
319 at the earliest stages of the brain's response to that stimulus. Moreover, the

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320 expectation signal contained enhanced information about the specific features of  
321 the stimulus that violated the expectation, in this case the orientation of the second  
322 grating. We conducted the same statistical tests on the three other parameters  
323 defining the Gaussian function (namely, the width, centre orientation and baseline)  
324 to determine how repetition suppression and expectation might affect other  
325 properties of the neural representation. There was no reliable influence of repetition  
326 suppression on any of these Gaussian parameters (all  $p > .32$ ). For expectation,  
327 there was a significant decrease in baseline activity over the same time period as  
328 observed for the increase in amplitude (79-185 ms,  $p = .001$ ), but there were no  
329 significant effects for the other parameters (all  $ps > .30$ ).

330 We followed up this initial analysis to ensure we did not miss any small  
331 effects of repetition suppression or expectation on any aspects of stimulus  
332 representation. We increased the signal-to-noise by averaging the stimulus  
333 reconstruction over this early time period (79-185 ms after stimulus presentation),  
334 and fitted Gaussians to each participant's data individually (Figure 4B). This again  
335 showed that the amplitude of the response was significantly ( $t(14) = 3.34, p = .005$ )  
336 higher for unexpected ( $M = 0.67, SE = 0.06$ ) than for expected ( $M = 0.41, SE = 0.03$ )  
337 stimuli. By contrast, the width of the representations was similar for unexpected ( $M$   
338 =  $29.62^\circ, SE = 4.72^\circ$ ) and expected ( $M = 26.72^\circ, SE = 2.74^\circ$ ) stimuli, ( $t(14) = 0.78,$   
339  $p = .45$ ). There was also a small but non-significant ( $t(14) = 1.94, p = .06$ ) trend for a  
340 smaller baseline response (i.e., non-orientation tuned activity) in the unexpected  
341 ( $M = -0.01, SE = 0.07$ ) than in the expected ( $M = 0.13, SE = 0.02$ ) condition. For  
342 comparison, we also averaged the same time period for the repetition suppression

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343 conditions, and found similar curves for the repeated and alternating trials (*all ps >*  
344 *.18*). This analysis confirms the previous result, which employed more conservative  
345 nonparametric cluster-based testing.

346 It might be argued that the particular baseline period we chose for the  
347 encoding analyses - namely from -100 to 0 ms before the onset of the second  
348 Gabor in each pair – biased the results by incorporating a purely top-down  
349 expectation template triggered by the orientation of the first Gabor (Kok et al.,  
350 2017). To rule out this possibility, we performed a further forward encoding analysis  
351 where we baselined the raw EEG data to the mean activity from -100 to 0 ms before  
352 the *first* Gabor in each pair. Critically, this control analysis involved a baseline period  
353 over which it was not possible to form a top-down expectation of the orientation of  
354 the second Gabor based on the orientation of the first. This analysis yielded the  
355 same pattern of results as the original analysis (Supplementary Figure 1), such that  
356 the unexpected stimulus evoked significantly greater orientation selectivity than the  
357 expected stimulus ( $p = .02$ ). Also in line with the original analyses, the width of the  
358 representation was not affected by expectation ( $p = .44$ ), and there was no effect of  
359 repetition suppression on orientation selectivity ( $p = .64$ ). We can thus be confident  
360 that the effect of expectation on orientation selectivity that we report here, based on  
361 our forward encoding analyses, is not an artefact of the baselining procedure.

362 We also used a number of approaches to determine whether repetition  
363 suppression and expectation interacted to affect orientation selectivity. First, we  
364 took the difference scores between the combination of factors (e.g., expected  
365 repetition minus unexpected repetition, and expected alternation minus unexpected

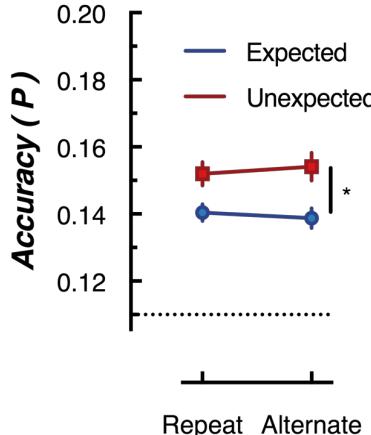
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366 alternation) and compared these using the same cluster-based permutation testing  
367 outlined above. This analysis revealed no significant interactions between the  
368 factors for any parameter (all  $ps > .10$ ). Second, we found the largest orientation-  
369 selectivity, defined by the amplitude of the fitted Gaussian, across the 600 ms  
370 following stimulus presentation. For each participant, this resulted in a single value  
371 for the four conditions. Each of these values was subjected to a two-way repeated-  
372 measures ANOVA, which again revealed no significant interaction between the  
373 factors (all  $ps > .30$ )

374 To further examine whether orientation-selectivity contained within the overall  
375 pattern of EEG activity differed for unexpected and expected stimuli, we used  
376 multivariate discriminant analysis to determine whether more traditional backward  
377 decoding (Grootswagers, Wardle, & Carlson, 2017; Kamitani & Tong, 2005; King,  
378 Gramfort, Schurger, Naccache, & Dehaene, 2014; Marti, King, & Dehaene, 2015)  
379 produces the same pattern of results as that yielded by the forward encoding  
380 approach described above. The same cross-validation procedure was used as in  
381 the forward encoding analysis, but accuracy was now defined as the proportion of  
382 trials labelled with the correct orientation. To facilitate comparison with the results  
383 of Kok et al., (2013), we took the peak classification accuracy within a 600 ms  
384 window after presentation of the second grating within each pair. This analysis  
385 confirmed the results of the forward encoding: orientations shown in unexpected  
386 trials were classified better than orientations shown in expected trials ( $F(1,14)$   
387  $76.42, p < .00001$ ). Again, there was no effect of repetition on classification  
388 accuracy ( $F(1,14) = 0.027, p = .87$ ); nor was there a significant interaction ( $F(1,14) =$

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389 2.52,  $p = .13$ ). This suggests the finding is not specific to the analysis method but  
390 rather reflects how expectation affects the representation of sensory information in  
391 general.



392

393 **Figure 5.** Peak (naive Bayes) classification accuracy of the presented grating  
394 orientation for expected and unexpected conditions. The dotted line indicates  
395 chance performance (1/9 orientations). The error bars indicate  $\pm 1$  standard error of  
396 the mean.

397

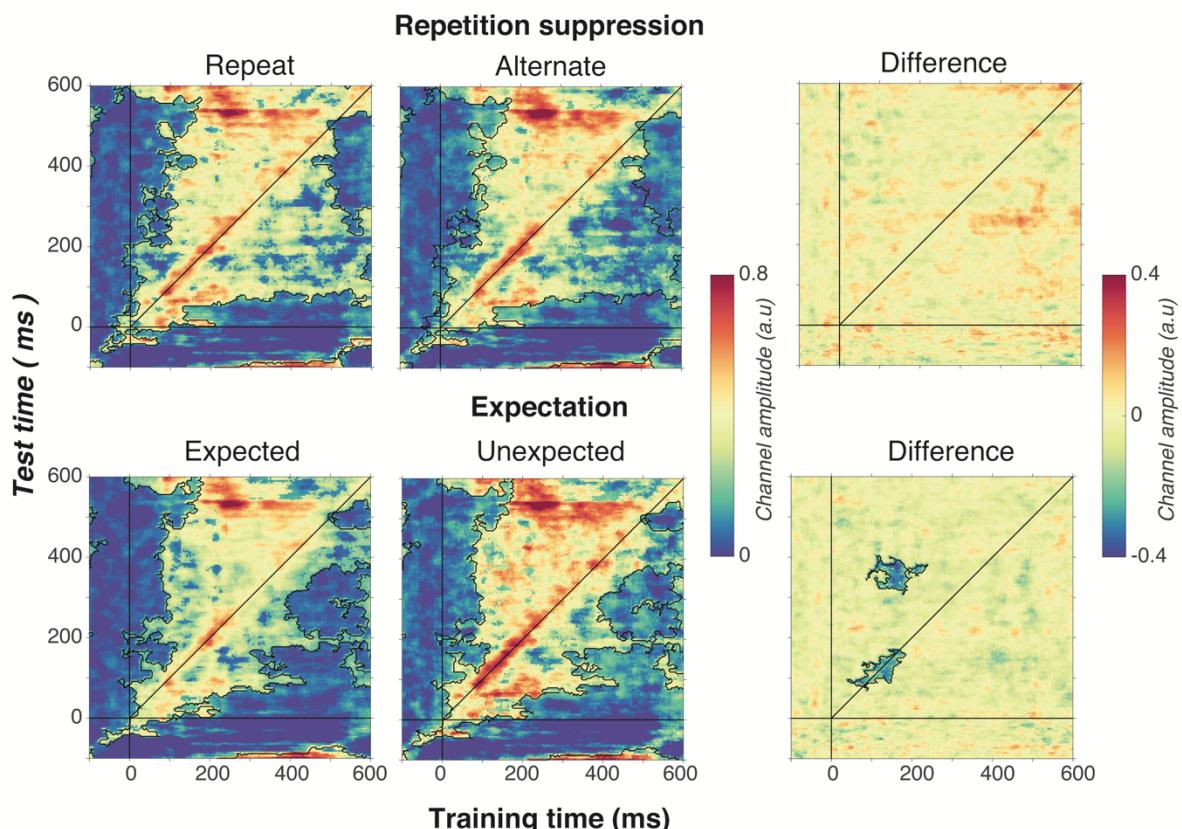
## 398 **Expectation affects the temporal stability of stimulus representations**

399 Next, we examined whether repetition suppression and expectation affected  
400 dynamic, ongoing stimulus representations by using cross-temporal generalization  
401 (King & Dehaene, 2014; King et al., 2014; Myers et al., 2015; Spaak, Watanabe,  
402 Funahashi, & Stokes, 2017; Stokes et al., 2013). To do this, we used the same  
403 forward encoding approach as in the previous analysis, but now the weights were  
404 derived from one time-point on one set of trials, and then applied at every time point  
405 in the test trials. Again, a cross-validation approach was used, with all trials serving  
406 as both training and test. This analysis examined whether the same spatial pattern  
407 of EEG activity that allows for orientation selectivity generalizes to other time points,  
408 thus revealing whether the pattern of orientation-selective activity is stable or

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409 changes over time.

410 As shown in Figure 6, optimal orientation selectivity was on-axis (training  
411 time equals test time) between 100 ms and 300 ms after stimulus presentation,  
412 suggesting that the stimulus representation changed dynamically over time (King &  
413 Dehaene, 2014). There was also significant off-axis orientation-selectivity from 100-  
414 500 ms after stimulus presentation, suggesting that some aspects of the neural  
415 representation of orientation were stable over time.



416  
417 **Figure 6.** Cross-temporal generalization of the forward encoding model based on  
418 grating orientations for the main effects of repetition suppression (upper panels) and  
419 expectation (lower panels). The maps have been thresholded (indicated by opacity)  
420 to show clusters (black outlines) of significant orientation selectivity (permutation  
421 testing, cluster threshold  $p < .05$ , corrected cluster statistic  $p < .05$ , 5,000  
422 permutations). The difference between the conditions is shown in the right-hand  
423 column (permutation testing, cluster threshold  $p < .05$ , corrected cluster statistic  $p <$   
424  $.05$ ). Opacity and outlines indicate significant differences.

425  
426

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427 There was no effect of repetition suppression on temporal generalization of  
428 orientation information (upper panels of Figure 6), suggesting that repetition  
429 suppression did not affect the temporal stability of neural representations of  
430 orientation. Examining the effect of expectation on cross-temporal generalization  
431 confirmed that there was significantly more on-axis orientation selectivity when the  
432 stimulus was unexpected than when it was expected (cluster  $p = .02$ ). This  
433 increased on-axis orientation selectivity generalized off-axis at around 300-400 ms  
434 after stimulus onset (cluster  $p = .01$ ), suggesting that the same representation that is  
435 activated to process the expectation is reactivated later as the stimulus continues to  
436 be processed. Such a signal could constitute the prior of the prediction, as this  
437 should be updated on the basis of incoming sensory evidence, which in turn would  
438 likely require reactivation of the unexpected stimulus.

## Discussion

440 Our findings demonstrate that repetition suppression and expectation have  
441 distinct effects on neural representations of simple visual stimuli. Repetition  
442 suppression had no effect on orientation selectivity, even though the neural  
443 response to repeated stimuli was significantly reduced over occipito-parietal areas.  
444 Unexpected stimuli, on the other hand, showed significantly increased orientation-  
445 selectivity relative to expected stimuli. This same early representation of the  
446 unexpected stimulus appeared to be reactivated at 200-300 ms after the initial  
447 neural response, supporting the idea that sensory expectations may be updated  
448 through comparison with incoming sensory evidence. These results suggest that

## Repetition suppression and prediction error

449 repetition suppression and expectation are separable and independent neural  
450 computations.

451 Our work provides a significant advance in understanding how predictions  
452 allow the brain to process incoming sensory information by comparing what is  
453 expected with what actually occurs. How expectations affect neural responses has  
454 been extensively investigated using mismatch negativity paradigms in which an  
455 unexpected stimulus causes a larger neural response than an expected stimulus  
456 (Bekinschtein et al., 2009; Garrido et al., 2009; Näätänen et al., 2007). Such  
457 mismatch responses to an unexpected stimulus have often been attributed to the  
458 generation of a prediction error that updates expectation based on a conflict  
459 between sensory evidence and the prior (Garrido et al., 2009). To date, however,  
460 most studies have focused exclusively on the overall magnitude of neural responses  
461 to unexpected events, rather than assessing the quality of stimulus-specific  
462 information potentially contained within such responses. As noted above, enhanced  
463 neural activity to unexpected visual events could reflect a differential response to  
464 one of a number of possible stimulus features, or simply an increase in baseline  
465 activity associated with a non-selective response. By examining how expectation  
466 affects the representation of an elementary feature dimension – in this case,  
467 orientation – our results imply the operation of at least two distinct neural processes  
468 at separate times following stimulus onset. Incoming sensory information is first  
469 evaluated against the prior (which occurs early after stimulus presentation). When  
470 an unexpected stimulus is detected and generates a prediction error, the  
471 representation is amplified through gain enhancement. Later, around 300 ms after

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472 stimulus presentation, this same representation is reactivated to update the  
473 expectation against the initially predicted representation.

474 According to predictive coding theory, expected stimuli should be more  
475 efficiently represented than unpredicted stimuli largely because the reduced neural  
476 response still encodes stimuli with the same fidelity (Friston, 2005). A more efficient  
477 response could be due to sharpening of neuronal tuning to stimulus features, or to a  
478 reduction in the gain of evoked neural responses. Our results strongly support the  
479 latter interpretation. Specifically, there was no evidence that a fulfilled expectation  
480 leads to a sharper representation of orientation information. Our findings might  
481 imply that the brain needs to have more information about an unexpected stimulus,  
482 so a correct response can be made. Our findings thus provide a novel insight into  
483 how predictive coding might change neural representations of sensory information.

484 The lack of evidence for sharpening of neural tuning in the current results is  
485 in contrast to the findings of a previous study (Kok et al., 2012), in which a high-level  
486 prediction error led to ‘sharper’ multivariate decoding for expected versus  
487 unexpected visual stimuli. In their study, Kok et al. (2012) used an auditory tone to  
488 cue the orientation of a subsequent visual stimulus, and found significantly reduced  
489 off-label classification accuracy for predicted than for unpredicted stimuli. They  
490 concluded that predictions cause sharpening of stimulus representations. More  
491 recently, using the same task combined with a forward encoding approach, Kok et  
492 al. (2017) showed that response gain is increased for a predicted stimulus.

493 It is natural to ask why the results of the current study differ from those of  
494 Kok and colleagues outlined above. One possible explanation lies in the different

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495 approaches used to generate expectations across the studies. Specifically, whereas  
496 Kok et al. manipulated expectations by pairing an auditory cue with a visual  
497 stimulus, we exploited the properties of the visual stimuli themselves (i.e., their  
498 orientation) to generate expectations within blocks of trials. An intriguing possibility  
499 is that predictions requiring integration of sensory events from two or more  
500 modalities lead to increased gain, whereas predictions made within a single sensory  
501 modality lead to decreased gain. This might in turn relate to the noted differences  
502 between simple ‘local’ and higher-order ‘global’ type predictions (Bekinschtein et  
503 al., 2009; King et al., 2014), which lead to distinct patterns of stimulus-selective  
504 decoding. A similar discrepancy relating to the effects of attention on sensory  
505 representations has been widely discussed, with some studies finding sharpening of  
506 stimulus representations with attention, and others showing gain enhancement (Liu,  
507 Larsson, & Carrasco, 2007; Maunsell, 2015; Maunsell & Treue, 2006; Treue &  
508 Trujillo, 1999). The differences between these results may potentially have arisen  
509 because the tasks relied upon different types of attention (e.g., spatial versus  
510 feature-based). Future studies could determine whether this same divergence  
511 occurs for prediction effects.

512 The current work applied multivariate model-based approaches to EEG data  
513 to determine how prediction and repetition suppression affect neural  
514 representations of perceptual information. We chose to use EEG so we could  
515 recover the temporal dynamics of these effects – something that would not be  
516 possible with the BOLD signal used in fMRI – and because EEG is the most widely-  
517 used tool for measuring expectation effects in human participants (see Garrido, et

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518 al., 2019 and Paavilainen, 2013 for review), thus facilitating comparison of our  
519 findings with those of other studies. We estimated orientation-selectivity using all  
520 EEG electrodes distributed across the scalp for two principal reasons. First, we  
521 wanted to limit experimenter degrees of freedom (Simmons, Nelson, & Simonsohn,  
522 2011) potentially introduced through the post-hoc selection of subsets of  
523 electrodes. Second, given the broad spatial resolution of EEG, we reasoned that  
524 activity recorded from electrodes at any given scalp location could potentially carry  
525 important feature-selective information from a number of neural sources. The results  
526 revealed that orientation-selective information appears largely driven by electrodes  
527 over occipital-parietal regions (Figure 3D), consistent with a number of previous  
528 studies that employed visual decoding of M/EEG data (Cichy, Pantazis, & Oliva,  
529 2014; Cichy, Ramirez, & Pantazis, 2015; Stokes, Wolff, & Spaak, 2015). As noted  
530 above, however, it is entirely possible that the effects we observed here arose from  
531 sources well beyond the occipital and parietal regions, or even potentially outside  
532 the visual cortical hierarchy. Limitations in the temporal and spatial resolution of  
533 current human imaging methods make it impossible to pinpoint the timing and  
534 location of interactions between visual areas that might reflect the cascade of  
535 predictions and prediction errors involved in sensory encoding. By combining the  
536 current paradigm and multivariate modelling with invasive recordings in animal  
537 models – for example using calcium imaging or extracellular electrode recordings –  
538 it should be possible to test some of the key claims of predictive coding theory that  
539 we have examined here, but at the level of individual neurons.

540 Surprisingly few studies have used invasive recording methods to test how

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541 predictive coding affects stimulus representations at the neuronal level. One study  
542 in macaques (Kaliukhovich & Vogels, 2010) used a design similar to that of  
543 Summerfield and colleagues, but with high-level objects (fractals and real-world  
544 objects) as stimuli. That study found that expectation did not attenuate repetition  
545 suppression in either spiking activity or local field potentials within the inferior  
546 temporal cortex. A later fMRI study in humans (Kovács, Kaiser, Kaliukhovich,  
547 Vidnyánszky, & Vogels, 2013) used a similar stimulus set, and also found no  
548 attenuation of repetition suppression by expectation in the same cortical region. A  
549 follow-up study provided a potential explanation for these findings by showing that  
550 the attenuation of neural responses associated with repetition suppression are  
551 found with familiar stimuli, but not with unfamiliar stimuli (Grotheer & Kovács, 2014).  
552 Viewed in this light, the stimulus sets used by Kaliukhovich and Vogels (2010) might  
553 not have been sufficiently familiar to yield effects of expectation in their non-human  
554 primate observers.

555 Other work has shown that context plays an important role in determining  
556 the magnitude of neuronal responses to sensory events. Thus, for example,  
557 (Ulanovsky, Las, & Nelken, 2003) found that rare auditory stimuli generate  
558 significantly larger responses in primary auditory cortical neurons than more  
559 commonly occurring stimuli. This result has been interpreted as a single-neuron  
560 analogue of the mismatch negativity, but the design used in the study did not  
561 control for adaptation effects, thus making it difficult to draw an unambiguous  
562 comparison with the current work. In the visual domain, oddball stimuli have also  
563 been found to modulate neuronal activity in rats, characterised by an enhancement

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564 of responses in the higher-order latero-intermediate area (Vinken, Vogels, & Op de  
565 Beeck, 2017). Moreover, Fiser et al. (2016) found that neurons in mouse primary  
566 visual cortex show a greater response when task-irrelevant visual stimuli that had  
567 been presented during training were omitted, suggesting that an established  
568 expectation had been violated. This result is consistent with the literature on the  
569 mismatch negativity, in which the omission of an expected stimulus results in a  
570 large prediction error (Garrido et al., 2009; Wacongne et al., 2011). In non-human  
571 primates, neurons in the inferior temporal cortex show an enhanced response to  
572 unexpected relative to expected stimuli (Kaposvari, Kumar, & Vogels, 2018), and  
573 population decoding accuracy is higher for unexpected compared with expected  
574 stimuli (Kumar, Kaposvari, & Vogels, 2017). Critically, however, no study has  
575 simultaneously recorded neuronal activity in multiple cortical regions to determine  
576 whether predictions generated in one area refine responses in a second area, as  
577 postulated by predictive coding theory (Friston, 2005; Rao & Ballard, 1999). Such a  
578 direct demonstration is necessary to provide a strong test of the central notion that  
579 cortical areas pass signals between themselves in order to generate expectations.

580 Unlike the effects of expectation, there is a large body of electrophysiological  
581 work showing that sensory adaptation influences neuronal activity (Adibi et al.,  
582 2013b; Adibi, Clifford, & Arabzadeh, 2013a; Felsen et al., 2002; Kohn & Movshon,  
583 2004; Patterson, Wissig, & Kohn, 2013). For instance, there is a sharpening of  
584 stimulus selectivity in MT neurons following 40 s of adaptation to a drifting grating  
585 (Kohn & Movshon, 2004). As we have highlighted, however, prolonged adaptation is  
586 likely also associated with a significant prediction that the next stimulus will be the

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587 same as the previous one. Perhaps more relevant to the current results, Patterson  
588 et al. (2013) found that the width of orientation tuning in V1 is only marginally  
589 sharpened following brief (400 ms) periods of adaptation. Again, however, their  
590 study did not control for expectation, so it is impossible to determine the role of  
591 predictive coding in their observations. Our finding that repetition suppression did  
592 not affect the bandwidth of orientation selectivity measured using EEG is also  
593 consistent with models of orientation adaptation based on human psychophysical  
594 data, which suggest that adaptation does not affect the tuning width of the adapted  
595 neural populations (Clifford, 2002; 2014; Dickinson, Almeida, Bell, & Badcock, 2010;  
596 Dickinson, Morgan, Tang, & Badcock, 2017; Tang, Dickinson, Visser, & Badcock,  
597 2015).

598 In summary, we have shown that repetition suppression and expectation  
599 differentially affect the neural representation of simple, but fundamental, sensory  
600 features. Our results further highlight how the context in which a stimulus occurs,  
601 not just its features, affect the way it is represented by the brain. Our findings  
602 suggest encoding priority through increased gain might be given to unexpected  
603 events, which in turn could potentially speed behavioural responses. This prioritized  
604 representation is then re-activated at a later time period, supporting the idea that  
605 feedback from higher cortical areas reactivates an initial sensory representation in  
606 early cortical areas.

607

## Repetition suppression and prediction error

608

### Method

609 **Participants**

610 A group of 15 healthy adult volunteers (9 females, median age = 20.5 yr,  
611 range = 18 to 37 yr) participated in exchange for partial course credit or financial  
612 reimbursement (AUD\$20/hr). We based our sample size on work that investigated  
613 the interaction between repetition suppression and prediction error (Summerfield et  
614 al., 2008), and that used forward encoding modelling to investigate orientation  
615 selectivity using MEG with a comparable number of trials as the current study  
616 (Myers et al., 2015). Each person provided written informed consent prior to  
617 participation, and had normal or corrected-to-normal vision. The study was  
618 approved by The University of Queensland Human Research Ethics Committee and  
619 was in accordance with the Declaration of Helsinki.

620 **Experimental setup**

621 The experiment was conducted inside a dimly illuminated room with the  
622 participants seated in a comfortable chair. The stimuli were displayed on a 22-inch  
623 LED monitor (resolution 1920 x 1080 pixels, refresh rate 120 Hz) using the  
624 PsychToolbox presentation software (Brainard, 1997; Pelli, 1997) for MATLAB  
625 (v7.3). Viewing distance was maintained at 45 cm using a chinrest, meaning the  
626 screen subtended 61.18° x 36.87° (each pixel 2.4' x 2.4').

627 **Visual task**

628 The stimuli were Gabors (diameter: 5°, spatial frequency: 2 c/°, 100%  
629 contrast) presented centrally in pairs for 100 ms, separated by 500 ms (600 ms  
630 stimulus onset asynchrony) with a variable (650 to 750 ms) inter-stimulus interval

## Repetition suppression and prediction error

631 between trials. Across the trials, the orientations of the Gabor were evenly spaced  
632 between 0° and 160° (in 20° steps) so we could reconstruct orientation selectivity  
633 contained within the EEG response using forward encoding modelling. The  
634 relationship of the orientations of the pairs Gabor was also used to construct the  
635 different repetition suppression and prediction conditions. The orientation presented  
636 in the second Gabor in the pair could either repeat or alternate with respect to the  
637 orientation of the first Gabor. In the alternation trials, the orientation of the first  
638 Gabor was drawn randomly, without replacement, from an even distribution of  
639 orientations that was different to the orientation of the second Gabor. To vary the  
640 degree of prediction, in half of the blocks 80% of the trials had repeated  
641 orientations and 20% of the trials had alternating orientations, whereas in the other  
642 half of the blocks these contingencies were reversed. This design allowed us to  
643 separately examine the effects of repetition suppression and prediction because of  
644 the orthogonal nature of the blocked design. The blocks of 135 trials (~3 mins)  
645 switched between the expectation of a repeating or alternating pattern, with the  
646 starting condition counterbalanced across participants.

647 The participants' task was to monitor the visual streams for rare, faintly  
648 coloured (red or green) Gabor and to discriminate the colour as quickly and  
649 accurately as possible. Any trial with a coloured target was excluded from analysis.  
650 The orientation match between the pairs was made to be consistent with the  
651 dominant contingency (i.e., repeated or alternating) within that block. Pilot testing  
652 was used prior to the main experiment to set the task at approximately threshold, to  
653 ensure that participants focused exclusively on the colour-discrimination task rather

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654 than the orientation contingencies associated with prediction and repetition. Only  
655 one participant reported being aware of the changing stimulus contingencies across  
656 the blocks when asked at the end of the experiment, and excluding this  
657 participant's data had no effect on the key results reported here. Self-paced breaks  
658 were provided between each of the 20 blocks within a session, at which time  
659 feedback was provided on performance in the preceding block. Each participant  
660 completed two sessions of 2700 trials each (5400 trials in total), with each session  
661 lasting around 70 mins of experimental time and 45 mins of EEG setup.

### 662 **EEG acquisition and pre-processing**

663 Continuous EEG data were recorded using a BioSemi Active Two system  
664 (BioSemi, Amsterdam, Netherlands). The signal was digitised at 1024 Hz sampling  
665 rate with a 24-bit A/D conversion. The 64 active scalp Ag/AgCl electrodes were  
666 arranged according to the international standard 10–20 system for electrode  
667 placement (Oostenveld & Praamstra, 2001) using a nylon head cap. As per BioSemi  
668 system design, the common mode sense and driven right leg electrodes served as  
669 the ground, and all scalp electrodes were referenced to the common mode sense  
670 during recording.

671 Offline EEG pre-processing was performed using EEGLAB in accordance  
672 with best practice procedures (Bigdely-Shamlo, Mullen, Kothe, Su, & Robbins,  
673 2015; Keil et al., 2014). The data were initially down-sampled to 256 Hz and  
674 subjected to a 0.5 Hz high-pass filter to remove slow baseline drifts. Electrical line  
675 noise was removed using *clean\_line.m*, and *clean\_rawdata.m* in EEGLAB (Delorme  
676 & Makeig, 2004) was used to remove bad channels (identified using Artifact

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677 Subspace Reconstruction), which were then interpolated from the neighbouring  
678 electrodes. Data were then re-referenced to the common average before being  
679 epoched into segments around each stimulus pair (-0.5 s to 1.25 s from the first  
680 stimulus in the pair). Systematic artefacts from eye blinks, movements and muscle  
681 activity were identified using semi-automated procedures in the SASICA toolbox  
682 (Chaumon, Bishop, & Busch, 2015) and regressed out of the signal. After this stage,  
683 any trial with a peak voltage exceeding  $\pm 100 \mu V$  was excluded from the analysis.  
684 The data were then baseline corrected to the mean EEG activity from -100 to 0 ms  
685 before the presentation of the second Gabor in the pair. Critically, the orientations  
686 of the first and second gratings were precisely balanced across the conditions to  
687 avoid any systematic bias in orientation information being carried forward by the  
688 first grating within each pair. Specifically, for every unexpected stimulus presented  
689 in the second grating there was an equal number of every other orientation that was  
690 expected to be presented. As the analysis we employed used a regression-based  
691 approach, any carry over of orientation-selective information from the first to the  
692 second grating therefore could not systematically bias the results.

## 693 Experimental Design

694 We used a modified version of a factorial design that has previously been  
695 used to separately examine the effects of repetition suppression and prediction  
696 error (Kaliukhovich & Vogels, 2010; Kovács et al., 2013; Summerfield et al., 2008;  
697 2011; Todorovic et al., 2011; Todorovic & de Lange, 2012). By comparing the two  
698 repeat conditions with the two alternating conditions, we could examine repetition  
699 suppression while controlling for different levels of expectation. Conversely, by

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700 comparing across the expected and unexpected trials, we could examine prediction  
701 error while controlling for repetition suppression.

702 The relationship between the pairs of orientations for the different  
703 expectation conditions was based on the original study (Summerfield et al., 2008),  
704 and on other studies (Kaliukhovich & Vogels, 2010; Kovács et al., 2013) that  
705 examined the interaction between repetition suppression and expectation. In the  
706 repeating condition, the orientation of the second Gabor is expected to be the same  
707 as the orientation of the first, whereas in the alternating condition the orientation of  
708 the second Gabor is expected to be *different* from that of the first. This relationship  
709 between the expected orientations of the stimuli in the alternating condition is  
710 slightly different to another modification of the paradigm which employed a more  
711 limited range of stimuli (Todorovic et al., 2011; Todorovic & de Lange, 2012).  
712 Specifically, the paradigm introduced by Todorovic and colleagues used two or  
713 three auditory tones of different frequencies. In the alternating condition, the  
714 expectation is that one tone will follow another (i.e. 1000 Hz and then 1032 Hz), then  
715 this is violated when a 1000 Hz tone is repeated. In this paradigm, an exact  
716 frequency is expected in the alternating condition, a design feature that differs from  
717 the paradigm used in the current work where there is no specific expectation of the  
718 orientation of the second Gabor based on the orientation of the first in the  
719 alternating condition. Instead the expectation in the alternating condition is that the  
720 orientation will change, and this can be violated by repeating the orientation. In this  
721 sense, there is no specific expectation about the second orientation in the  
722 alternating condition. Instead, the rule is about alternating or repeating the first

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723 orientation. We did not implement the Todorovic et al. paradigm because the  
724 combinatorial explosion of stimulus conditions needed to measure orientation  
725 selectivity (such that every orientation is predicted by another orientation). Future  
726 work could investigate how this subtle change in paradigm design affects the  
727 encoding of stimulus information.

### 728 **Forward encoding modelling**

729 We used a forward encoding approach to estimate the amount of orientation-  
730 selective information contained in the EEG data at each time point of the trial. This  
731 approach differs from standard decoding approaches by modelling each presented  
732 orientation as a continuous variable of a set of tuned orientation-selective channels.  
733 The forward-encoding technique has been successfully used to reconstruct colour  
734 (Brouwer & Heeger, 2009), spatial (Sprague & Serences, 2013) and orientation  
735 (Ester, Sutterer, Serences, & Awh, 2016) selectivity in fMRI data. More recently the  
736 same approach has been applied to EEG and MEG data, which have inherently  
737 better temporal resolution than fMRI (Garcia et al., 2013; Kok et al., 2017; Myers et  
738 al., 2015; Wolff, Jochim, Akyürek, & Stokes, 2017b).

739 We applied forward encoding modelling to determine how repetition  
740 suppression and prediction error affected orientation selectivity. To do this, the  
741 second orientation (Figure 7A) in the Gabor pair in each trial was used to construct a  
742 regression matrix, with separate regressors for the 9 orientations used across the  
743 experiment. This regression matrix was convolved with a set of basis functions (half  
744 cosines raised to the 8<sup>th</sup> power (Figure 7C), which allowed complete and unbiased  
745 coverage of orientation space) to allow us to pool similar information patterns

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746 across nearby orientations (Brouwer & Heeger, 2009). We used this tuned  
747 regression matrix to estimate time-resolved orientation selectivity contained within  
748 the EEG activity in a 16 ms sliding window, in 4 ms steps (Figure 8B; Myers et al.,  
749 2015). To avoid overfitting, we used a leave-one-out cross-validation procedure  
750 where the regression weights were estimated for a training set and applied to an  
751 independent test set (Figure 8D). All trial types (including target trials) were used in  
752 training and test sets. This was done by solving the linear equation:

753 
$$B_1 = WC_1 \quad (1)$$

754 Where  $B_1$  (64 sensors x N training trials) is the electrode data for the training set,  $C_1$   
755 (9 channels x N training trials) is the tuned channel response across the training  
756 trials, and  $W$  is the weight matrix for the sensors we want to estimate (64 sensors x  
757 9 channels).  $W$  can be estimated using least square regression to solve equation (2):

758 
$$W = (C_1 C_1^T)^{-1} C_1^T B_1 \quad (2)$$

759 The channel response in the test set  $C_2$  (9 channels x N test trials) was estimated  
760 using the weights in (2) and applied to activity in  $B_2$  (64 sensors x N test trials).

761 
$$C^2 = (W W^T) W^T B^2 \quad (3)$$

762 We repeated this process by holding one trial out as test, and training on the  
763 remaining trials until all trials had been used in test and training. The procedure was  
764 repeated for each trial within the trial epoch. We then shifted all trials to a common  
765 orientation, meaning that 0° corresponded to the orientation presented on each trial.  
766 The reconstructed channel activations were separated into the four conditions, and  
767 averaged over trials. These responses were then smoothed with a Gaussian kernel

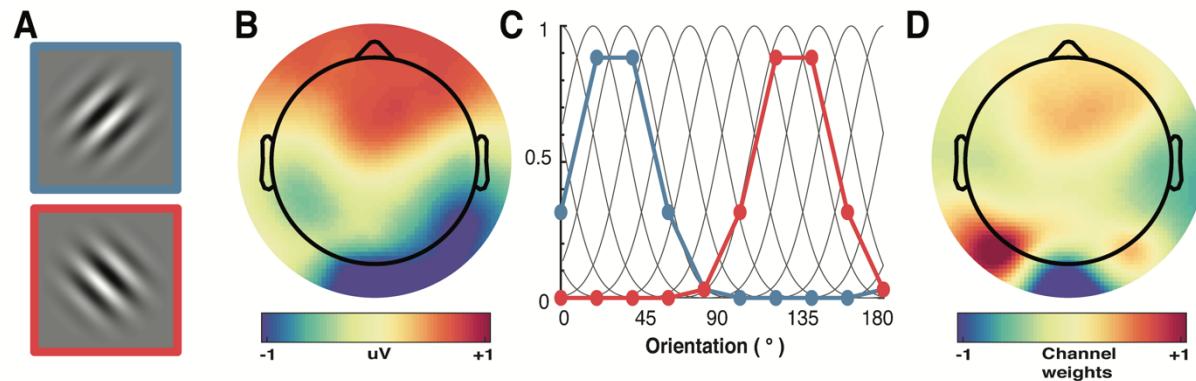
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768 with a 16 ms window, and fitted with a Gaussian function (4) using non-linear least  
769 square regression to quantify the amount of orientation selective activity.

770

$$G(x) = A \exp\left(-\frac{(x-\varphi)^2}{2\sigma^2}\right) + C \quad (4)$$

771 Where  $A$  is the amplitude representing the amount of orientation selective activity,  
772 is the orientation the function is centred on (in degrees),  $\sigma$  is the width (degrees) and  
773  $C$  is a constant used to account for non-orientation selective baseline shifts.



774

775 **Figure 7.** A schematic of the forward-encoding approach applied to EEG activity.  
776 **(A)** Participants viewed individual gratings at fixation, each with a specific  
777 orientation. **(B)** Neural activity evoked by each grating was measured over the entire  
778 scalp. **(C)** Evoked neural responses were convolved with canonical orientation-  
779 selective functions (grey lines in C) to determine coefficients for the different  
780 orientations (coloured dots and lines, which match the colours of the outlined  
781 gratings in A). These coefficients were then used to generate a regression matrix.  
782 **(D)** General linear modelling was used on a subset of training trials to generate  
783 weights for each channel. These weights were inverted and simultaneously applied  
784 to an independent test set of data to recover orientation selectivity in the EEG  
785 activity. As EEG activity has high temporal resolution, we can apply the procedure  
786 to many epochs following stimulus presentation to determine the temporal  
787 dynamics of orientation processing (see Figure 3).  
788

## 789 Multivariate pattern analysis

790 We conducted a multivariate pattern analysis to build upon the initial forward  
791 encoding results which showed that unexpected stimuli elicit greater orientation  
792 selectivity than expected stimuli. This analysis used the same data as the forward

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793 encoding analysis. We used the *classify* function from *Matlab 2017a* with the  
794 ‘diaglinear’ option to implement a Naive Bayes classifier. For each time point, we  
795 used the same cross-validation procedure as the forward encoding modelling with  
796 the same averaging procedure to select train and test sets of data. The classifier  
797 was given the orientations of the training data and predicted the orientation of the  
798 test data. A trial was labelled correct if the presented orientation was produced. To  
799 facilitate comparison of the results with those of (Kok et al., 2012), we found the  
800 peak classification accuracy for each participant in the 600 ms following stimulus  
801 presentation. The same wide time window was used across conditions to  
802 accommodate large inter-individual differences in peak classification without  
803 biasing the results toward one particular condition.

804 **Statistical testing**

805 A non-parametric sign permutation test was used to determine the null  
806 distribution for testing (Wolff, Jochim, Akyürek, & Stokes, 2017b). This method  
807 makes no assumptions about the underlying shape of the null distribution. This was  
808 done by randomly flipping the sign of the data for the participants with equal  
809 probability. Fifty thousand (50,000) permutations were used for the time-series data,  
810 whereas only 5000 were used for the temporal generalization plots because of the  
811 significantly greater computational demands.

812 Cluster-based non-parametric correction (50,000 permutations for timeseries  
813 and 5,000 for temporal generalization) was used to account for multiple  
814 comparisons, and determined whether there were statistical differences between  
815 the contrasting conditions. Paired-samples t-tests were used to follow up the

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816 analysis in Figure 4 within a specified time window, and no correction was applied.  
817 A two-way repeated measures ANOVA (implemented using GraphPad Prism 7.0c,  
818 La Jolla California, USA) was used to analyse the multivariate pattern analysis  
819 results shown in Figure 5.

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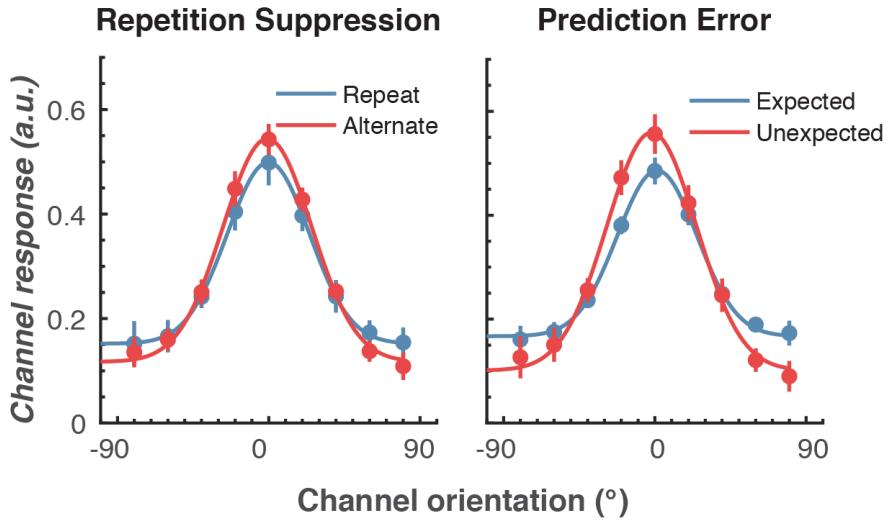
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826

### Supplementary Information



827

828 **Supplementary Figure 1.** The effect of a different baseline period (-100 to 0 ms  
829 before onset of the first Gabor) on orientation selectivity for the two main conditions.  
830 Population tuning curves averaged over the significant time period (79 – 150 ms)  
831 shown in Figure 4A. The curves, shown as fitted Gaussians, illustrate how overall  
832 stimulus representations are affected by repetition and expectation. While there was  
833 no difference in orientation tuning for repeated versus alternate stimuli (left panel),  
834 the amplitude of the orientation response increased significantly, and the baseline  
835 decreased, for unexpected relative to expected stimuli (right panel). Error bars  
836 indicate  $\pm 1$  standard error.  
837

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