Repetition suppression and prediction error

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

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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

24   **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.

40

Introduction

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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 (Diederen, 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, Trittschuh,

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

4

Repetition suppression and prediction error

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).

Repetition suppression and prediction error

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   Gabors. 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 Gabors 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   Gabors 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

155   expectation form 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).
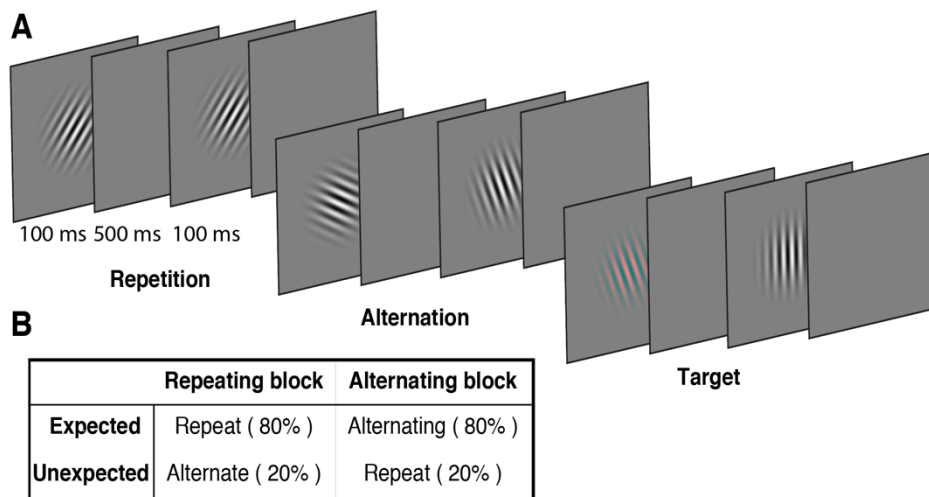
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160   **Figure 1.** Example stimulus displays and task design. **(A)** Schematic of the stimuli
161   and timing used in the experiment. Participants viewed a rapid stream of pairs of
162   Gabors and monitored for an infrequent coloured target (10% 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).
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Repetition suppression and prediction error
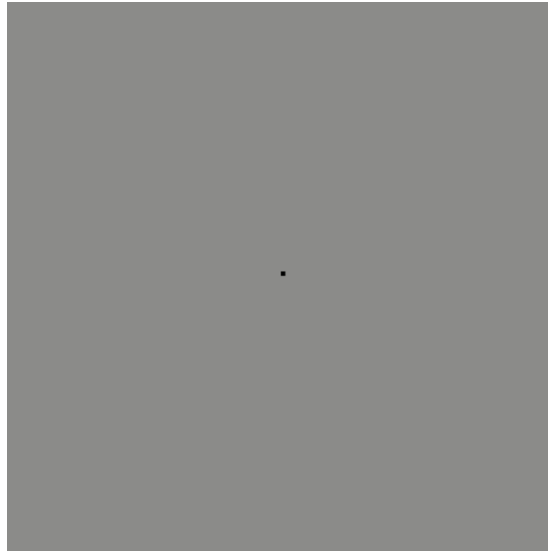
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171   **Movie 1.** Example of a stimulus sequence of Gabors in a typical repetition block.

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

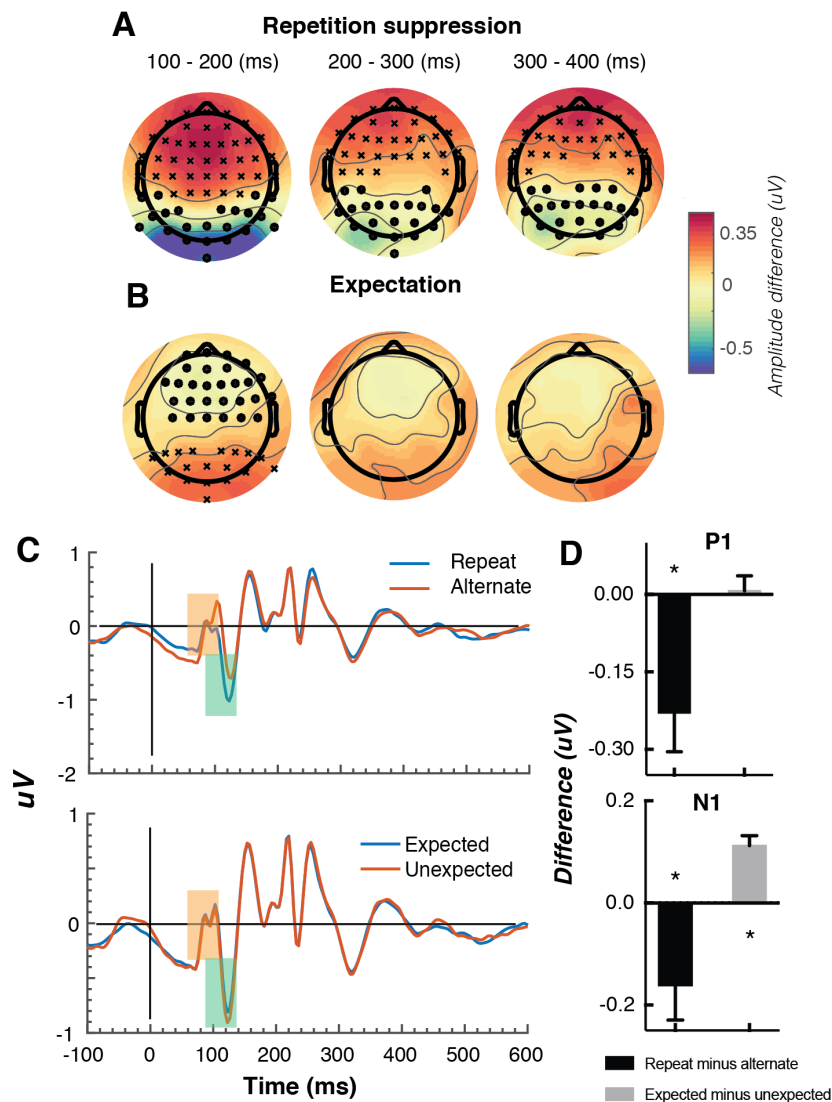185   electrodes mirrored the repetition suppression effect with a similar time course: the

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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Repetition suppression and prediction error

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

11

Repetition suppression and prediction error

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.

12

Repetition suppression and prediction error

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

13

Repetition suppression and prediction error

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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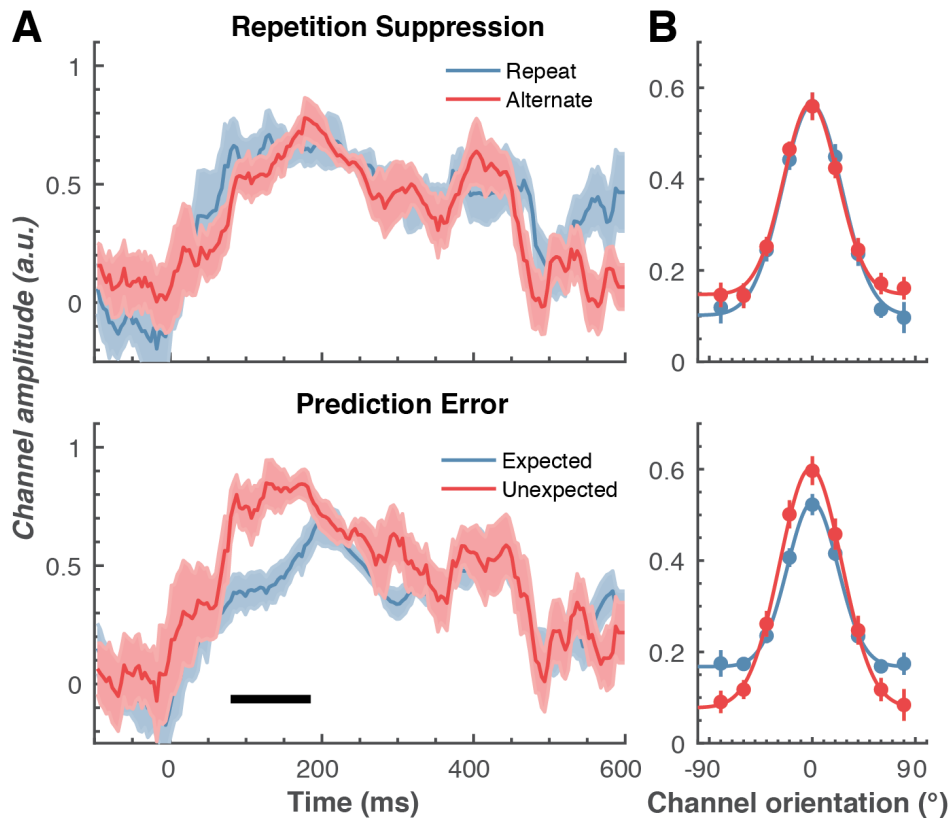**Repetition suppression and prediction error**
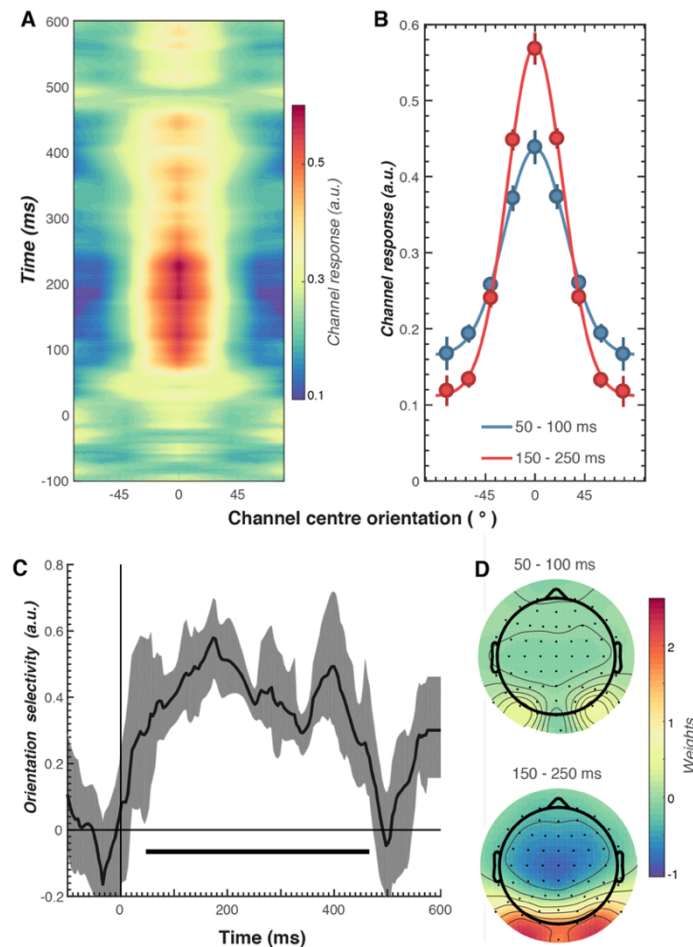
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266 **Figure 3.** Results of the forward encoding modelling for orientation-selectivity. **(A)**
267 Time-resolved orientation tuning curve across all participants and conditions in
268 response to the second Gabor in the pair. The forward encoding 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 ±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).

15

Repetition suppression and prediction error

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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16

Repetition suppression and prediction error

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

Examining the effect of expectation revealed a markedly different pattern of

results. As shown in Figure 4A, at 79 - 185 ms after the onset of the second

stimulus in the pair, orientation-selectivity increased significantly ($p < .0001$) when

the stimulus was unexpected relative to when it was expected, and this effect arose

at the earliest stages of the brain's response to that stimulus. Moreover, the

17

Repetition suppression and prediction error

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°, SE = 4.72°) and expected (M = 26.72°, SE = 2.74°) 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

19

Repetition suppression and prediction error

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) =

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.

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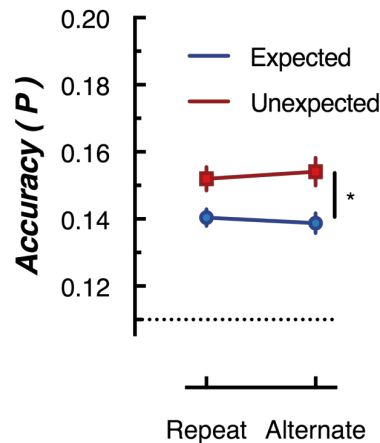
Figure 5. Peak (naive Bayes) classification accuracy of the presented grating
orientation for expected and unexpected conditions. The dotted line indicates
chance performance (1/9 orientations). The error bars indicate ±1 standard error of
the mean.

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

21

Repetition suppression and prediction error

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.
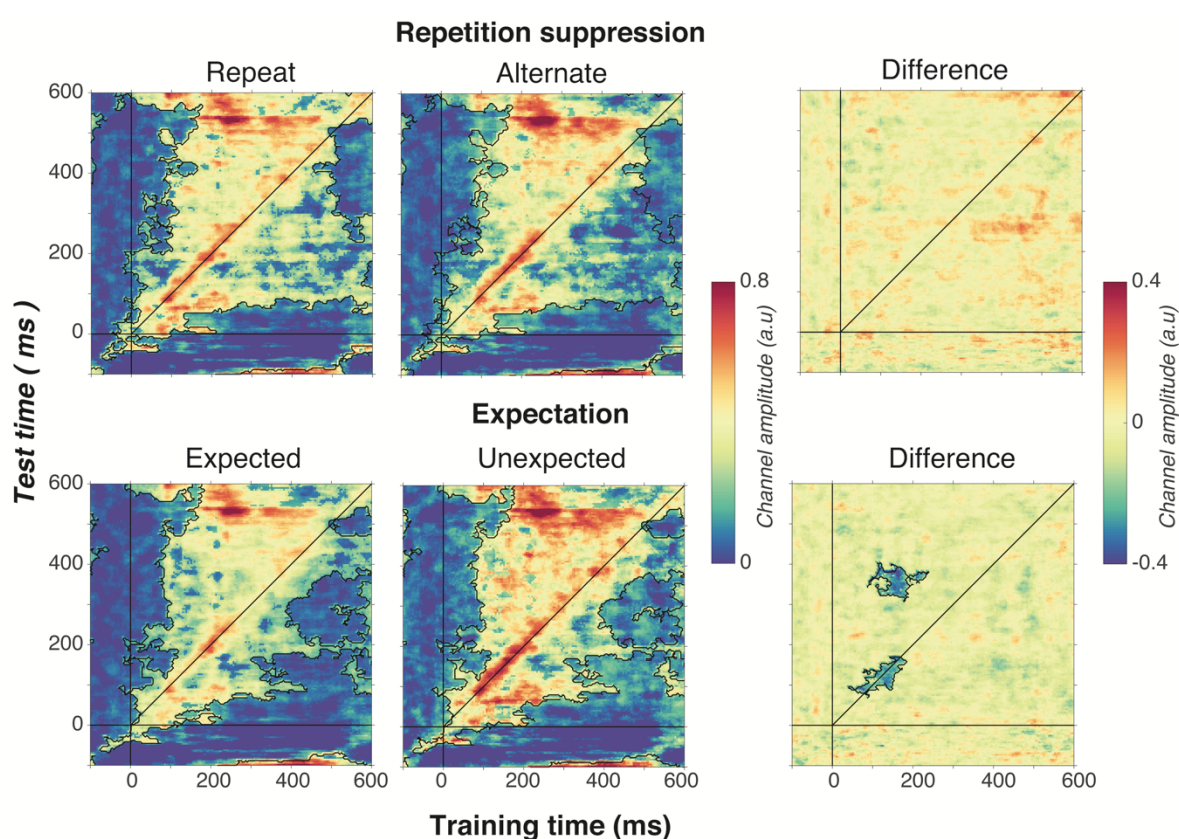
416

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

22

Repetition suppression and prediction error

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.

439   **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

23

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

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

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

26

Repetition suppression and prediction error

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

27

Repetition suppression and prediction error

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

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 predictio8n that the next stimulus will be the

Repetition suppression and prediction error

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

31

Repetition suppression and prediction error

631   between trials. Across the trials, the orientations of the Gabors were evenly spaced

632   between 0º and 160º (in 20º 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 Gabors 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) Gabors 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

32

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

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 ±100 *uV* 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

Repetition suppression and prediction error

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

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 8th power (Figure 7C), which allowed complete and unbiased

745   coverage of orientation space) to allow us to pool similar information patterns

Repetition suppression and prediction error

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:

$$B_1 = WC_1 \qquad (1)$$

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):

$$W = (C_1 \, C_1^T)^{-1} \, C_1^T \, B_1 \qquad (2)$$

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).

$$C^2 = (W \, W^T) \, W^T \, B^2 \qquad (3)$$

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

Repetition suppression and prediction error

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

771 Where *A* is the amplitude representing the amount of orientation selective activity,

772 is the orientation the function is centred on (in degrees), is the width (degrees) and

773 *C* is a constant used to account for non-orientation selective baseline shifts.
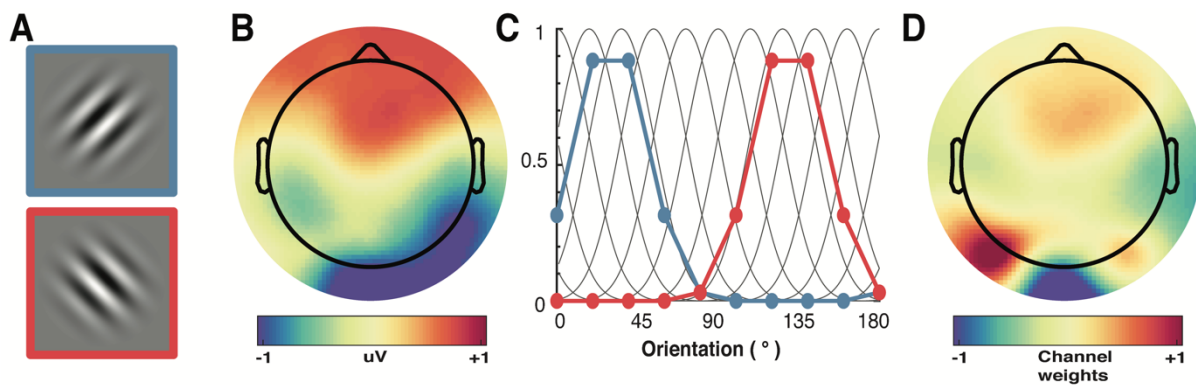
774

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

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

Repetition suppression and prediction error

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.

Acknowledgements

825

826   **Supplementary Information**
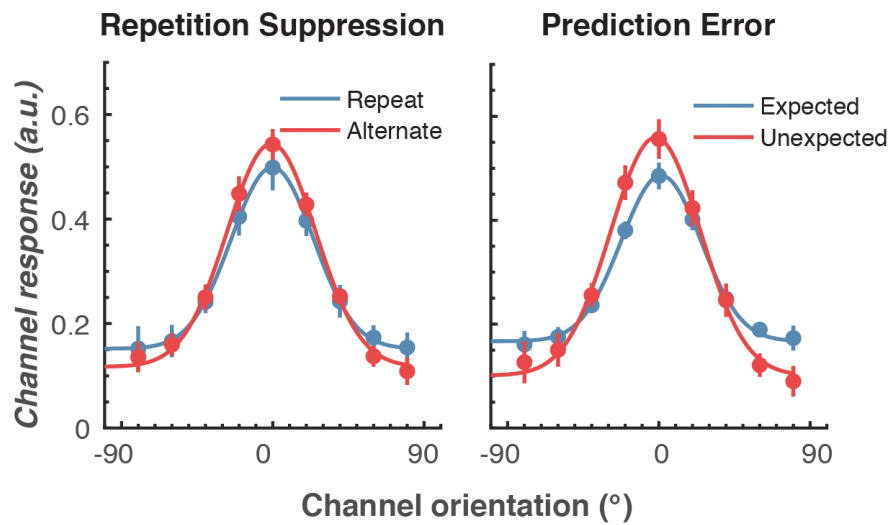
827

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 ±1 standard error.
837

838   **Reference**

839   Adibi, M., McDonald, J. S., Clifford, C. W. G., & Arabzadeh, E. (2013). Adaptation
840   improves neural coding efficiency despite increasing correlations in variability.
841   *The Journal of Neuroscience, 33*(5), 2108–2120.
842   http://doi.org/10.1523/JNEUROSCI.3449-12.2013
843   Auksztulewicz, R., & Friston, K. (2016). Repetition suppression and its contextual
844   determinants in predictive coding. *Cortex, 80*, 125–140.
845   http://doi.org/10.1016/j.cortex.2015.11.024
846   Barron, H. C., Garvert, M. M., & Behrens, T. E. J. (2016). Repetition suppression: a
847   means to index neural representations using BOLD? *Philosophical Transactions
848   of the Royal Society of London Series B, Biological Sciences, 371*(1705),
849   20150355. http://doi.org/10.1098/rstb.2015.0355
850   Bekinschtein, T. A., Dehaene, S., Rohaut, B., Tadel, F., Cohen, L., & Naccache, L.
851   (2009). Neural signature of the conscious processing of auditory regularities.
852   *Proceedings of the National Academy of Sciences, 106*(5), 1672–1677.
853   http://doi.org/10.1073/pnas.0809667106
854   Benucci, A., Saleem, A. B., & Carandini, M. (2013). Adaptation maintains population
855   homeostasis in primary visual cortex, *16*(6), 724–729.
856   http://doi.org/10.1038/nn.3382
857   Bigdely-Shamlo, N., Mullen, T., Kothe, C., Su, K.-M., & Robbins, K. A. (2015). The
858   PREP pipeline: standardized preprocessing for large-scale EEG analysis.
859   *Frontiers in Neuroinformatics, 9*, B153. http://doi.org/10.3389/fninf.2015.00016
860   Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436.
861   http://doi.org/10.1163/156856897X00357
862   Brouwer, G. J., & Heeger, D. J. (2009). Decoding and reconstructing color from
863   responses in human visual cortex. *The Journal of Neuroscience, 29*(44), 13992–
864   14003. http://doi.org/10.1523/JNEUROSCI.3577-09.2009
865   Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., et
866   al. (1998). Functional-Anatomic Correlates of Object Priming in Humans
867   Revealed by Rapid Presentation Event-Related fMRI. *Neuron, 20*(2), 285–296.
868   http://doi.org/10.1016/S0896-6273(00)80456-0
869   Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early
870   adaptation to repeated unfamiliar faces across viewpoint changes in the right
871   hemisphere: Evidence from the N170 ERP component. *Neuropsychologia, 47*(3),
872   639–643. http://doi.org/10.1016/j.neuropsychologia.2008.11.016
873   Chaumon, M., Bishop, D. V. M., & Busch, N. A. (2015). A practical guide to the
874   selection of independent components of the electroencephalogram for artifact
875   correction. *Journal of Neuroscience Methods, 250*, 47–63.
876   http://doi.org/10.1016/j.jneumeth.2015.02.025
877   Cichy, R. M., Pantazis, D., & Oliva, A. (2014). Resolving human object recognition in
878   space and time. *Nature Publishing Group*. http://doi.org/10.1038/nn.3635
879   Cichy, R. M., Ramirez, F. M., & Pantazis, D. (2015). Can visual information encoded
880   in cortical columns be decoded from magnetoencephalography data in humans?
881   *NeuroImage, 121*, 193–204. http://doi.org/10.1016/j.neuroimage.2015.07.011

Repetition suppression and prediction error

882 Clifford, C. W. G. (2002). Perceptual adaptation: motion parallels orientation. *Trends*
883   *in Cognitive Sciences*, 6(3), 136–143.
884 Clifford, C. W. G. (2014). The tilt illusion: phenomenology and functional implications.
885   *Vision Research*, 104, 3–11. http://doi.org/10.1016/j.visres.2014.06.009
886 Cui, Y., Wang, Y. V., Park, S. J. H., Demb, J. B., & Butts, D. A. (2016). Divisive
887   suppression explains high-precision firing and contrast adaptation in retinal
888   ganglion cells. *eLife*, 5. http://doi.org/10.7554/eLife.19460
889 Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., &
890   Rivière, D. (2001). Cerebral mechanisms of word masking and unconscious
891   repetition priming. *Nature Publishing Group*, 4(7), 752–758.
892   http://doi.org/10.1038/89551
893 Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of
894   single-trial EEG dynamics including independent component analysis. *Journal of*
895   *Neuroscience Methods*, 134(1), 9–21.
896   http://doi.org/10.1016/j.jneumeth.2003.10.009
897 Dickinson, J. E., Almeida, R. A., Bell, J., & Badcock, D. R. (2010). Global shape
898   aftereffects have a local substrate: A tilt aftereffect field. *Journal of Vision*,
899   10(13), 5–5. http://doi.org/10.1167/10.13.5
900 Dickinson, J. E., Morgan, S. K., Tang, M. F., & Badcock, D. R. (2017). Separate
901   banks of information channels encode size and aspect ratio. *Journal of Vision*,
902   17(3), 27. http://doi.org/10.1167/17.3.27
903 Diederen, K. M. J., Spencer, T., Vestergaard, M. D., Fletcher, P. C., & Schultz, W.
904   (2016). Adaptive Prediction Error Coding in the Human Midbrain and Striatum
905   Facilitates Behavioral Adaptation and Learning Efficiency. *Neuron*, 90(5), 1127–
906   1138. http://doi.org/10.1016/j.neuron.2016.04.019
907 Ester, E. F., Sutterer, D. W., Serences, J. T., & Awh, E. (2016). Feature-Selective
908   Attentional Modulations in Human Frontoparietal Cortex. *The Journal of*
909   *Neuroscience*, 36(31), 8188–8199. http://doi.org/10.1523/JNEUROSCI.3935-
910   15.2016
911 Fairhall, A. L., Lewen, G. D., Bialek, W., & de Ruyter van Steveninck, R. R. (2001).
912   Efficiency and ambiguity in an adaptive neural code. *Nature*, 412(6849), 787–
913   792. http://doi.org/10.1038/35090500
914 Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the*
915   *Royal Society of London B: Biological Sciences*, 360(1456), 815–836.
916   http://doi.org/10.1098/rstb.2005.1622
917 Garcia, J. O., Srinivasan, R., & Serences, J. T. (2013). Near-real-time feature-
918   selective modulations in human cortex. *Current Biology*, 23(6), 515–522.
919   http://doi.org/10.1016/j.cub.2013.02.013
920 Garrido, M. I., Kilner, J. M., Stephan, K. E., & Friston, K. J. (2009). The mismatch
921   negativity: A review of underlying mechanisms. *Clinical Neurophysiology*, 120(3),
922   453–463. http://doi.org/10.1016/j.clinph.2008.11.029
923 Garrido, M. I., Sahani, M., & Dolan, R. J. (2013). Outlier Responses Reflect
924   Sensitivity to Statistical Structure in the Human Brain. *PLOS Comput Biol*, 9(3),
925   e1002999. http://doi.org/10.1371/journal.pcbi.1002999

926   Gotts, S. J., Chow, C. C., & Martin, A. (2012). Repetition priming and repetition
927   suppression: A case for enhanced efficiency through neural synchronization.
928   *Cognitive Neuroscience*. http://doi.org/10.1080/17588928.2012.691277
929   Grootswagers, T., Wardle, S. G., & Carlson, T. A. (2017). Decoding Dynamic Brain
930   Patterns from Evoked Responses: A Tutorial on Multivariate Pattern Analysis
931   Applied to Time Series Neuroimaging Data. *Journal of Cognitive Neuroscience*,
932   *29*(4), 677–697. http://doi.org/10.1162/jocn_a_01068
933   Gross, C. G., Schiller, P. H., Wells, C., & Gerstein, G. L. (1967). Single-unit activity in
934   temporal association cortex of the monkey. *Journal of Neurophysiology*, *30*(4),
935   833–43.
936   Grotheer, M., & Kovács, G. (2014). Repetition probability effects depend on prior
937   experiences. *The Journal of Neuroscience*, *34*(19), 6640–6646.
938   http://doi.org/10.1523/JNEUROSCI.5326-13.2014
939   Henson, R. N. A., & Rugg, M. D. (2003). Neural response suppression,
940   haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*,
941   *41*(3), 263–270. http://doi.org/10.1016/S0028-3932(02)00159-8
942   Kaliukhovich, D. A., & Vogels, R. (2010). Stimulus Repetition Probability Does Not
943   Affect Repetition Suppression in Macaque Inferior Temporal Cortex. *Cerebral*
944   *Cortex*, *21*(7), 1547–1558. http://doi.org/10.1093/cercor/bhq207
945   Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the
946   human brain, *8*(5), 679–685. http://doi.org/10.1038/nn1444
947   Kaposvari, P., Kumar, S., & Vogels, R. (2018). Statistical Learning Signals in
948   Macaque Inferior Temporal Cortex. *Cerebral Cortex*, *28*(1), 250–266.
949   http://doi.org/10.1093/cercor/bhw374
950   Kay, K. N., Naselaris, T., Prenger, R. J., & Gallant, J. L. (2008). Identifying natural
951   images from human brain activity. *Nature*, *452*(7185), 352–355.
952   http://doi.org/10.1038/nature06713
953   Keil, A., Debener, S., Gratton, G., Junghöfer, M., Kappenman, E. S., Luck, S. J., et
954   al. (2014). Committee report: Publication guidelines and recommendations for
955   studies using electroencephalography and magnetoencephalography.
956   *Psychophysiology*, *51*(1), 1–21. http://doi.org/10.1111/psyp.12147
957   Keller, A. J., Houlton, R., Kampa, B. M., Lesica, N. A., Mrsic-Flogel, T. D., Keller, G.
958   B., & Helmchen, F. (2017). Stimulus relevance modulates contrast adaptation in
959   visual cortex. *eLife*, *6*, e21589. http://doi.org/10.7554/eLife.21589
960   King, J. R., & Dehaene, S. (2014). Characterizing the dynamics of mental
961   representations: the temporal generalization method. *Trends in Cognitive*
962   *Sciences*, *18*(4), 203–210. http://doi.org/10.1016/j.tics.2014.01.002
963   King, J.-R., Gramfort, A., Schurger, A., Naccache, L., & Dehaene, S. (2014). Two
964   Distinct Dynamic Modes Subtend the Detection of Unexpected Sounds. *PloS*
965   *One*, *9*(1), e85791. http://doi.org/10.1371/journal.pone.0085791
966   King, J.-R., Pescetelli, N., & Dehaene, S. (2016). Brain Mechanisms Underlying the
967   Brief Maintenance of Seen and Unseen Sensory Information. *Neuron*, *92*(5),
968   1122–1134. http://doi.org/10.1016/j.neuron.2016.10.051
969   Kohn, A., & Movshon, J. A. (2004). Adaptation changes the direction tuning of
970   macaque MT neurons., *7*(7), 764–772. http://doi.org/10.1038/nn1267

Repetition suppression and prediction error

971   Kok, P., Jehee, J. F. M., & de Lange, F. P. (2012). Less Is More: Expectation
972   Sharpens Representations in the Primary Visual Cortex. *Neuron*, *75*(2), 265–
973   270. http://doi.org/10.1016/j.neuron.2012.04.034
974   Kok, P., Mostert, P., & de Lange, F. P. (2017). Prior expectations induce prestimulus
975   sensory templates. *Proceedings of the National Academy of Sciences of the*
976   *United States of America*, *26*, 201705652.
977   http://doi.org/10.1073/pnas.1705652114
978   Kourtzi, Z., & Kanwisher, N. (2001). Representation of Perceived Object Shape by
979   the Human Lateral Occipital Complex. *Science*, *293*(5534), 1506–1509.
980   http://doi.org/10.1126/science.1061133
981   Kovács, G., Kaiser, D., Kaliukhovich, D. A., Vidnyánszky, Z., & Vogels, R. (2013).
982   Repetition probability does not affect fMRI repetition suppression for objects. *The*
983   *Journal of Neuroscience*, *33*(23), 9805–9812.
984   http://doi.org/10.1523/JNEUROSCI.3423-12.2013
985   Kumar, S., Kaposvari, P., & Vogels, R. (2017). Encoding of Predictable and
986   Unpredictable Stimuli by Inferior Temporal Cortical Neurons. *Journal of Cognitive*
987   *Neuroscience*, *29*(8), 1445–1454. http://doi.org/10.1162/jocn_a_01135
988   Kvale, M. N., & Schreiner, C. E. (2004). Short-Term Adaptation of Auditory
989   Receptive Fields to Dynamic Stimuli. *Journal of Neurophysiology*, *91*(2), 604–
990   612. http://doi.org/10.1152/jn.00484.2003
991   Larsson, J., & Smith, A. T. (2012). fMRI repetition suppression: neuronal adaptation
992   or stimulus expectation? *Cerebral Cortex*, *22*(3), 567–576.
993   http://doi.org/10.1093/cercor/bhr119
994   Liu, T., Larsson, J., & Carrasco, M. (2007). Feature-Based Attention Modulates
995   Orientation-Selective Responses in Human Visual Cortex. *Neuron*, *55*(2), 313–
996   323. http://doi.org/10.1016/j.neuron.2007.06.030
997   Maravall, M., Petersen, R. S., Fairhall, A. L., Arabzadeh, E., & Diamond, M. E.
998   (2007). Shifts in Coding Properties and Maintenance of Information Transmission
999   during Adaptation in Barrel Cortex. *PLoS Biology*, *5*(2), e19.
1000   http://doi.org/10.1371/journal.pbio.0050019
1001   Marti, S., King, J. R., & Dehaene, S. (2015). Time-Resolved Decoding of Two
1002   Processing Chains during Dual-Task Interference. *Neuron*, *88*(6), 1297–1307.
1003   http://doi.org/10.1016/j.neuron.2015.10.040
1004   Maunsell, J. (2015). Neuronal Mechanisms of Visual Attention. *Annual Review of*
1005   *Vision Science*, *1*(1), 373–391. http://doi.org/10.1146/annurev-vision-082114-
1006   035431
1007   Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex.
1008   *Trends in Neurosciences*, *29*(6), 317–322.
1009   http://doi.org/10.1016/j.tins.2006.04.001
1010   Movshon, J. A., & Lennie, P. (1979). Pattern-selective adaptation in visual cortical
1011   neurones. *Nature*, *278*(5707), 850–852.
1012   Myers, N. E., Rohenkohl, G., Wyart, V., Woolrich, M. W., Nobre, A. C., Stokes, M.
1013   G., & Frank, M. J. (2015). Testing sensory evidence against mnemonic
1014   templates. *eLife*, *4*, e09000. http://doi.org/10.7554/eLife.09000
1015   Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity
1016   (MMN) in basic research of central auditory processing: A review. *Clinical*

Neurophysiology, 118(12), 2544–2590.
http://doi.org/10.1016/j.clinph.2007.04.026

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology*, *112*(4), 713–719.

Paavilainen, P. (2013). The mismatch-negativity (MMN) component of the auditory event-related potential to violations of abstract regularities: A review. *International Journal of Psychophysiology*, *88*(2), 109–123. http://doi.org/10.1016/j.ijpsycho.2013.03.015

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects, *2*(1), 79–87. http://doi.org/10.1038/4580

Rasmussen, R. G., Schwartz, A., & Chase, S. M. (2017). Dynamic range adaptation in primary motor cortical populations. *eLife*, *6*, e21409. http://doi.org/10.7554/eLife.21409

Rentzeperis, I., Nikolaev, A. R., Kiper, D. C., & Van Leeuwen, C. (2012). Relationship between neural response and adaptation selectivity to form and color: an ERP study. *Frontiers in Human Neuroscience*, *6*. http://doi.org/10.3389/fnhum.2012.00089

Saarinen, J., Paavilainen, P., Schöger, E., Tervaniemi, M., & Näätänen, R. (1992). Representation of abstract attributes of auditory stimuli in the human brain. *NeuroReport*, *3*(12), 1149–1151.

Salti, M., Monto, S., Charles, L., King, J.-R., Parkkonen, L., Dehaene, S., & Johansen-Berg, H. (2015). Distinct cortical codes and temporal dynamics for conscious and unconscious percepts. *eLife*, *4*, e05652. http://doi.org/10.7554/eLife.05652

Schacter, D. L., & Buckner, R. L. (1998). Priming and the Brain. *Neuron*, *20*(2), 185–195.

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-Positive Psychology: Undisclosed Flexibility in Data Collection and Analysis Allows Presenting Anything as Significant. *Psychological Science*, *22*(11), 1359–1366. http://doi.org/10.1177/0956797611417632

Smirnakis, S. M., Berry, M. J., Warland, D. K., Bialek, W., & Meister, M. (1997). Adaptation of retinal processing to image contrast and spatial scale. *Nature*, *386*(6620), 69–73. http://doi.org/10.1038/386069a0

Spaak, E., Watanabe, K., Funahashi, S., & Stokes, M. G. (2017). Stable and Dynamic Coding for Working Memory in Primate Prefrontal Cortex. *The Journal of Neuroscience*, *37*(27), 6503–6516. http://doi.org/10.1523/JNEUROSCI.3364-16.2017

Sprague, T. C., & Serences, J. T. (2013). Attention modulates spatial priority maps in the human occipital, parietal and frontal cortices, *16*(12), 1879–1887. http://doi.org/10.1038/nn.3574

Repetition suppression and prediction error

1061 Stokes, M. G., Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., & Duncan, J. (2013).
1062   Dynamic Coding for Cognitive Control in Prefrontal Cortex. *Neuron*, *78*(2), 364–
1063   375. http://doi.org/10.1016/j.neuron.2013.01.039
1064 Stokes, M. G., Wolff, M. J., & Spaak, E. (2015). Decoding Rich Spatial Information
1065   with High Temporal Resolution. *Trends in Cognitive Sciences*, *19*(11), 636–638.
1066   http://doi.org/10.1016/j.tics.2015.08.016
1067 Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008).
1068   Neural repetition suppression reflects fulfilled perceptual expectations, *11*(9),
1069   1004–1006. http://doi.org/10.1038/nn.2163
1070 Summerfield, C., Wyart, V., Mareike Johnen, V., & de Gardelle, V. (2011). Human
1071   Scalp Electroencephalography Reveals that Repetition Suppression Varies with
1072   Expectation. *Frontiers in Human Neuroscience*, *5*.
1073   http://doi.org/10.3389/fnhum.2011.00067
1074 Tang, M. F., Dickinson, J. E., Visser, T. A. W., & Badcock, D. R. (2015). The broad
1075   orientation dependence of the motion streak aftereffect reveals interactions
1076   between form and motion neurons. *Journal of Vision*, *15*(13), 4.
1077   http://doi.org/10.1167/15.13.4
1078 Todorovic, A., & de Lange, F. P. (2012). Repetition suppression and expectation
1079   suppression are dissociable in time in early auditory evoked fields. *The Journal*
1080   *of Neuroscience*, *32*(39), 13389–13395.
1081   http://doi.org/10.1523/JNEUROSCI.2227-12.2012
1082 Todorovic, A., van Ede, F., Maris, E., & de Lange, F. P. (2011). Prior Expectation
1083   Mediates Neural Adaptation to Repeated Sounds in the Auditory Cortex: An
1084   MEG Study. *The Journal of Neuroscience*, *31*(25), 9118–9123.
1085   http://doi.org/10.1523/JNEUROSCI.1425-11.2011
1086 Tootell, R. B., Hadjikhani, N. K., Vanduffel, W., Liu, A. K., Mendola, J. D., Sereno, M.
1087   I., & Dale, A. M. (1998). Functional analysis of primary visual cortex (V1) in
1088   humans. *Proceedings of the National Academy of Sciences of the United States*
1089   *of America*, *95*(3), 811–817. http://doi.org/10.1038/340386a0
1090 Tootell, R., Reppas, J. B., Dale, A. M., & Look, R. B. (1995). Visual motion aftereffect
1091   in human cortical area MT revealed by functional magnetic resonance imaging.
1092   *Nature*.
1093 Treue, S., & Trujillo, J. (1999). Feature-based attention influences motion processing
1094   gain in macaque visual cortex. *Nature*. http://doi.org/10.1038/21176
1095 Ulanovsky, N., Las, L., & Nelken, I. (2003). Processing of low-probability sounds by
1096   cortical neurons, *6*(4), 391–398. http://doi.org/10.1038/nn1032
1097 Vinken, K., Vogels, R., & Op de Beeck, H. (2017). Recent Visual Experience Shapes
1098   Visual Processing in Rats through Stimulus-Specific Adaptation and Response
1099   Enhancement. *Current Biology*, *27*(6), 914–919.
1100   http://doi.org/10.1016/j.cub.2017.02.024
1101 Wacongne, C., Labyt, E., van Wassenhove, V., Bekinschtein, T., Naccache, L., &
1102   Dehaene, S. (2011). Evidence for a hierarchy of predictions and prediction errors
1103   in human cortex. *Proceedings of the National Academy of Sciences of the United*
1104   *States of America*, *108*(51), 20754–20759.
1105   http://doi.org/10.1073/pnas.1117807108

Repetition suppression and prediction error

1106   Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017a). Dynamic hidden
1107   states underlying working-memory-guided behavior, *20*(6), 864–871.
1108   http://doi.org/10.1038/nn.4546
1109   Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017b). Dynamic hidden
1110   states underlying working-memory-guided behavior, *20*(6), 864–871.
1111   http://doi.org/10.1038/nn.4546
1112