Repetition suppression and prediction error

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

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4 # Prediction Error and Repetition Suppression Have Distinct

5 # Effects on Neural Representations of Visual Information

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Repetition suppression and prediction error

25   **Abstract**

26   Predictive coding theories argue recent experience establishes expectations in the

27   brain that when violated generate *prediction errors*. Prediction errors provides a

28   possible explanation for *repetition suppression* where repeated stimulus

29   presentations yield reduced neural responses. On a predictive coding account,

30   repetition suppression arises because the repeated stimuli are expected whereas

31   non-repeated stimuli are unexpected, eliciting larger neural responses. Here we

32   employed electroencephalography in human to test the predictive coding account of

33   repetition suppression. In different blocks, streams of gratings were presented whose

34   orientations were expected either to repeat or change. Uniquely, we applied

35   multivariate forward modelling to determine how orientation selectivity was affected

36   by repetition and prediction. Prediction errors were associated with significantly

37   enhanced orientation selectivity, whereas there was no such influence on selectivity

38   during repetition suppression. Our findings also suggest that when a prediction error

39   is registered in the visual system, representations of expected stimulus features are

40   transiently reactivated.

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Introduction

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43   At any moment in time, the brain receives more sensory information than can

44   be responded to, creating the need for selection and efficient processing of the

45   incoming signals. One mechanism by which the brain reduces its information

46   processing load is to encode successive presentations of the same stimulus in a

47   more efficient form, a process known as neural adaptation. Such adaptation has

48   been observed across different sensory modalities and species, and provides a

49   mechanism to enhance the coding efficiency of individual neurons and neuronal

50   populations (Maravall et al., 2007; Barlow, 2012; Benucci et al., 2013; Adibi et al.,

51   2013b). A specific form of neuronal adaptation is known as repetition suppression, in

52   which the neural responses evoked by a given stimulus decline with repeated

53   exposure to that stimulus (Gross et al., 1967; Movshon and Lennie, 1979; Diederen

54   et al., 2016; Keller et al., 2017; Rasmussen et al., 2017). Here we asked whether a

55   predictive coding theory can account for the changes in neural representations

56   observed with repetition suppression.

57   The phenomenon of repetition suppression has been widely exploited to

58   investigate neural representations of sensory information. Repeated exposures allow

59   for more efficient representation of subsequent stimuli, as manifested in improved

60   behavioural performance despite a significant reduction in neural activity (Schacter

61   and Buckner, 1998; Henson and Rugg, 2003). Repetition suppression paradigms

62   have been used extensively in human neuroimaging because they are commonly

63   believed to be analogous to the single-cell adaptation effects observed in animal

64   studies (see Barron et al., 2016 for review). The exact relationship between the

65   effects seen in human neuroimaging studies and animal neurophysiology has,

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66   however, yet to be fully established.

67   The view that repetition suppression measured in human neuroimaging

68   reflects neuronal adaptation has recently been challenged by hierarchical predictive

69   coding theories (Summerfield et al., 2008; Auksztulewicz and Friston, 2016). These

70   theories argue that the brain interprets incoming sensory events based on what

71   would be expected from the recent history of exposure to such stimuli (Rao and

72   Ballard, 1999; Friston, 2005). Predictions are generated within each cortical area,

73   and are bi-directionally propagated from higher to lower areas, including to primary

74   sensory regions, allowing for more efficient representation of expected stimuli. When

75   there is a precise expectation, incoming information can be efficiently represented by

76   recruiting a small pool of relevant neurons (Friston, 2005). Some of the most

77   compelling evidence for predictive coding comes from human neuroimaging

78   experiments in which the presentation of an unexpected stimulus generates a larger

79   response than the presentation of an expected stimulus. In studies employing

80   electroencephalography (EEG) and magnetoencephalography (MEG), this effect is

81   known as the *mismatch negativity* (Näätänen et al., 2007; Garrido et al., 2009;

82   Wacongne et al., 2011).

83   To test the hypothesis that prediction error can account for repetition

84   suppression effects, Summerfield and colleagues (2008) introduced an experimental

85   paradigm in which the identity of a face stimulus was either repeated in 80% of trials

86   (making the repetition *expected*) or was changed in 80% of trials (making the

87   repetition *unexpected*). There was a greater reduction of the BOLD response in

88   fusiform face area when a face repetition was expected, compared to when it was

89   unexpected. This attenuation of repetition suppression by prediction has also been

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90   replicated using fMRI (Larsson and Smith, 2012) and M/EEG, using high-level stimuli

91   such as faces (Summerfield et al., 2011), and simple stimuli such as tones

92   (Todorovic et al., 2011; Todorovic and de Lange, 2012).

93   A potential reconciliation of the relationship between prediction error and

94   repetition suppression comes from work showing that while expectations decrease

95   the overall amount of neural activity, they may also yield sharper representations of

96   sensory stimuli (Kok et al., 2012). Typical neuroimaging analyses only examine

97   overall levels of activity (Tootell et al., 1995; Buckner et al., 1998; Tootell et al., 1998;

98   Kourtzi and Kanwisher, 2001), which could be produced by several different types of

99   change in neural representation. For instance, both sharpening, where response to

100   only unpredicted features is suppressed, and gain reduction, where a multiplicative

101   suppression occurs for all features, could be associated with decreased population

102   activity, even though the amount of information carried by the representations will be

103   markedly different. Recently introduced multivariate pattern analytic approaches to

104   human neuroimaging, such as forward encoding modelling, allow quantification of

105   stimulus-selective information contained within patterns of neural activity in human

106   observers (Brouwer and Heeger, 2009; Garcia et al., 2013; Myers et al., 2015; Salti

107   et al., 2015; King et al., 2016; Wolff et al., 2017).

108   Here we used multivariate methods to determine whether repetition

109   suppression and prediction error similarly affect the way the brain represents visual

110   orientation information. To anticipate our findings, we found that repetition

111   suppression had no effect on visual orientation selectivity, but that prediction error

112   was associated with a significantly increased orientation-selective response through

113   a gain modulation soon after the stimulus was presented. This representation was
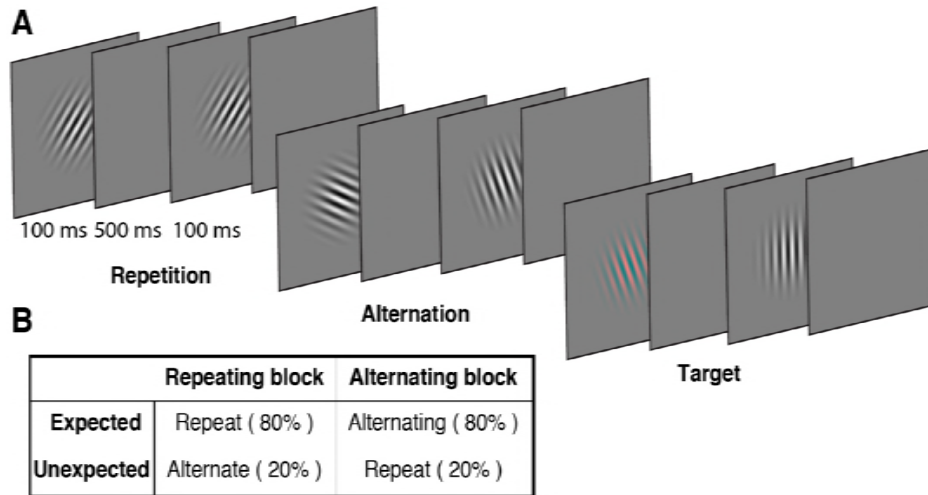
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114   then transiently re-activated ~200 ms afterwards.

115   **Results**

116   We used a modified version of the paradigm introduced by Summerfield and

117   colleagues (2008), replacing the face stimuli used in that study with oriented Gabors.

118   These low-level stimuli allowed us to quantify the degree of orientation selectivity in

119   EEG activity to determine how representations of orientation are affected by

120   prediction error and repetition suppression. Each of fifteen observers participated in

121   two EEG sessions where on each trial, two Gabors were presented sequentially (100

122   ms presentation, 600 ms stimulus onset asynchrony), and these stimulus pairs either

123   repeated or alternated in their orientation (Figure 1A, Movie 1). The predictability of

124   the repeated and alternating pairs was varied in a block-wise manner to manipulate

125   expectation. In a *repeating* block, the orientations of the two Gabors in a pair

126   repeated in 80% of trials, and alternated for the remaining 20%. These contingencies

127   were reversed in the *alternating* block (Figure 1B). The orientations of successive

128   stimuli across a block were randomized to limit any accumulated effects of

129   adaptation and prediction. As repetition suppression and prediction error form

130   orthogonal dimensions of the task, the design allowed us to isolate their respective

131   contributions to neural responses. Participants completed an unrelated task of

132   discriminating (red vs blue) rare (10%) coloured Gabors.

Repetition suppression and prediction error

A

100 ms 500 ms 100 ms

Repetition

B

Alternation

Target

	Repeating block	Alternating block
Expected	Repeat (80%)	Alternating (80%)
Unexpected	Alternate (20%)	Repeat (20%)

133

134 **Figure 1.** Example stimulus displays and task design. **(A)** Schematic of the stimuli
135 and timing used in the experiment. Participants viewed a rapid stream of pairs of
136 Gabors and monitored for an infrequently occurring coloured target (10% of trials).
137 The stimulus orientations varied pseudorandomly across trials between 0° and 160°
138 (in 20° steps), allowing orientation-selective information contained within patterns of
139 EEG activity to be estimated. **(B)** The orientation of the pairs of Gabors could either
140 repeat or alternate. In one type of block, 80% of trials were orientation repeats and
141 the remaining 20% alternated (Repeating blocks); in the other type of block these
142 contingencies were reversed (Alternating blocks).

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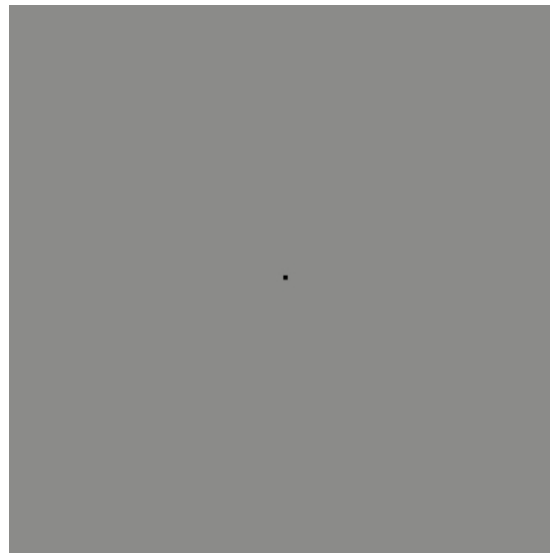
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145 **Movie 1.** Example of the stimulus sequence in a typical repetition block.

146

147 **Repetition suppression and prediction error affect the overall level of neural**

148 **activity**

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

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Repetition suppression and prediction error

150   Consistent with previous work (Tootell et al., 1998; Summerfield et al., 2011;

151   Todorovic et al., 2011; Rentzeperis et al., 2012; Todorovic and de Lange, 2012; Cui

152   et al., 2016; Keller et al., 2017), there was a significant repetition suppression effect

153   (Repeat < Alternating), such that the response to repeated stimuli was significantly

154   reduced compared with the response to alternating stimuli (Figure 2A). The repetition

155   suppression effect was evident over a large cluster of occipital-parietal electrodes at

156   two time intervals: an early effect from 79 to 230 ms, and a later effect at 250 to 540

157   ms after the onset of the second stimulus (cluster $p < .025$; Figure 2B and caption). A

158   large cluster of frontal electrodes mirrored the repetition suppression effect with a

159   similar time course: the ERP over these frontal sites had the same pattern, but was

160   reversed in sign, suggesting it originated from the same dipole as the occipital

161   response.

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Repetition suppression and prediction error
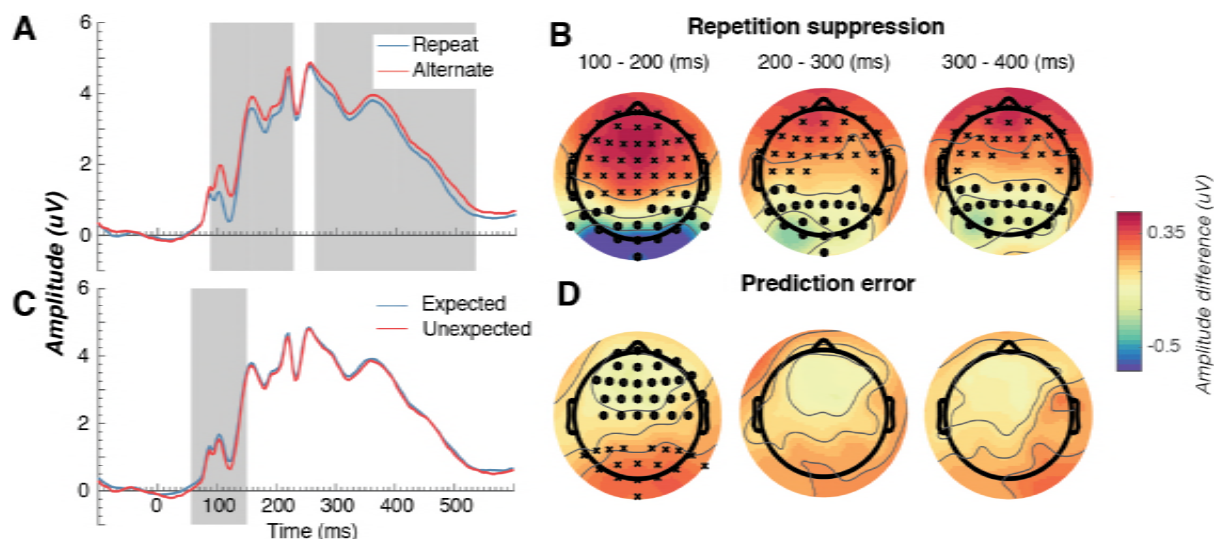
Figure 2. Univariate EEG results for the effect of repetition suppression and prediction error on the second stimulus in a pair (T2). Grand average ERP time courses for repetition suppression **(A)** and prediction error **(C)** averaged over occipital-parietal electrodes (O1, O2, Oz, POz, PO7, PO3, PO8, PO4). The shaded region indicates significant differences between the conditions (two-tailed cluster-permutation, alpha $p < .05$, cluster alpha $p < .05$, N permutations = 20,000). The main effects of repetition suppression **(B)** and prediction error **(D)** over three time periods and across all electrodes. The main effect of repetition suppression is displayed as Repeating minus Alternating trials. The main effect of prediction error is displayed as Expected minus Unexpected. 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).

Also consistent with previous results (Garrido et al., 2009; Summerfield et al.,

2011; Todorovic et al., 2011; Todorovic and de Lange, 2012), there was a significant

prediction error effect (Expected < Unexpected), with a larger neural response over a

cluster of frontal electrodes 75-150 ms after stimulus presentation (Figure 2C). As

with the repetition suppression result described above, there was a prediction error

effect of opposite polarity over occipital-parietal electrodes. This effect was

significant at an early time point post-stimulus (79-130 ms), but not at later time

points (320-390 ms; Figure 2D). Finally, there was no interaction between repetition

suppression and prediction error (no significant positive or negative clusters, all $p >$

9

187   .05). Taken together, these results reveal both repetition suppression and prediction

188   error effects in the neural data, which were indexed separately as shown in Figure 2.

189   **Prediction errors increase the amount of orientation-selective information**

190   **contained within patterns of EEG activity**

191   We next examined the key question of whether repetition suppression and

192   prediction error differentially affect the neural representation of orientation

193   information. To do this, we used a forward encoding approach to reconstruct

194   orientation-selective information contained within the multivariate pattern of EEG

195   activity distributed across the scalp (see Methods for details). Briefly, this technique

196   transforms sensor-level responses into tuned 'feature' channels (Kay et al., 2008;

197   Brouwer and Heeger, 2009; Garcia et al., 2013; Myers et al., 2015), in this case,

198   orientation-selective features. For each trial, the presented orientation was

199   convolved with a canonical, orientation-selective tuning function and regressed

200   against the pattern of EEG activity across all sensors at each time point. This

201   created a spatial filter of the multivariate EEG activity that differentiated orientations

202   (Figure 3D). These weights were then inverted to reconstruct the model, and

203   multiplied against an independent set of test trials to produce responses in the

204   modelled orientation channels. These sets of responses were then used to evaluate

205   the degree of orientation selectivity in those trials. The procedure was repeated for

206   all time points in the trial, and a cross-validated approach was used until all trials had

207   been used for both training and testing.

208   As shown in Figure 3, the forward encoding revealed a strong, orientation-

209   selective response derived from the multivariate pattern of EEG activity. This

210   orientation-tuned response was evident from ~50 to 470 ms after stimulus onset, and

Repetition suppression and prediction error

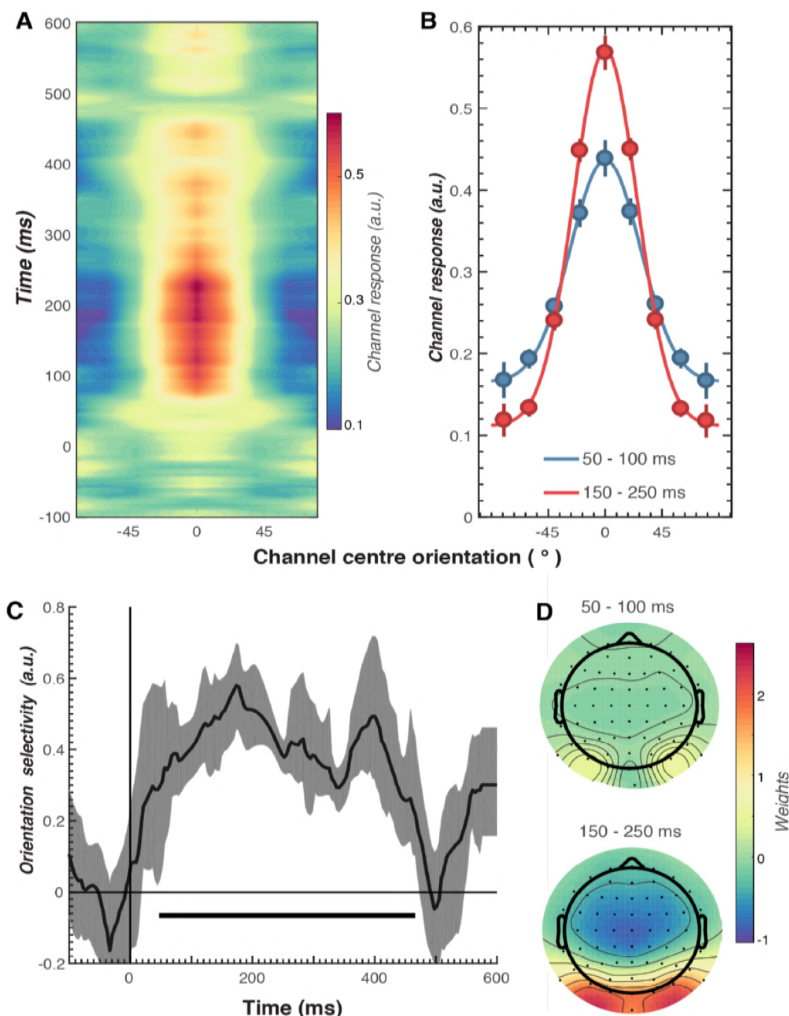211   peaked between ~120-250 ms (Figure 3C). Examination of the regression weights

212   revealed that this response was largely driven by activity centred over occipital-

213   parietal areas (Figure 3D).

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Repetition suppression and prediction error

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

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Repetition suppression and prediction error

236   To examine our central question of whether repetition suppression and

237   prediction error have differential effects on neural representations of orientation, we

238   split and averaged the results of the forward encoding by trial type, and fitted these

239   with Gaussians (see Methods) to quantify orientation selectivity (Figure 4). Repetition

240   suppression did not affect the amount of orientation selectivity contained within the

241   EEG data, as trials with repeated and alternating orientations could be decoded with

242   similar accuracies. This was the case even though the repeated trials had a

243   markedly smaller EEG response over occipital and parietal electrodes, where the

244   forward encoding model was maximally sensitive (Figure 2A). This result is

245   consistent with the 'efficient representation' hypothesis of repetition suppression,

246   which argues that the overall neural response is smaller with repetition suppression

247   due to more efficient coding of stimulus information (Gotts et al., 2012).

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Repetition suppression and prediction error
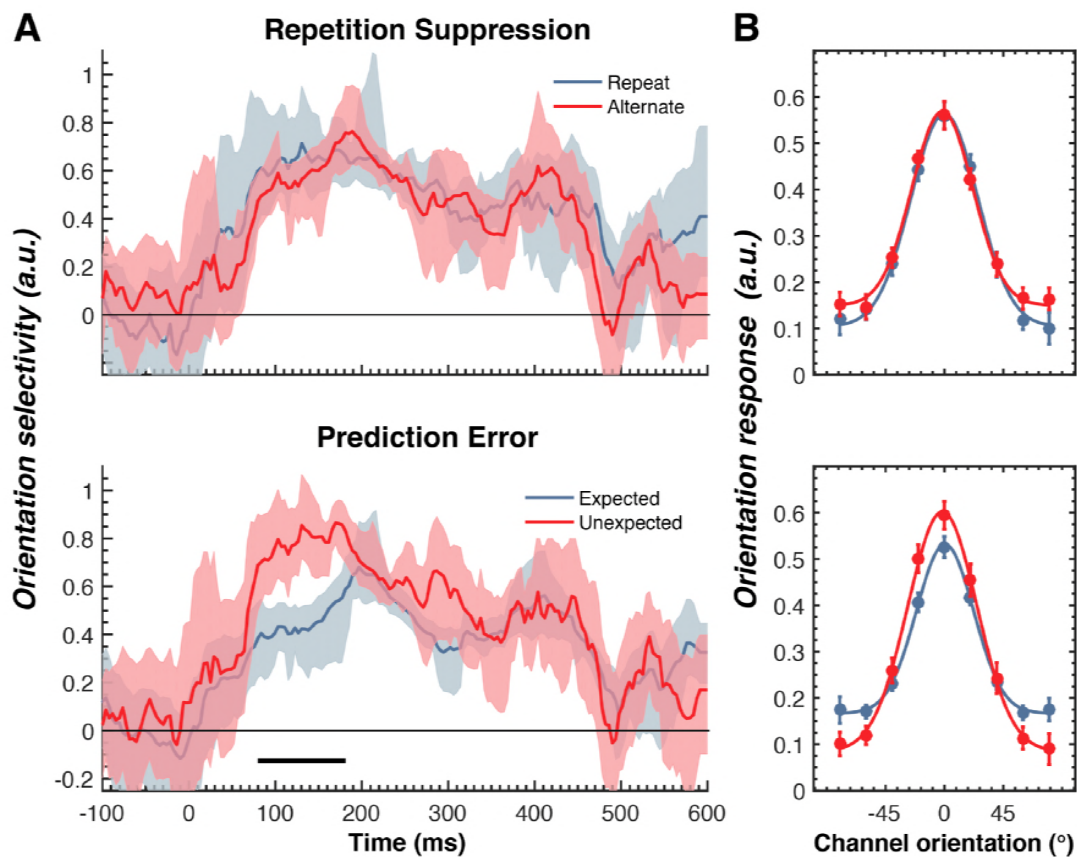
Figure 4. The effect of repetition suppression and prediction error on orientation selectivity measured using forward encoding modelling. **(A).** Amount of orientation-selective information reconstructed from the EEG signal in response to the second Gabor in a pair, shown separately for repetition suppression (upper panel) and prediction error (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). Error shading indicates bootstrapped 95% confidence intervals of the mean. **(B)** The population tuning curve averaged over the significant time period (79 – 185 ms) to show how the overall stimulus representation is affected with a fitted Gaussian. For prediction error, the amplitude increased and the baseline decreased. There was no effect for the repetition suppression condition. Error bars indicate ±1 standard error.

Examining the effect of prediction error revealed a markedly different pattern

of results. At 79 - 185 ms after the onset of the second stimulus in the pair,

orientation-selectivity increased significantly when the stimulus was unexpected

relative to when it was expected, i.e., the prediction error was associated with an

increased representation of the stimulus at the earliest stages of the brain's

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**Repetition suppression and prediction error**

268   response to that stimulus. Moreover, the prediction error signal contained enhanced

269   information about the specific features of the stimulus that violated expectation, in

270   this case the orientation of the second grating.

271   To determine how the orientation representation was affected by prediction

272   error, we averaged the stimulus reconstruction over this early time period (79-185

273   ms after stimulus presentation) to increase signal-to-noise, and fitted Gaussians to

274   each participant's data individually (Figure 3B). This again showed that the amplitude

275   of the response was significantly ($t(14) = 3.34$, $p = .0049$) higher for unexpected

276   ($M = 0.67$, $SE = 0.06$) than for expected ($M = 0.41$, $SE = 0.03$) stimuli. By contrast,

277   the width of the representations was similar for unexpected ($M = 29.62°$, $SE = 4.72°$)

278   and expected ($M = 26.72°$, $SE = 2.74°$) stimuli, paired t-test ($t(14) = 0.78$, $p = .45$).

279   There was also a small, but non-significant ($t(14) = 1.94$, $p = .072$) trend for a smaller

280   baseline response (i.e., non-orientation tuned activity) in the unexpected ($M = -0.01$,

281    $SE = 0.07$) than in the expected ($M = 0.13$, $SE = 0.02$) condition. For comparison, we

282   also averaged the same time period for the repetition suppression conditions, and

283   found similar curves for the repeated and alternating trials (*all ps > .05*).

284   To further examine whether orientation-selectivity contained within the overall

285   pattern of EEG activity differed for unexpected and expected stimuli, we used

286   multivariate linear discriminant analysis to determine whether backward decoding

287   produces the same pattern of results as that yielded by the forward encoding

288   approach described above. A similar cross-validation procedure was used as in the

289   forward encoding approach, but accuracy was now defined as proportion correct

290   accuracy of the presented orientation on the test trials. This analysis confirmed the

291   results of the forward encoding: orientations shown in unexpected trials were

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292   classified better than orientations shown in expected trials ($p <$. 05). Again, there was

293   no effect of repetition on classification accuracy (paired t-test $p > .05$).
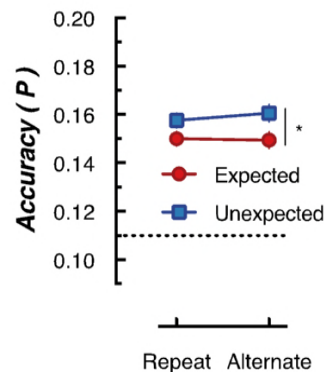
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295   **Figure 5.** Peak linear discriminant classification accuracy of the presented grating
296   orientation for expected and unexpected conditions. The dotted line indicates chance
297   performance (1/9 orientations). The error bars indicate ±1 standard error of the
298   mean.
299
300   **Prediction error affects the temporal stability of stimulus representations**

301   Next, we examined whether repetition suppression and prediction error

302   affected dynamic, ongoing stimulus representations by using cross-temporal

303   generalization (Stokes et al., 2013; King et al., 2014; King and Dehaene, 2014;

304   Myers et al., 2015; Spaak et al., 2017). To do this, we used the same forward

305   encoding approach as in the previous analysis, but now the weights were derived

306   from one time-point on one set of trials, and then applied at every time point in the

307   test trials. Again, a cross-validation approach was used, with all trials serving as both

308   training and test. This analysis examined whether the same spatial pattern of EEG

309   activity that allows for orientation selectivity generalizes to other time points, thus

310   revealing whether there was a stable or dynamic neural representation of the stimuli

311   over time.

312   As shown in Figure 6, the best orientation selectivity was on-axis between 100

313   ms and 300 ms after stimulus presentation, suggesting that the stimulus

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Repetition suppression and prediction error

314   representation changed dynamically over time (King and Dehaene, 2014). There

315   was also significant off-axis orientation-selectivity from 100-500 ms after stimulus

316   presentation, suggesting that some aspects of the neural representation of

317   orientation were stable over time.
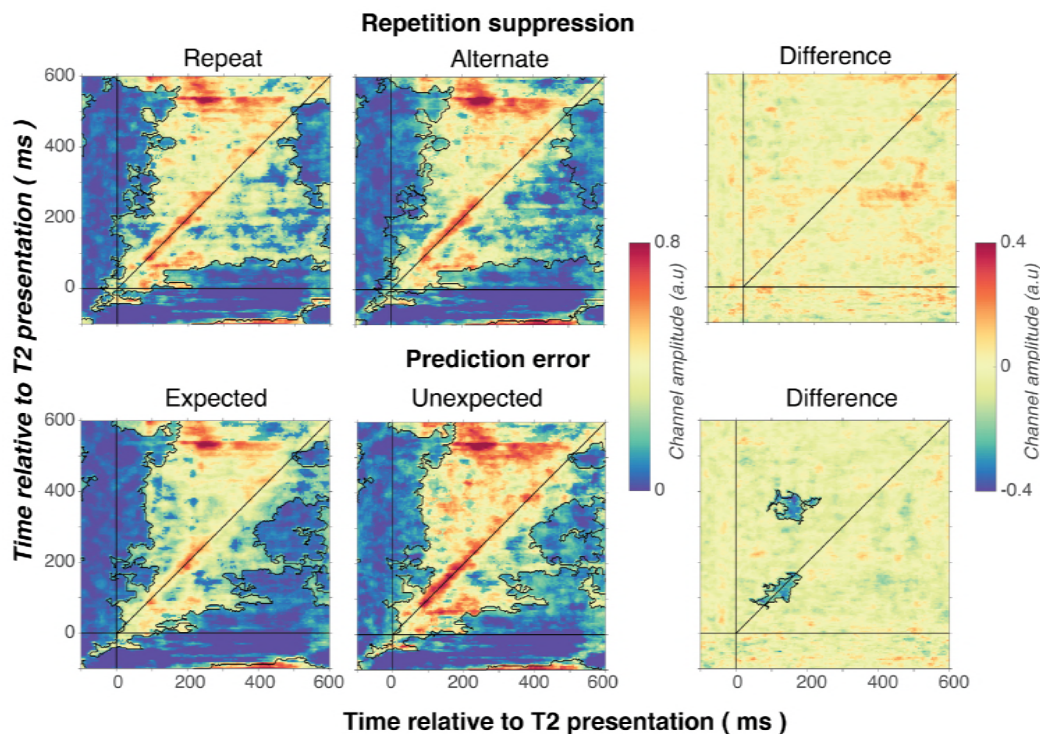
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319   **Figure 6.** Cross-temporal generalization of the forward encoding model based on T2
320   orientations for the main effects of repetition suppression (upper panels) and
321   prediction error (lower panels). The maps have been thresholded (indicated by
322   opacity) to show clusters (black outlines) of significant orientation selectivity
323   (permutation testing, cluster threshold p < .05, corrected cluster statistic $p < .05$,
324   5,000 permutations). The difference between the conditions is shown in the right-
325   hand column (permutation testing, cluster threshold $p < .05$, corrected cluster
326   statistic $p < .05$). Opacity and outlines indicate significant differences.
327
328   There was no effect of repetition suppression on the temporal generalization

329   of orientation information (upper panels of Figure 6), suggesting that repetition

330   suppression did not affect the temporal stability of neural representations of the

331   Gabors. Examining the effect of prediction error on cross-temporal generalization

332   confirmed that there was significantly more on-axis orientation selectivity when the

333   stimulus was unexpected than when it was expected. This increased on-axis

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334 orientation selectivity generalized off-axis at around 300-400 ms after stimulus onset.

335 This finding suggests that the same representation that is activated to process the

336 prediction error is reactivated later as the stimulus continues to be processed. Such

337 a signal could constitute the prior of the prediction, as this should be updated on the

338 basis of the incoming sensory evidence, which in turn would likely require

339 reactivation of the unexpected stimulus.

340 **Representation of the expected feature is activated even when it is not**

341 **presented**

342 In a final set of analyses, we investigated how prediction error signals affect

343 the interpretation of incoming sensory information, one of the key questions of

344 predictive coding theory (Rao and Ballard, 1999; Friston, 2005). To do this, we

345 focused on trials in which the orientation of the first Gabor within a pair did not match

346 the orientation of the second Gabor (i.e., the alternating trials), and examined the

347 EEG response to the second stimulus (see Figure 7). Here, we trained the forward

348 encoding model on the orientation of the Gabor that was actually presented (stimulus
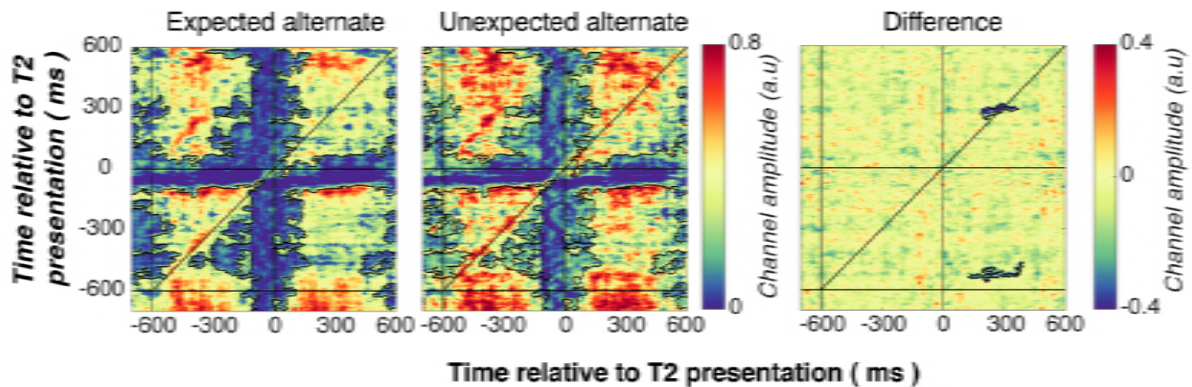
349 driven), or on the orientation that was *expected* based on the first Gabor in the pair

350 (non-stimulus driven). We did not combine data across the repeat and alternating

351 conditions because the orientations were now different upon presentation of the

352 second Gabor in the pair.

Repetition suppression and prediction error

Figure 7. Cross-temporal generalization of the forward encoding model for the orientations presented in T1 relative to the onset of T2 (T1 was presented at -600 ms). The orientation in the T2 period is randomized but there are still periods for the unexpected alternation in which there is significant orientation selectivity. These 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 opacity in the right-hand column indicates areas of statistically significant difference between the two conditions (permutation testing ($n = 5,000$), cluster threshold p < .05, corrected cluster statistic $p < .05$).

In the case of unexpected alternation trials (central panel in Figure 7), the

orientation presented in the first Gabor would be expected to repeat, so when a

different orientation occurred as T2 this prediction had to be suppressed and the

prior updated. Inspecting the plot for the difference between expected and

unexpected trials (right panel in Figure 7) provides clues as to how this process

might occur. As expected, for the time that T1 was presented there was significant

on- and off-axis encoding for T1 orientation, with little difference between expectation

conditions. More interestingly, in the unexpected alternation condition there was

significantly better on-axis orientation selectivity for the T1 orientation between 150

and 300 ms after the onset of T2, relative to the expected alternation condition

(upper right quadrant of right panel in Figure 7). Furthermore, over the same time

period, there was significantly better off-axis generalization of the T1 representation

to the T2 epoch (lower right quadrant of right panel in Figure 7). This is confirmed by

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379   the occurrence of significantly increased off-axis orientation selectivity between

380   training time of -500 ms and +300 ms. The time course of this effect is consistent

381   with our earlier findings, as the unexpected condition yielded better orientation

382   selectivity for the presented (T2) orientation between 79 and 150 ms after the

383   second Gabor presentation. An intriguing possibility is that the relevant neural

384   circuits re-activate the representation of the expected stimulus when faced with

385   unexpected sensory signals.

386   **Discussion**

387   Our findings demonstrate that repetition suppression and prediction error

388   have distinct effects on neural representations of simple visual stimuli. We found that

389   repetition suppression had no effect on orientation selectivity, even though the neural

390   response to repeated stimuli was significantly decreased over occipital-parietal

391   areas. Prediction error, on the other hand, significantly increased the amount of

392   feature-selective information contained within patterns of EEG activity very soon

393   after stimulus onset. This same early representation of the unexpected stimulus was

394   reactivated at 200-300 ms after the initial neural response, supporting the idea that

395   sensory prior expectations may be updated through comparison with the incoming

396   sensory evidence.

397   The present work provides a significant advance in our understanding of how

398   predictive coding allows the brain to process incoming sensory information by

399   comparing what is expected with what actually occurs. Prediction errors have been

400   extensively investigated using mismatch negativity protocols in which an unexpected

401   stimulus causes a significantly larger response than an expected stimulus (Näätänen

402   et al., 2007; Bekinschtein et al., 2009; Garrido et al., 2009). Typically, this increased

Repetition suppression and prediction error

403   response to an unexpected stimulus has been attributed to the need to update the

404   prediction based on sensory evidence (Garrido et al., 2009). However, our results

405   suggest that the increased response may reflect two distinct processes that occur at

406   separate times. Incoming sensory information is first evaluated against the prior

407   (which occurs very early after stimulus presentation). Later, around 300 ms after

408   stimulus presentation, this same representation is reactivated to update the

409   expectation against the initially predicted representation. The present work thus

410   provides a novel insight into how predictive coding might change neural

411   representations of sensory information.

412   Multivariate pattern classification methods have been widely used to examine

413   BOLD activity (Kamitani and Tong, 2005; 2006; Kriegeskorte et al., 2008; Haxby et

414   al., 2014), but have only recently been applied to EEG and MEG data (Garcia et al.,

415   2013; King et al., 2013; 2014; King and Dehaene, 2014; Cichy et al., 2015; Myers et

416   al., 2015; King et al., 2016; Wolff et al., 2017). These kinds of analyses permit non-

417   invasive neuroimaging to move beyond the measurement of overall levels of neural

418   activity, and instead to uncover subtle patterns of neural activity associated with

419   specific stimuli or task demands, and which are more directly comparable with those

420   obtained from invasive neurophysiological recordings of neuronal activity (Kamitani

421   and Tong, 2006; Doeller et al., 2010; Sprague and Serences, 2013; Constantinescu

422   et al., 2016). Such model-based approaches are especially appealing since changes

423   in overall activity levels could be consistent with many different changes in the nature

424   of the underlying neural representation. For instance, sharpening and gain reduction

425   could both reduce the magnitude of the overall neural response but cause very

426   different effects on the amount of information conveyed by those representations.

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427   Surprisingly few studies have used invasive recording methods to examine

428   how predictive coding affects stimulus representations at the neuronal level. One

429   study in macaques (Kaliukhovich and Vogels, 2010) used the same design as

430   Summerfield and colleagues but found no attenuation of repetition suppression by

431   expectation on spiking and local field potentials in inferior temporal cortex when

432   using high-level objects as stimuli (fractals and real-world objects). A later fMRI study

433   in humans (Kovács et al., 2013), used a similar stimulus set and also found no

434   attenuation of repetition suppression by expectation in the same cortical region. A

435   follow-up study explained the apparent conflict finding that the attenuation effects of

436   repetition suppression are only found with familiar but not unfamiliar stimuli (Grotheer

437   and Kovács, 2014). Taken together, these results potentially suggests that the

438   stimulus sets used by (2010) were sufficiently unfamiliar to the animals to induce

439   expectation effects on repetition suppression.

440   Some other work has, however, found that context plays a large role in

441   determining the magnitude of single neuron responses, with rare stimuli generating

442   significantly larger responses than more commonly-occurring stimuli (Ulanovsky et

443   al., 2003). This result has been considered a single-neuron equivalent of the

444   mismatch negativity, but the design did not control for adaptation effects, thus

445   making it difficult to draw an unambiguous comparison with the current work. A more

446   recent study found that neurons in mouse visual cortex show a large response when

447   task-irrelevant visual stimuli presented during training were omitted, suggesting a

448   strong expectation had been violated (Fiser et al., 2016). This result is consistent

449   with the literature on the mismatch negativity, in which the omission of an expected

450   stimulus results in a large prediction error (Garrido et al., 2009; Wacongne et al.,

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451   2011). Future single-unit work characterising how response selectivity of neural

452   populations is affected by prediction would help illuminate the neuronal

453   underpinnings of expectation effects derived from non-invasive imaging in human

454   observers.

455   Unlike the effects of prediction, there is a large body of electrophysiological

456   work showing how adaptation affects neuronal stimulus representations across

457   various sensory modalities in different species (Dragoi et al., 2000; Felsen et al.,

458   2002; Kohn and Movshon, 2004; Patterson et al., 2013; Adibi et al., 2013a; 2013b).

459   For instance, there is a sharpening of stimulus selectivity in MT neurons following 40

460   s of adaptation to a drifting grating (Kohn and Movshon, 2004). As we have

461   highlighted, however, prolonged adaptation is likely also associated with a significant

462   prediction that the next stimulus will be the same as the previous one. Perhaps more

463   relevant to the current results, the width of the orientation tuning in V1 is only

464   marginally sharpened with brief (400 ms) adaptation (Patterson et al., 2013). Again,

465   however, this latter work did not control for expectation, so it is impossible to

466   determine the role of predictive coding in these results. Our result where repetition

467   suppression did not affect the bandwidth of orientation selectivity measured using

468   EEG is also consistent with models of orientation adaptation based on human

469   psychophysical data, which suggest that adaptation does not affect the width of the

470   adapted neurons (Clifford, 2002; Dickinson et al., 2010; Clifford, 2014; Tang et al.,

471   2015; Dickinson et al., 2017).

472   We found that a prediction error increased the gain of early stimulus

473   representations, but did not affect the sharpness of their tuning. This lack of

474   sharpening is in contrast with the findings of a previous study (Kok et al., 2012), in

23

475 which a high-level prediction error led to 'sharper' multivariate decoding for expected

476 versus unexpected visual stimuli. Kok and colleagues used an auditory tone to cue

477 the orientation of a subsequent visual stimulus, and found significantly less off-label

478 classification accuracy for predicted than for unpredicted stimuli. They concluded

479 that predictions cause sharpening of stimulus representations. It is noteworthy,

480 however, that in their study Kok et al. (2012) employed a 'backward' decoding

481 analysis to quantify sharpness, rather than forward encoding as here, which might

482 account for the discrepant findings. It has been argued that the forward encoding

483 approach, which reconstructs feature representations, is more appropriate than

484 decoding for determining how stimulus selectivity is changed (Cichy et al., 2015).

485 Another possible reason for the different results relates to the manner in which

486 predictions are generated within a task. Kok and colleagues generated predictions

487 by pairing an auditory cue with a visual stimulus, whereas we exploited the

488 properties of the visual stimuli themselves (i.e., their orientation) to generate

489 predictions. An intriguing possibility is that combining predictions generated across

490 distinct cortical areas (e.g., visual and auditory) leads to sharpening of tuning,

491 whereas predictions generated within a single cortical area lead to gain modulation.

492 In summary, we have shown that repetition suppression and prediction error

493 differentially affect the neural representation of simple, but fundamental, sensory

494 features. Our results further highlight how the context in which a stimulus occurs, not

495 just its features, affect the way it is represented by the brain. Our findings suggest

496 encoding priority through increased gain may be given to unexpected events which

497 could potentially speed responses. This prioritized representation is then re-activated

498 at a later time period supporting the idea that the feedback from higher cortical areas

24

499   reactivates an initial sensory representation in early cortical areas.

Method

Participants

502   A group of 15 healthy adult volunteers (9 females, median age = 20.5 yr,

503   range = 18 to 37 yr) participated in exchange for partial course credit or financial

504   reimbursement (AUD$20/hr). We based our sample size based on work that

505   investigated the interaction between repetition suppression and predictive error (N =

506   16; Summerfield et al., 2008) and that used forward encoding modelling to

507   investigate orientation selectivity using MEEG with a comparable number of trials as

508   the current study (N =10; Myers et al., 2015). Each person provided written informed

509   consent prior to participation, and had normal or corrected-to-normal vision. The

510   study was approved by The University of Queensland Human Research Ethics

511   Committee and was in accordance with the Declaration of Helsinki.

Experimental setup

513   The experiment was conducted inside a dimly illuminated room with the

514   participants seated in a comfortable chair. The stimuli were displayed on a 22-inch

515   LED monitor (resolution 1920 x 1080 pixels, refresh rate 120 Hz) using the

516   PsychToolbox presentation software (Brainard, 1997; Pelli, 1997) for MATLAB

517   (v7.3). Viewing distance was maintained at 45 cm using a chinrest, meaning the

518   screen subtended 61.18^o x 36.87^o (each pixel 2.4' x 2.4').

Task

520   The stimuli were Gabors (diameter: 5°, spatial frequency: 2 c/^{o}, 100%

521   contrast) presented centrally in pairs for 100 ms, separated by 500 ms (600 ms

522   stimulus onset asynchrony) with a variable (650 to 750 ms) inter-stimulus interval

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

524 between 0º and 160º (in 20º steps) so we could reconstruct orientation selectivity

525 contained within the EEG response using forward encoding modelling. The

526 relationship of the orientations of the pairs Gabors was also used to construct the

527 different repetition suppression and prediction conditions. The orientation presented

528 in the second Gabor in the pair could either repeat or alternate with respect to the

529 orientation of the first Gabor. In the alternation trials, the orientation of the first Gabor

530 was drawn randomly, without replacement, from an even distribution of orientations

531 that was different to the orientation of the second Gabor. To vary the degree of

532 prediction, in half of the blocks 80% of the trials had repeated orientations and 20%

533 of the trials had alternating orientations, whereas in the other half of the blocks these

534 contingencies were reversed. This design allowed us to separately examine the

535 effects of repetition suppression and prediction because of the orthogonal nature of

536 the blocked design. The blocks of 135 trials (~3 mins) switched between the

537 expectation of a repeating or alternating pattern, with the starting condition

538 counterbalanced across participants.

539   The participants' task was to monitor the stream for rare, faintly coloured red

540 or green Gabors, and to discriminate the colour as quickly and accurately as

541 possible. Any trial with a coloured target was excluded from analysis. The orientation

542 match between the pairs was made to be consistent with the dominant contingency

543 (i.e., repeated or alternating) within that block. Pilot testing was used prior to the

544 main experiment to set the task at approximately threshold, to ensure that

545 participants focused exclusively on the colour-discrimination task rather than the

546 orientation contingencies associated with prediction and repetition. Only one

26

547 participant reported being aware of the changing stimulus contingencies across the

548 blocks when asked at the end of the experiment. Self-paced breaks were provided

549 between each of the 20 blocks within a session, at which time feedback was

550 provided on performance in the preceding block. Each participant completed two

551 sessions of 2700 trials each (5400 trials in total), with each session lasting around 70

552 mins of experimental time and 45 mins of EEG setup.

553 **EEG acquisition and pre-processing**

554 Continuous EEG data were recorded using a BioSemi Active Two system

555 (BioSemi, Amsterdam, Netherlands). The signal was digitised at 1024 Hz sampling

556 rate with a 24-bit A/D conversion. The 64 active scalp Ag/AgCl electrodes were

557 arranged according to the international standard 10–20 system for electrode

558 placement (Oostenveld and Praamstra, 2001) using a nylon head cap. As per

559 BioSemi system design, the common mode sense and driven right leg electrodes

560 served as the ground, and all scalp electrodes were referenced to the common mode

561 sense during recording.

562 Offline EEG pre-processing was performed using EEGLAB in accordance with

563 best practice procedures (Keil et al., 2014; Bigdely-Shamlo et al., 2015). The data

564 were initially down sampled to 256 Hz and subjected to a 0.5 Hz high-pass filter to

565 remove slow baseline drifts. Electrical line noise was removed using the

566 *clean_line.m,* and *clean_rawdata.m* in EEGLAB (Delorme and Makeig, 2004) was

567 used remove bad channels (identified using Artifact Subspace Reconstruction),

568 which were then interpolated from the neighbouring electrodes. Data were then re-

569 referenced to the common average before being epoched into segments around

570 each stimulus pair (-0.5 s to 1.25 s from the first stimulus in the pair). Systematic

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571   artefacts from eye blinks, movements and muscle activity were identified using semi-

572   automated procedures in the SASICA toolbox (Chaumon et al., 2015) and regressed

573   out of the signal. After this stage, any trial with a peak voltage exceeding ±100 uV

574   was excluded from the analysis. The data were then baseline corrected to the

575   average EEG activity from -100 to 0 ms before the presentation of the second Gabor

576   pair.

577   **Design**

578   We used a modified version of a factorial design that has previously been

579   used to separately examine the effects of repetition suppression and prediction error

580   (Summerfield et al., 2008; Kaliukhovich and Vogels, 2010; Summerfield et al., 2011;

581   Todorovic et al., 2011; Todorovic and de Lange, 2012; Kovács et al., 2013). By

582   comparing the two repeat conditions with the two alternating conditions, we could

583   examine repetition suppression while controlling for different levels of expectation.

584   Conversely, by comparing across the expected and unexpected trials, we could

585   examine prediction error while controlling for repetition suppression.

586   **Measuring orientation selectivity**

587   We used a forward encoding approach to estimate the amount of orientation-

588   selective information contained in the EEG data at each time point of the trial. This

589   approach differs from standard decoding approaches by modelling each presented

590   orientation as a continuous variable of a set of tuned orientation-selective channels.

591   The forward-encoding technique has been successfully used to reconstruct colour

592   (Brouwer and Heeger, 2009) and spatial (Sprague and Serences, 2013) selectivity in

593   fMRI data. More recently it has been extended to orientation (Garcia et al., 2013;

594   Myers et al., 2015; Wolff et al., 2017) and space (Foster et al., 2016) encoding of

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595   MEG and EEG data, which allows for far greater temporal resolution than fMRI.

596   We applied forward encoding modelling to determine how repetition

597   suppression and prediction error affected orientation selectivity. To do this, the

598   second orientation in the Gabor pair in each trial was used to construct a regression

599   matrix, with a separate regressor for the 9 orientations used across the experiment.

600   This regression matrix was convolved with a set of basis functions (half cosines

601   raised to the 8th power, which allowed complete and unbiased coverage of

602   orientation space) to allow us to pool similar information patterns across nearby

603   orientations (Brouwer and Heeger, 2009). We used this tuned regression matrix to

604   estimate time-resolved orientation selectivity contained within the EEG activity in a

605   16 ms sliding window, in 4 ms steps (Myers et al., 2015). To avoid overfitting, we

606   used a cross-validation procedure where the regression weights were estimated for

607   a training set and applied to an independent test set. This was done by solving the

608   linear equation:

609 $$B_1 = WC_1 \tag{1}$$

610   Where B_1 (64 sensors x N training trials) is the electrode data for the training set, C_1

611   (9 channels x N training trials) is the tuned channel response across the training

612   trials, and W is the weight matrix for the sensors we want to estimate (64 sensors x 9

613   channels). W can be estimated using least square regression to solve equation (2):

614                                $$W = (C_1 \ C_1^{T})^{-1} \ C_1^{T} \ B_1 \tag{2}$$

615   The channel response in the test set C_2 (9 channels x N test trials) was estimated

616   using the weights in (2) and applied to activity in B_2 (64 sensors x N test trials).

617                                $$C^2 = (W \ W^{T}) \ W^{T} \ B^2 \tag{3}$$

618   We repeated this process by holding one trial out as test, and training on the

29

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619   remaining trials until all trials had been used in test and training. The procedure was

620   repeated for each trial within the trial epoch. We then shifted all trials to a common

621   orientation, meaning that 0º corresponded to the orientation presented on each trial.

622   The reconstructed channel activations were separated into the four

623   conditions, and averaged over the trials. These responses were then smoothed with

624   a Gaussian kernel with a 16 ms window, and fit with a Gaussian function (4) using

625   least square regression to quantify the amount of orientation selective activity.

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

627   Where A is the amplitude representing the amount of orientation selective activity, φ

628   is the orientation the function is centred on (in degrees), σ is the standard deviation

629   (degrees) and C is a constant used to account for non-orientation selective baseline

630   shifts.

References

638   Adibi M, Clifford CWG, Arabzadeh E (2013a) Informational basis of sensory
639   adaptation: entropy and single-spike efficiency in rat barrel cortex. J Neurosci
640   33:14921–14926.

641   Adibi M, McDonald JS, Clifford CWG, Arabzadeh E (2013b) Adaptation improves
642   neural coding efficiency despite increasing correlations in variability. J Neurosci
643   33:2108–2120.

644   Auksztulewicz R, Friston K (2016) Repetition suppression and its contextual

645   determinants in predictive coding. Cortex 80:125–140.

646   Barlow HB (2012) Possible Principles Underlying the Transformations of Sensory
647   Messages. In: Sensory Communication, pp 216–234. The MIT Press.

648   Barron HC, Garvert MM, Behrens TEJ (2016) Repetition suppression: a means to
649   index neural representations using BOLD? Philos Trans R Soc Lond, B, Biol Sci
650   371:20150355.

651   Bekinschtein TA, Dehaene S, Rohaut B, Tadel F, Cohen L, Naccache L (2009)
652   Neural signature of the conscious processing of auditory regularities.
653   Proceedings of the National Academy of Sciences 106:1672–1677.

654   Benucci A, Saleem AB, Carandini M (2013) Adaptation maintains population
655   homeostasis in primary visual cortex. Nat Neurosci 16:724–729.

656   Bigdely-Shamlo N, Mullen T, Kothe C, Su K-M, Robbins KA (2015) The PREP
657   pipeline: standardized preprocessing for large-scale EEG analysis. Front
658   Neuroinform 9:B153.

659   Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433–436.

660   Brouwer GJ, Heeger DJ (2009) Decoding and reconstructing color from responses in
661   human visual cortex. J Neurosci 29:13992–14003.

662   Buckner RL, Goodman J, Burock M, Rotte M, Koutstaal W, Schacter D, Rosen B,
663   Dale AM (1998) Functional-Anatomic Correlates of Object Priming in Humans
664   Revealed by Rapid Presentation Event-Related fMRI. Neuron 20:285–296.

665   Chaumon M, Bishop DVM, Busch NA (2015) A practical guide to the selection of
666   independent components of the electroencephalogram for artifact correction. J
667   Neurosci Meth 250:47–63.

668   Cichy RM, Ramirez FM, Pantazis D (2015) Can visual information encoded in
669   cortical columns be decoded from magnetoencephalography data in humans?
670   NeuroImage 121:193–204.

671   Clifford CWG (2002) Perceptual adaptation: motion parallels orientation. Trends
672   Cogn Sci 6:136–143.

673   Clifford CWG (2014) The tilt illusion: phenomenology and functional implications. Vis
674   Res 104:3–11.

675   Constantinescu AO, O'Reilly JX, Behrens TEJ (2016) Organizing conceptual
676   knowledge in humans with a gridlike code. Science 352:1464–1468.

677   Cui Y, Wang YV, Park SJH, Demb JB, Butts DA (2016) Divisive suppression
678   explains high-precision firing and contrast adaptation in retinal ganglion cells.
679   eLife Sciences 5.

Repetition suppression and prediction error

680 Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-
681   trial EEG dynamics including independent component analysis. J Neurosci Meth
682   134:9–21.

683 Dickinson JE, Almeida RA, Bell J, Badcock DR (2010) Global shape aftereffects
684   have a local substrate: A tilt aftereffect field. J Vis 10:5–5.

685 Dickinson JE, Morgan SK, Tang MF, Badcock DR (2017) Separate banks of
686   information channels encode size and aspect ratio. J Vis 17:27.

687 Diederen KMJ, Spencer T, Vestergaard MD, Fletcher PC, Schultz W (2016) Adaptive
688   Prediction Error Coding in the Human Midbrain and Striatum Facilitates
689   Behavioral Adaptation and Learning Efficiency. Neuron 90:1127–1138.

690 Doeller CF, Barry C, Burgess N (2010) Evidence for grid cells in a human memory
691   network. Nature 463:657–661.

692 Dragoi V, Sharma J, Sur M (2000) Adaptation-Induced Plasticity of Orientation
693   Tuning in Adult Visual Cortex. Neuron 28:287–298.

694 Felsen G, Shen Y-S, Yao H, Spor G, Li C, Dan Y (2002) Dynamic Modification of
695   Cortical Orientation Tuning Mediated by Recurrent Connections. Neuron 36:945–
696   954.

697 Fiser A, Mahringer D, Oyibo HK, Petersen AV, Leinweber M, Keller GB (2016)
698   Experience-dependent spatial expectations in mouse visual cortex. Nat Neurosci
699   19:1658–1664.

700 Foster JJ, Sutterer DW, Serences JT, Vogel EK, Awh E (2016) The topography of
701   alpha-band activity tracks the content of spatial working memory. J Neurophysiol
702   115:168–177.

703 Friston K (2005) A theory of cortical responses. Philosophical Transactions of the
704   Royal Society of London B: Biological Sciences 360:815–836.

705 Garcia JO, Srinivasan R, Serences JT (2013) Near-real-time feature-selective
706   modulations in human cortex. Current Biology 23:515–522.

707 Garrido MI, Kilner JM, Stephan KE, Friston KJ (2009) The mismatch negativity: A
708   review of underlying mechanisms. Clinical Neurophysiology 120:453–463.

709 Gotts SJ, Chow CC, Martin A (2012) Repetition priming and repetition suppression:
710   A case for enhanced efficiency through neural synchronization. Cogn Neurosci.

711 Gross CG, Schiller PH, Wells C, Gerstein GL (1967) Single-unit activity in temporal
712   association cortex of the monkey. J Neurophysiol 30:833–843.

713 Grotheer M, Kovács G (2014) Repetition probability effects depend on prior
714   experiences. J Neurosci 34:6640–6646.

Repetition suppression and prediction error

715 Haxby JV, Connolly AC, Guntupalli JS (2014) Decoding neural representational
716   spaces using multivariate pattern analysis. Annu Rev Neurosci 37:435–456.

717 Henson RNA, Rugg MD (2003) Neural response suppression, haemodynamic
718   repetition effects, and behavioural priming. Neuropsychologia 41:263–270.

719 Kaliukhovich DA, Vogels R (2010) Stimulus Repetition Probability Does Not Affect
720   Repetition Suppression in Macaque Inferior Temporal Cortex. Cereb Cortex
721   21:1547–1558.

722 Kamitani Y, Tong F (2005) Decoding the visual and subjective contents of the human
723   brain. Nat Neurosci 8:679–685.

724 Kamitani Y, Tong F (2006) Decoding seen and attended motion directions from
725   activity in the human visual cortex. Current Biology 16:1096–1102.

726 Kay KN, Naselaris T, Prenger RJ, Gallant JL (2008) Identifying natural images from
727   human brain activity. Nature 452:352–355.

728 Keil A, Debener S, Gratton G, Junghöfer M, Kappenman ES, Luck SJ, Luu P, Miller
729   GA, Yee CM (2014) Committee report: Publication guidelines and
730   recommendations for studies using electroencephalography and
731   magnetoencephalography. Psychophysiology 51:1–21.

732 Keller AJ, Houlton R, Kampa BM, Lesica NA, Mrsic-Flogel TD, Keller GB, Helmchen
733   F (2017) Stimulus relevance modulates contrast adaptation in visual cortex. eLife
734   Sciences 6:e21589.

735 King J-R, Gramfort A, Schurger A, Naccache L, Dehaene S (2014) Two Distinct
736   Dynamic Modes Subtend the Detection of Unexpected Sounds Kiebel S, ed.
737   PLoS ONE 9:e85791.

738 King J-R, Pescetelli N, Dehaene S (2016) Brain Mechanisms Underlying the Brief
739   Maintenance of Seen and Unseen Sensory Information. Neuron 92:1122–1134.

740 King JR, Dehaene S (2014) Characterizing the dynamics of mental representations:
741   the temporal generalization method. Trends Cogn Sci 18:203–210.

742 King JR, Faugeras F, Gramfort A, Schurger A, Karoui El I, Sitt JD, Rohaut B,
743   Wacongne C, Labyt E, Bekinschtein T, Cohen L, Naccache L, Dehaene S (2013)
744   Single-trial decoding of auditory novelty responses facilitates the detection of
745   residual consciousness. NeuroImage 83:726–738.

746 Kohn A, Movshon JA (2004) Adaptation changes the direction tuning of macaque MT
747   neurons. Nat Neurosci 7:764–772.

748 Kok P, Jehee JFM, de Lange FP (2012) Less Is More: Expectation Sharpens
749   Representations in the Primary Visual Cortex. Neuron 75:265–270.

750 Kourtzi Z, Kanwisher N (2001) Representation of Perceived Object Shape by the
751   Human Lateral Occipital Complex. Science 293:1506–1509.

752 Kovács G, Kaiser D, Kaliukhovich DA, Vidnyánszky Z, Vogels R (2013) Repetition
753   probability does not affect fMRI repetition suppression for objects. J Neurosci
754   33:9805–9812.

755 Kriegeskorte N, Mur M, Ruff DA, Kiani R, Bodurka J, Esteky H, Tanaka K, Bandettini
756   PA (2008) Matching Categorical Object Representations in Inferior Temporal
757   Cortex of Man and Monkey. Neuron 60:1126–1141.

758 Larsson J, Smith AT (2012) fMRI repetition suppression: neuronal adaptation or
759   stimulus expectation? Cerebral Cortex 22:567–576.

760 Maravall M, Petersen RS, Fairhall AL, Arabzadeh E, Diamond ME (2007) Shifts in
761   Coding Properties and Maintenance of Information Transmission during
762   Adaptation in Barrel Cortex Ebner FF, ed. PLoS Biol 5:e19.

763 Movshon JA, Lennie P (1979) Pattern-selective adaptation in visual cortical
764   neurones. Nature 278:850–852.

765 Myers NE, Rohenkohl G, Wyart V, Woolrich MW, Nobre AC, Stokes MG, Frank MJ
766   (2015) Testing sensory evidence against mnemonic templates. eLife Sciences
767   4:e09000.

768 Näätänen R, Paavilainen P, Rinne T, Alho K (2007) The mismatch negativity (MMN)
769   in basic research of central auditory processing: A review. Clinical
770   Neurophysiology 118:2544–2590.

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

773 Patterson CA, Wissig SC, Kohn A (2013) Distinct Effects of Brief and Prolonged
774   Adaptation on Orientation Tuning in Primary Visual Cortex. J Neurosci 33:532–
775   543.

776 Pelli DG (1997) The VideoToolbox software for visual psychophysics: Transforming
777   numbers into movies. Spat Vis 10:437–442.

778 Rao RPN, Ballard DH (1999) Predictive coding in the visual cortex: a functional
779   interpretation of some extra-classical receptive-field effects. Nat Neurosci 2:79–
780   87.

781 Rasmussen RG, Schwartz A, Chase SM (2017) Dynamic range adaptation in
782   primary motor cortical populations. eLife Sciences 6:e21409.

783 Rentzeperis I, Nikolaev AR, Kiper DC, Van Leeuwen C (2012) Relationship between
784   neural response and adaptation selectivity to form and color: an ERP study.
785   Front Hum Neurosci 6.

Repetition suppression and prediction error

786 Salti M, Monto S, Charles L, King J-R, Parkkonen L, Dehaene S, Johansen-Berg H
787   (2015) Distinct cortical codes and temporal dynamics for conscious and
788   unconscious percepts Johansen-Berg H, ed. eLife Sciences 4:e05652.

789 Schacter DL, Buckner RL (1998) Priming and the Brain. Neuron 20:185–195.

790 Spaak E, Watanabe K, Funahashi S, Stokes MG (2017) Stable and Dynamic Coding
791   for Working Memory in Primate Prefrontal Cortex. J Neurosci 37:6503–6516.

792 Sprague TC, Serences JT (2013) Attention modulates spatial priority maps in the
793   human occipital, parietal and frontal cortices. Nat Neurosci 16:1879–1887.

794 Stokes MG, Kusunoki M, Sigala N, Nili H, Gaffan D, Duncan J (2013) Dynamic
795   Coding for Cognitive Control in Prefrontal Cortex. Neuron 78:364–375.

796 Summerfield C, Trittschuh EH, Monti JM, Mesulam MM, Egner T (2008) Neural
797   repetition suppression reflects fulfilled perceptual expectations. Nat Neurosci
798   11:1004–1006.

799 Summerfield C, Wyart V, Mareike Johnen V, de Gardelle V (2011) Human Scalp
800   Electroencephalography Reveals that Repetition Suppression Varies with
801   Expectation. Front Hum Neurosci 5.

802 Tang MF, Dickinson JE, Visser TAW, Badcock DR (2015) The broad orientation
803   dependence of the motion streak aftereffect reveals interactions between form
804   and motion neurons. J Vis 15:4.

805 Todorovic A, de Lange FP (2012) Repetition suppression and expectation
806   suppression are dissociable in time in early auditory evoked fields. J Neurosci
807   32:13389–13395.

808 Todorovic A, van Ede F, Maris E, de Lange FP (2011) Prior Expectation Mediates
809   Neural Adaptation to Repeated Sounds in the Auditory Cortex: An MEG Study. J
810   Neurosci 31:9118–9123.

811 Tootell R, Reppas JB, Dale AM, Look RB (1995) Visual motion aftereffect in human
812   cortical area MT revealed by functional magnetic resonance imaging. Nature.

813 Tootell RB, Hadjikhani NK, Vanduffel W, Liu AK, Mendola JD, Sereno MI, Dale AM
814   (1998) Functional analysis of primary visual cortex (V1) in humans. Proc Natl
815   Acad Sci USA 95:811–817.

816 Ulanovsky N, Las L, Nelken I (2003) Processing of low-probability sounds by cortical
817   neurons. Nat Neurosci 6:391–398.

818 Wacongne C, Labyt E, van Wassenhove V, Bekinschtein T, Naccache L, Dehaene S
819   (2011) Evidence for a hierarchy of predictions and prediction errors in human
820   cortex. Proc Natl Acad Sci USA 108:20754–20759.

Repetition suppression and prediction error

821   Wolff MJ, Jochim J, Akyürek EG, Stokes MG (2017) Dynamic hidden states
822   underlying working-memory-guided behavior. Nat Neurosci 20:864–871.

823